PHYLOGENY OF NEORNITHES

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Source: Bulletin of Carnegie Museum of Natural History, Number 37:1-544. 2006.
Published By: Carnegie Museum of Natural History
DOI: http://dx.doi.org/10.2992/0145-9058(2006)37[1:PON]2.0.CO;2
URL: http://www.bioone.org/doi/full/10.2992/0145-9058%282006%2937%5B1%3APON%5D2.0.CO%3B2

ABSTRACT

This work serves as a compendium of anatomical resources upon which a companion phylogenetic analysis of Aves and related Theropoda (Avialae) was based (Livezey and Zusi 2006). Following a brief historical overview of avian anatomy and avian systematics, the rich published literature pertinent to these topics is classified chronologically and geographically. The former also was organized with respect to eras of predominant methodologies in avian systematics, with an emphasis on recent paleontological finds bearing importantly on the origins of modern birds (Neornithes). This was followed by an exposition on the theoretical and abstract underpinnings of morphological characterization for purposes of phylogenetic reconstructions (to be published separately), with aspects of analysis for phylogenetic inference (e.g., tactics for employment of currently available software, ordering, criteria for optimization of trees) considered elsewhere.

The principal contribution of this exposition is a listing of characters and states manifesting what was inferred to hold promise with respect to phylogenetic or historical signal. In total, 2,954 anatomical characters were defined—2,451 osteological, 256 myological, and 247 miscellaneous—of which 981 (approximately one-third) were multiple-state (i.e., comprised three or more states), the latter including 537 characters treated as ordered. Bibliographic provenance for characters was provided, where possible, but exact equivalence of characters and states among workers was seldom feasible. In many cases, previously published characters were listed on the grounds that these pertained most closely to the structure or complex at hand in the present study, and that such listings provided at least a historical grasp of the magnitude of prior usages of a given character. We also summarized, to the extent feasible, previously published characters for which inclusion in the present work was judged to be unreliable or lacking sufficient clarity.

In addition to the descriptions of characters, a limited series of figures are provided, in no small part to ameliorate the challenges posed by new terms and formal anatomical nomenclature. We are adherents to nomenclatural formalism (Livezey and Zusi 2001) in anatomical contexts *sensu* the ICAAN (International Committee on Avian Anatomical Nomenclature; Baumel 1993). I.e., we consider that characters and states—implicitly proposals of homology—warrant clarity with respect to surrounding text in the same sense that binomial taxa—i.e., as hypotheses of historical lineages—are subject to formal conventions.

Finally, literature cited herein is listed, as a work of this kind is impossible without access to the wealth of information and insight provided by such a resource. As this literature is integrated by citation with the descriptions of characters, it is hoped that the bibliography will lessen the challenges posed by a deep, multilingual, and variably technical literature for systematists using these descriptions. The dimension of the character matrix also led us to enclose a CD of the data set in the present work to assist those seeking to improve, append, or refine our efforts.

A phylogenetic (cladistic) analysis of these data will appear separately (Livezey and Zusi 2006). Soon thereafter a collaboration with an unparalleled compilation of molecular data (i.e., DNA sequences) and confirmatory paleontological data is planned to conclude with the publication of a total-evidence analysis of avian phylogeny under the auspices of the NSF "Tree of Life" program, one to encompass extant birds (Neornithes), avian relatives from the Mesozoic (outgroups), and nonavialian fossil taxa from the Mesozoic ("deep" outgroups).

KEY WORDS: Arthrology, Aves, Characters, Integument, Morphology, Myology, Neornithes, Osteology, Pennation, Phylogenetics, Theropoda

INTRODUCTION

Background for Compendium and Companion Analysis

Episodes of Avian Systematics

Osteology, like much of comparative anatomy, has been the subject of comparably intense study throughout the history of ornithological systematics, and led to a long-standing, virtual monopoly of anatomy for diagnoses of avian taxa (Coues 1872, 1927; A. Newton 1893, 1894, 1895, 1896; Holmgren 1955; Short 1976; Van Tyne and Berger 1976). Nevertheless, within five years of the publication of the classic work by Darwin (1859), Wallace (1864) was moved to note the value of osteology for ornithological systematics. A century later, E. Mayr (1955) was critical of the progress in phylogenetics of Passeriformes, and Stresemann (1959) lamented the failure of comparative anatomy to resolve higher-order relationships of birds. The latter sentiments were to be echoed by systematists to the present day (Paton et al. 2002; G. Mayr et al. 2003; Sorenson et al. 2003; Chubb 2004; Dyke and van Tuinen 2004).

Many systematists averred that birds, purportedly constrained by the requirements of flight, would manifest little anatomical variation meaningful for phylogenetics (Colbert 1955; Romer 1968; Stahl 1974). E. Mayr (1976, 1980) chronicled perennial problems of avian classification. Despite a widespread perception that avian fossils are rare because of fragility and poor preservation (Romer 1968), a diminished confidence in comparative anatomy to resolve avian systematics was accompanied by a grandiose vision of paleontology, anatomical study of fossilized elements. This optimism held that vital insights (especially higher-order relationships) and transcendent "laws" of evolution (Shideler 1952) are to be gained *only* through the discovery of new fossils (Feduccia 1995). The empirical limits of paleontological inferences for Neornithes—exemplified by Howard (1950) and S. L. Olson (1985)—derived principally from undemonstrated (perhaps if not undemonstrable) ancestral status of fossil taxa (Cracraft 1980).

A tradition of intuitive assessments of "convergence" in morphological characters, notably among taxa sharing obvious aspects of life history, has haunted a reliance on comparative anatomy for reconstruction of phylogenetic relationships (Bock 1967, 1977; Cracraft 1979, 1981b). A broad consensus and empirical foundation supports the likelihood of functional similarities in some morphological features—e.g., appendicular resemblances related to locomotion in distantly related diving birds (Storer 1960a–b; Harrison 1977), but these convergences were essentially assumptions and failed to support the contention that occult homoplasy afflicts appendicular anatomy of birds. Sibley and Ahlquist (1970, 1972, 1990) perpetuated a claim of evidentiary superiority of molecular evidence, a subject of continued controversy (Cracraft 1987; Harshman 1994).

Despite an inauspicious record of accomplishment in the avian context in terms of robust placements of problematic taxa or uniformity of inferences, a molecular chauvinism persists in some systematic circles (Hedges and Maxson 1992, 1996; Hedges and Sibley 1994; Hedges et al. 1995; McCracken and Sheldon 1998; Van Tuinen et al. 2001), primarily with respect to a superiority of sequence data. Perhaps the most egregious perspective offered by this school is the proposal that morphological data be relegated to attributes mapped *a posteriori* onto phylogenies solely inferred by molecular means (e.g., Hedges and Maxson 1992). This prejudice at times suggests an unlimited credulity toward unprecedented groupings only weakly supported by single studies (e.g., Van Tuinen et al. 2001; Fain and Houde 2004). Fortunately, this unilateralism has been balanced, at least in part, by a more objective perspective regarding diverse sources of phylogenetic data (Wiens and Reeder 1995; Huelsenbeck et al. 1996; Wiens and Hillis 1996; K. Lee et al. 1997; Jenner 2004; Wiens 2004), enumeration of advantages of both classes of data (Wiens 2004), and an emphasis on areas of agreement among methodologies (Bledsoe and Raikow 1990). The most encouraging sign is a genuine recognition of the magnitude of the problem that prompts the use of diverse sources of historical signal for resolution (Crowe 1988; Cracraft et al. 2004).

Genesis of Current Project

The present venture—a morphologically based phylogenetic analysis of modern birds (Neornithes)—originated in 1993, although both authors held interests of long standing in comparative avian anatomy and systematics (e.g., Zusi 1962, 1967, 1984, 1993; Livezey 1986, 1991, 1997a, 1998a–b). In brief, we believed that comparative anatomy deserved a multisystemic, uniformly characterized, and taxonomically inclusive assessment to provide balance to the enthusiasm and widespread resources being bestowed upon molecular techniques. Therefore, we decided to provide an empirically detailed, morphological counterproposal to phylogenetic reconstructions based on molecular evidence, at least to obviate comparisons of molecular reconstructions with traditional avian classifications, the latter not qualifying as phylogenetic hypotheses *per se*.

The first two years of the study were critical in the organization of synoptic series of specimens and the adoption of a standardized method of characterization. The latter was achieved primarily through collaborative study of unparalleled series of specimens, the formal terminology outlined in the *Nomina Anatomica Avium* (Baumel et al. 1993), and reference to the primary anatomical literature, notably recent descriptions of new fossil avialians. Several two-week periods of intensive study resulted in several hundred characters of the skull and vertebral column and the basis for two ancillary works (Zusi and Livezey 2000; Livezey and Zusi 2006), but it became evident that a formal commitment of effort and external financial resources would be considerable in order to see the phylogenetic project to completion.

The signal captured in this preliminary survey of axial characters—based on a primary analysis performed for inclusion in a proposal for funds—was encouraging even given its provisionally rooted, preliminary nature. This truly heuristic exercise, reprinted by Livezey and Zusi (2001), unfortunately prompted unintended citations of the work as a genuine hypothesis of avian phylogeny (e.g., G. Mayr et al. 2003), despite an explicit disclaimer given in the paper. Nonetheless, this demonstration of potential of avian morphology for phylogenetic reconstruction proved successful in securing funding by Livezey from the National Science Foundation (NSF) for the core project on Neornithes.

These resources permitted opportunities and travel to complete mutual study of the axial and hyoid skeleton and critical fossil taxa, followed by largely independent study of the appendicular skeleton and pectoral musculature by Livezey and the cranial and pelvic musculature by Zusi. The original award, followed by two one-year extensions, was supplemented in 2004 for the present publication of characters. This compendium forms the empirical basis for a companion phylogenetic analysis (Livezey and Zusi 2006) and will serve as formal morphological component, in combination with paleontological and molecular contributions, for subsequent reconstructions based on "total evidence" (Bininda-Emonds et al. 2002), and part of the crown-theropod component of the NSF "Tree of Life" program.

Descriptions of Avian Anatomy: An Episodic Perspective

POST-LINNEAN SURVEYS

The earliest anatomical sources authored by ornithologists were largely taxonomic in focus, typically addressing generalities of osteological or other anatomical aspects for representatives of a higher taxon or group thereof. With few exceptions—e.g., Brandt (1839 [1840]a–c), Eyton (1867), Suschkin (1899a–b, 1905), and F. A. Lucas (1904)—ornithological works of anatomical emphasis during the 19th century were dominated by comparatively few, prolific workers. Moreover, with the notable exceptions of the classic works by Gadow (e.g., 1877, 1879a–b, 1891a–b, 1892, 1893) and Fürbringer (1888, 1889, 1902), most anatomical resources of the century were authored by a dozen Anglo-ornithologists. These, and an American (Shufeldt), are listed below with samples of representative works:

- **Owen** (1836, 1838, 1839, 1841, 1842, 1843, 1844, 1846a–b, 1848a–c, 1849a–b, 1851, 1852, 1856a–b, 1858a–b, 1863, 1866a–c, 1869a–c, 1870a–c, 1871a–b, 1872, 1873a–b, 1875, 1877, 1879, 1882, 1883a–b, 1886);
- **Huxley** (1859, 1867, 1868a–b);
- **W. K. Parker** (1860, 1861, 1862, 1864, 1866, 1868, 1869a–b, 1875a–b, 1879, 1883, 1887, 1888a–d, 1889a–d, 1890, 1891a–b);
- **Garrod** (1872a–b, 1873a–d, 1874a–e, 1875a–b, 1876a–f, 1877a–d, 1878a–b, 1879a–b);
- **Gadow** (1877, 1879a–b, 1880, 1882a–b, 1883, 1885, 1888, 1889, 1891a–b, 1892, 1893);
- **Forbes** (1879, 1880a–c, 1881a–c, 1882a–f);
- **Shufeldt** (1881a–d, 1882, 1883, 1884a–c, 1885a–b, 1886a–d, 1888a–e, 1889a–g, 1890, 1891a–e, 1892, 1893a–c, 1894a–b, 1900a–b, 1901a–i, 1902a–c, 1903a–b, 1904a–b, 1907, 1909, 1913a–b, 1914, 1915a–b, 1918a–b, 1919a–b, 1920, 1922);
- **Beddard** (1884, 1885a–b, 1886a–d, 1888a–b, 1889a–d, 1890a–c, 1891, 1892, 1893a–b, 1894, 1896a–e, 1897a–b, 1898a–b, 1899, 1901a–d, 1902a–c, 1903a–b, 1911);
- **Seebohm** (1888, 1889, 1890a–c, 1895);
- **T. J. Parker** (1891, 1892, 1895);
- **Mitchell** (1895, 1896, 1899, 1901a–c, 1905, 1913a–b, 1915);
- **Pycraft** (1895, 1898a–d, 1899a–c, 1900, 1901, 1902, 1903a–d, 1905a–c, 1906a–b, 1907a–c, 1909, 1910);
- **Lowe** (1915a–c, 1916a–b, 1922, 1923, 1924, 1925a–b, 1926a–b, 1927, 1928a–b, 1930, 1931a–d, 1933, 1935, 1938, 1939a–b, 1942, 1943, 1944a–b, 1946, 1948).

A survey of these authors and the years of their publications delimits a golden era of ornithological anatomy and systematics derived therefrom.

Mere numbers of works predictably are a poor indicator of the importance of their contributions, as the impressive series by Owen were dominated by almost two dozen dedicated primarily to the moas (Dinornithiformes) and were comparatively superficial with respect to systematic inferences. A similar generality clearly applies to the works by Shufeldt.

The systematics and biogeography of the ratites—flightless, acarinate, palaeognathous birds—were to remain topics of lasting interest (Romer 1968: 146). At the other extreme were the comparatively few but influential works by Garrod, who published seminal classics on four key anatomical systems—osteorhiny (Garrod 1873a), crural muscles (Garrod 1873b), carotid arteries (Garrod 1873c), and crural tendons (Garrod 1875a)—during a period of less than three years. Similarly, Huxley was not as prolific with respect to anatomical treatises, but his exploration of the osseous palate of birds (Huxley 1867) arguably was the single most-influential paper (excluding monographic works) in avian systematics of the 19th century (Zusi and Livezey 2006). The monographic work by Fürbringer (1888) has proven indispensable for following generations of avian anatomists and systematists, and the work is so rich in detail and taxonomic scale that its use appears to have been limited largely by the ambition, anatomical expertise, and primary languages of subsequent workers.

Intuitive Syntheses and Eclectics

The early to mid 20th century was characterized by a more-explicit emphasis on the systematic implications of anatomical descriptions, and a more-subtle increase in studies of greater taxonomic scale. Several authors produced works of primarily anatomical (as opposed to taxonomic) focus and lasting importance, including: Lönnberg (1904), Van Oort (1905), Lebedinsky (1913, 1919), Böker (1927, 1935), Schüz (1927), Boetticher (1928, 1929), Boas (1929, 1934), Lemmrich (1931), Technau (1936), Hofer (1945, 1949, 1950, 1955), Tiermeier (1950), Goebloed (1958), and Goodge (1972). Bock (1956, 1958, 1959, 1960a–b, 1963a–b, 1969) was known for meticulous anatomy and the articulation of an adaptational-functional approach to characters and their utility for systematics, a framework that was to attract few adherents.

The next few decades were to be dominated by avian systematists having explicitly systematic goals only variably related to function, e.g., Jollie (1953, 1958, 1976, 1977a–c), Verheyen (1953a–b, 1955a–c, 1956a–h, 1957a–d, 1958a–f, 1959a–d, 1960a–g, 1961), Johnsgard (1961), Brodkorb (1971a, 1976), Burton (1971a–b, 1974a–b, 1978, 1984), S. L. Olson (1973, 1976, 1977, 1979, 1980, 1983, 1985, 1987b), Feduccia (1976a, 1977a–c, 1978, 1985), Elzanowski (1977a–b, 1987, 1991), S. L. Olson and Feduccia (1980a–b), L. D. Martin (1983a–b, 1984, 1985, 1987), Kurochkin (1985).

During the two decades following the American publication of cladistic methodology (Hennig 1966), some avian systematists—e.g., Houde and Olson (1981), Houde (1986, 1987, 1988), W. E. Lanyon (1986, 1988a–b), and Houde and Haubold (1987)—persisted in what Raikow (1985c) dubbed "eclectic" methods, an amalgam of descriptive anatomy, functional morphology, and intuitive systematics or quantitative phenetics (e.g., Hecht 1976; E. Mayr 1976, 1982). By the early 1990s, however, most ornithological systematists had adopted cladistic methods (Wiley 1981), varying principally in focus (neontological *vs.* paleontological), evidence (morphological *vs.* molecular), or taxonomic scale (interfamilial *vs.* intrageneric).

Contemporary Morphological Cladistics

Paleontological Emphases

Paleornithological workers adopted cladistic techniques more slowly than their neontological colleagues. Excluding alpha-descriptive works for newly discovered fossil taxa, explicit phylogenetic analyses of significant scale in paleornithology were few during the early 1990s (e.g., Holdaway 1991, 1994). With the revolutionary finds of Mesozoic fossils (below), paleornithologists embraced cladistic techniques for inferences regarding the basalmost divergences in the avian clade. Important works, most associated with explicit data sets but varying moderately in methodological details, include: Chiappe (1995a–b, 1996a–b, 2001a–b, 2002), Chatterjee (1998a, 1999), Dyke (2001a–b), Chiappe and Dyke (2002), J. M. Clark et al. (2002a), G. Mayr (2002a, 2003a–c, 2004a–b), and Dyke et al. (2003). In addition, an increasing number of systematists recognized the importance of including both fossil and modern taxa in phylogenetic reconstructions, e.g., Livezey and Martin (1988), Houde (1994), K. Lee et al. (1997), Livezey (1997a, 1998b), Cracraft and Clarke (2001), J. A. Clarke and Norell (2002), G. Mayr and Clarke (2003), and J. A. Clarke et al. (2005).

Neontological Emphases

Ornithological systematists having primary interests in modern taxa adopted cladistics comparatively rapidly, in part because of the wealth of anatomical material that was available. At least a decade prior to widespread paleontological applications, phylogenetic analysis was the preferred if not sole formal method of choice among neontologists. Important works of this kind include: Raikow (1976, 1977a–b, 1978, 1982, 1987, 1993, 1994), Strauch (1978, 1985), Bentz (1979), Cracraft (1981a, 1982, 1985, 1986, 1988), McKitrick (1985a–b, 1986, 1991a–b, 1992), Cannell (1986), Livezey (1986, 1989, 1990, 1991, 1995a–c, 1996a–c, 1997a–b, 1998a–b), Prum (1988, 1990, 1992, 1993), Siegel-Causey (1988, 1997), Cracraft and Mindell (1989), Chu (1995, 1998, 2002), Ericson (1996, 1997), Ericson et al. (1998), Hughes (2000), G. Mayr et al. (2003), and G. Mayr and Ericson (2004). Several of the last in the foregoing series incorporated both molecular and morphological data.

Scrutiny of this sample reflects that studies of this kind were largely limited to the United States, and more specifically to the two largest U.S. museums (American Museum of Natural History, New York, AMNH; Smithsonian Institution, Washington, D.C., USNM) and several universities or private institutes having strong anatomical traditions—University of Michigan; Carnegie Museum of Natural History, CMNH; and University of Kansas. Important European collections and/or systematic traditions include the Natural History Museum, U.K., BMNH; Forschungsinstitut Senckenberg, Frankfurt, Germany; Swedish Museum of Natural History; and Muséum national d'Histoire naturelle, France.

PALEORNITHOLOGICAL REVOLUTION AND HYPOTHESES OF ORIGINS

Virtually coincident with our initial surveys of osteological characters for Neornithes, paleontological discoveries provided both a deeper sample of outgroups for modern taxa and stimulated an expansion of fossil taxa to be included in the project. Prior to the last decade of the 20th century, only a handful of Mesozoic Aves were known, and the quality of which often was wanting (Boetticher 1928; Swinton 1960; Bock 1969; Cracraft 1971a; L. D. Martin and Tate 1976; L. D. Martin and Stewart 1982; Fox 1984; Raath 1985, 1990; Elzanowski 1991; Elzanowski and Galton 1991; L. D. Martin 1995).

During the last decade of the 20th century, a spate of discoveries of Mesozoic forms confirming a diverse cladogenesis of Avialae and allies (Chiappe 1995a, 1997, 2001a–b, 2002; Hou et al. 1995, 1996, 1999a–b; Chiappe and Dyke 2002) emerged from several key regions:

- **Asia** (Sereno and Rao 1992; Zhou et al. 1992, 2000; Norell et al. 1993, 1994, 1995; Perle et al. 1993, 1994; J. M. Clark et al. 1994, 1999, 2002a; Dasheveg et al. 1995; Zhou 1995a–b; Chiappe et al. 1996, 1997, 1998, 2001; Dong and Currie 1996; Ji and Ji 1996, 1997; Ji et al. 1998, 1999, 2001, 2003a–b; Hou and Chen 1999; Barsbold et al. 2000a–b; Zhou and Wang 2000; J. M. Clark et al. 2001; Currie and Chen 2001; Norell and Clarke 2001; Sereno 2001; J. A. Clarke and Norell 2002; Sereno et al. 2002; Suzuki et al. 2002; Zhou and Zhang 2002, 2003; Gong et al. 2004);
- **Europe** (Sanz and Bonaparte 1992; Sanz and Buscalioni 1992; Sanz et al. 1995, 1996, 1997, 2002; J. A. Clarke and Chiappe 2001);
- **South America** (A. D. Walker 1980; Chiappe 1991a–b, 1992, 1993, 1995b, 1996a–b; Novas 1994 [1993], 1996, 1997; Novas and Puerta 1997; Holtz 2001a–b; Norell et al. 2001; Chiappe and Walker 2002; Chiappe et al. 2002; Novas and Pol 2002);
- **Madagascar** (Forster et al. 1996, 1998).

This paleornithological renaissance—fortuitous in both timing and magnitude—provided the empirical foundation for a robust resurrection of the dinosaurian origin for Aves as prevailing hypothesis (Chiappe 1995a, 1997; Padian 1998; J. M. Clark et al. 2002b; Prum 2002), a proposal of varying focus dating from the 19th century (Seeley 1866, 1871, 1874, 1891; Cope 1867, 1885; Huxley 1868a, 1870; Vogt 1880; Marsh 1881; Baur 1883, 1884, 1885c–e; Dames 1884, 1885, 1897; W. K. Parker 1887, 1888a) and revived repeatedly (at times controversially) during the interim, either stimulated by new specimens, renewed interpretation of earlier collections, or shifts in inferential paradigms (Gasch 1888; Osborn 1900; Funncius 1909; Hay 1910; Versluys 1910, 1912; Wamich 1913; Heilmann 1926; Boas 1930; Galton 1970; Ostrom 1973, 1975a–b, 1976a–b, 1979, 1991; Thulborn 1975, 1984; Cracraft 1977; Tarsitano and Hecht 1980; Thulborn and Hamley 1982; Hou and Liu 1984; Currie 1985, 1987; Kurochkin 1985; Gauthier 1986; Molnar 1986; Kurzanov 1987; Witmer 1991; Elzanowski and Wellnhofer 1992, 1993; Wellnhofer 1994).

The resultant shift in perspective regarding the phylogenetic origins of Aves as being among traditionally delimited Theropoda—by strong consensus of systematists (Padian and Chiappe 1997, 1998a–b; Witmer 2002)—permitted increased efficiency of study and improved estimates of basal polarities for osteological characters and provided insights into osteohistology (Chinsamy et al. 1994, 1995; Ricqlès et al. 2003), integument (P. G. Davis and Briggs 1995, 1998; Chen et al. 1998; Ji et al. 1998, 2001; Chiappe et al. 1999; Schweitzer et al. 1999; Xu et al. 1999a–b; Currie and Chen 2001; Schweitzer 2001; Xu et al. 2003), and breeding behavior (Norell et al. 1994, 1995; Dong and Currie 1996; Varricchio et al. 1997). As recently as the 1980s, the potential outgroups for Neornithes were limited to a handful of moderately represented taxa—*Archaeopteryx*, *Hesperornis*, and *Ichthyornis* (J. T. Gregory 1951, 1952; Gingerich 1972, 1973, 1976; Ostrom 1972; Harrison 1973; Harrison and Walker 1976a–b; Parris and Echols 1992)—limiting phylogenetic works in detailing of avian plesiomorphy (cf. Brodkorb 1971a; Cracraft 1981a, 1982, 1986, 1988; Witmer and Martin 1987; Cracraft and Mindell 1989; Witmer 1991; Elzanowski 1995). However, the turn of the millenium witnessed an increase in taxonomic diversity by an order of magnitude (Kurochkin 1995a; Chiappe 2001b; Cracraft and Clarke 2001).

In addition, during this period, a wealth of new avian fossils from the Cenozoic was described, principally from Messel, Germany (Feduccia and Martin 1976; Mourer-Chauviré 1980, 1983, 2000; Hesse 1988, 1990, 1992; Alvarenga and Bonaparte 1992; Cheneval 1995, 2000; G. Mayr 1996, 1998a–b, 1999a–b, 2000a–d, 2001a–g, 2002b–e, 2003d, 2004c; G. Mayr and Daniels 1998; G. Mayr and Peters 1998, 1999; Dyke and Waterhouse 2000; G. Mayr and Mourer-Chauviré 2000; Dyke 2001a–b; Dyke and Gulas 2002; G. Mayr and Smith 2002; Alvarenga and Guiherme 2003), but most were referred preliminarily to extant orders and few if any of these augured resolution of higher-order relationships among Neornithes.

This new diversity of outgroup taxa both provided insights and posed challenges, e.g., insights into transformation of many morphological characters and polarities (Barriel and Tassy 1997, 1998) were accompanied by expansion of the size of the most challenging analytical task at hand—number of terminal taxa in the phylogeny to be reconstructed (Swofford et al. 1996). The latter analytical burden was exacerbated by a disproportionate increase of missing data in these otherwise welcome Mesozoic terminals (Wiens 1998a, 2003; Kearney 2002; Kearney and Clark 2003; Wilkinson 2003), including whole suites of characters important for phylogenetic reconstructions among modern Neornithes.

Renewed Relevance of Traditional Dinosauria

With the approachment if not attainment of consensus regarding theropod origins of Aves, osteological characters and relationships of archosaurs traditionally dubbed "Dinosauria" became critical. Very quickly those systematists in opposition to the theropod hypothesis were in the minority, and their arguments turned more on a methodological opposition to cladistics and traditional scenarios concerning the evolution of avian flight than on the growing morphological evidence at hand (e.g., Bock 1985a). This quasi-philosophical debate was confounded by the popular resistance toward the taxonomic legalism that birds not only derived from dinosaurs but that, by nomenclatural rules, birds themselves *were* dinosaurs. Many important outgroup taxa were described well before the "paleornithological revolution," whereas others constituted an important part of this episode of discovery. Nevertheless, descriptions of pertinent characters remained of approximately uniform utility throughout the literature of recent decades.

This enlarged and diverse, extended outgroup posed both practical and strategic issues for the present analysis of Aves. Of primary importance among outgroups were other Tetanurae, with secondary references to Coelurosauria, "carnosaurs," and basal Theropoda; very conservative structures permitted reference to more distant relatives, including the Sauropoda, Ornithischia, and basalmost Dinosauria. Only for myological polarities not reconstructed by osteological remnants on theropods (e.g., Hutchinson 2001a–b), the Crocodylomorpha and basalmost Archosauria were included for comparisons. These deep roots were not necessary for purposes of rooting with respect to most avian characters, but primarily were valuable to deeply root myological characters and thereby solidify the polarities of characters relevant to the Avialae.

Logical Partition of Analysis

The presentation of this analysis in two separate works—one comparatively lengthy compilation of characters and a shorter, subsequent work summarizing the phylogenetic analysis of these data—represents a logistic necessity of publication and the essentially bipartite nature of phylogenetic analysis (Mishler 2005). Not only are these endeavors practically divisible, but objectivity of characterization is approached most effectively when performed independently of analysis of characters. We agree with Mishler (2005) that the first stage—characterization and construction of the data matrix—typically is the more important of the two efforts, despite the fact that substantially less literature treats derivation of the character (data) matrix than the analysis of the data or inference of phylogenetic trees (the latter a diagrammatic summary of the former). It may be instructive to view the disparity in lengths of the two publications in view of this assessment of relative significance of the components of study.

METHODS

Exemplars

Specific taxonomy of modern Aves followed, with few exceptions, the classification by Dickinson (2003). Higher-level classifications were followed only for purposes of selection of exemplars, and all available classifications (e.g., Storer 1960a, 1971a; Wetmore 1960) required working revisions in order to encompass controversial or otherwise critical taxa. Cognizant of dynamics of ornithological classification (Gauthier and de Queiroz 2001), we followed the taxonomy of Mesozoic avialians of Chiappe (2002), taxonomy of fossil birds of the Cenozoic largely followed Brodkorb (1963, 1964, 1967, 1971b, 1978), that of other Dinosauria after Benton (1990a–b), K. Carpenter and Currie (1990), Sereno (1997, 1999), and Norell et al. (2001).

The taxonomic scope of the project, combined with progressive affirmation of minimal variation between exemplars and excluded confamilials, validated the utility of exemplars (Yeates 1995) as terminal taxa for the reconstruction of higher-order phylogeny of Aves. Cognizant of the advantages of dense sampling of taxa for phylogenetic inference (Zwickl and Hillis 2002), logistic limitations were considered less burdensome in a morphological context in which comparatively conservative rates of change and greater diversity of potential states reduced likelihood of error (e.g., long-branch attraction) relative to molecular applications (e.g., limitation of all characters to same four states).

Limitations of exemplars (*sensu* surrogacy for higher-order taxa) as terminals for phylogenetic estimates are substantially understood (Yeates 1995; Wiens 1998b, 2000; Prendini 2001), therefore notable departures from exemplary states among confamilials or atypicality of exemplars for specific characters were noted. All preferences, however, were conditional on availabilities of specimens (D. S. Wood et al. 1982; D. S. Wood and Schnell 1986). These details were not intended to serve as equivalents for descriptions of morphological variation inclusive of all modern neornithine families sampled, but rather to ameliorate the shortcomings of exemplars for purposes of reconstruction of higher-order phylogenetic inferences.

Synoptic Series and Reference Specimens

Fossil Taxa and Specimens

Direct study of specimens and surveys of published analyses and description served as the basis for morphological characterizations summarized herein. For Neornithes, first-hand comparison of specimens composed the primary source of characters, with supplementary proposals from the literature considered subsequently. A select group of fossil (mostly Mesozoic) taxa were subjects of direct study of specimens (see below), whereas most Mesozoic taxa were characterized primarily based on published descriptions and figures.

A reliance on the paleontological literature reflected: (*i*) the primary focus of our study, relationships among Neornithes; (*ii*) necessities imposed by time constraints; and (*iii*) general thoroughness of prior paleontological studies. A few (sub)fossil taxa originally included for analysis were determined subsequently to be too poorly represented (e.g., *Sylviornis, Plotopterum*). Study of *Archaeopteryx* included direct examination of specimens in London, Berlin, Eichstätt, Härlem (cast), and Münich.

Our primary concern in the study of fossil birds in the present work was to amalgamate traditionally established characters, typically informally described using terms derived from those of Howard (1929), into the context of our anatomical study of Neornithes and a revised anatomical nomenclature for Aves (Baumel et al. 1993). Awareness of the difficulties of interpretation of paleontological characters within a formal nomenclatural context and published information prompted a documentation of literature deemed relevant to the characters cited (under *Note*). Employment of a uniform nomenclature, extended even to characters of long vernacular traditions (J. D. Harris 2004), was intended to avoid a divergent terminology that has diminished an anatomically precise discourse between disciplines, e.g., paleontological and neontological schools (Livezey and Zusi 2001).

However, fossil Aves and nonavialian Theropoda offer insights of enormous interest in themselves, and this potential, as well as that for refined rooting, argued for the inclusion of as many well-represented fossil taxa as feasible. Despite limited potential as additional outgroups (Holtz 2000 [1998]), a number of Mesozoic taxa, including *Utahraptor* (Kirkland et al. 1993), *Afrovenator* (Sereno et al. 1994), *Elaphrosaurus* (Janensch 1920), *Shenzhouraptor* (Ji et al. 2003a), *Therizinosaurus sensu generis* (Maleev 1954), *Unenlagia* (Novas and Puerta 1997), *Protoavis* (Chatterjee 1991, 1999), *Alxasaurus* (Russell and Dong 1994a [1993]), *Vorona* (Forster et al. 1996), and *Limenavis* (J. A. Clarke and Chiappe 2001), were excluded because of limited descriptions or access. Also excluded for reasons of poor representation were several Enatiornithes (Chiappe and Walker 2002): *Lectavis*, *Soroavisaurus*, *Yungavolucris*, and *Avisaurus*.

We primarily coded exemplar species for modern taxa (Appendix 1) based on synoptic series of specimens. A primary synoptic set of specimens, listed as "voucher" specimens (Appendix 1), were bolstered by examination of additional specimens where variation or damage required; polymorphism in exemplar taxa was so coded, thereby recording the variation observed in the terminal taxa (N. B. Simmons 2001). Although less definitive than a single, fixed state for a given taxon (Wiens 2000) and not recommended for intraspecific variation (Swofford 1998), it was preferable to arbitrarily assigning a single state for a polyspecific terminal potentially manifesting variation at multiple taxonomic levels. For some characterizations, especially those requiring access to exceptionally rare specimens, permission to dissect rare spirit specimens, or requiring special preparations, we resorted to characterizations based on secondary exemplar taxa (Appendix 1). Published works (e.g., W. K. Parker 1862, 1868; 1891a–b; T. J. Parker 1895; Pycraft 1900; Archey 1941; H. J. Müller 1961b, 1963) proved essential for characterization of structures posing special challenges—e.g., suturae cranii (obscured with age) and conchae nasalis (involving variably cartilaginous components).

Contrary to characters developed primarily through study of our primary synoptic specimens of modern taxa, most characters originating from paleontological material were based on published descriptions. These sources are exhaustively listed with each character so derived. This documentary work was facilitated by two semicomplementary data sets, both slightly exceeding 200 characters and in comparatively wide use: (*i*) a matrix originated by Chiappe and colleagues (e.g., Chiappe 2001a, 2002) for Mesozoic Avialiae; and (*ii*) a matrix originally compiled by Norell and collaborators (e.g., Norell et al. 2001, J. M. Clark et al. 2002a), subsequently revised and circulated by the Theropod Research Group (e.g., Hwang et al. 2002, 2004). To date, the most comprehensive synthesis of characters pertaining to Theropoda was cited in an analytical overview of basal Tetanurae *fide* Hwang et al. (2004), which consisted of 75 taxa and 638 characters drawn from the literature and unpublished; representation of birds was limited to a single taxon Avialae *fide* Hwang et al. (2004).

Skeletal Specimens

Primary reference was made with respect to a series of voucher specimens arranged for simultaneous, comparative study. For most taxa, additional specimens of conspecifics or less-closely related taxa were available where assessments proved challenging. The primary synoptic series was retained at the USNM, whereas a secondary series was maintained at CMNH. Important use also was made of specimens held at the BMNH and AMNH.

Traditional or "complete" skeletons formed the primary series of skeletons examined in this project. We also went to significant effort to procure for study synoptic series of: (*i*) juvenile skeleton specimens in which suturae normally obscured with age were preserved, (*ii*) disarticulated ossa quadrati, (*iii*) crania freed from ossa quadrati, (*iv*) serially arranged vertebrae, and (*v*) articulated trunks for examination of costae. We studied characters of the internum cranii in specimens of appropriate condition or specially prepared by parasagittal section.

Spirit Specimens

Fluid-preserved specimens formed the primary resource for myological characterizations. Logistical limitation required that we use the published literature to the extent that we were confident of expertise, and focus our dissections on the remaining taxa. Myological study of the cranial and pelvic musculature was performed by Zusi, whereas pectoral myology was undertaken by Livezey. All myological examinations were performed using dissecting microscopes, surgical equipment, and pertinent literature. Staining permitted improved resolution of smaller muscles and details of fibers (Bock and Shear 1972).

Availability of Specimens

(Sub)fossil taxa, for obvious reasons, were not available for dissection, and inferences based on impressiones musculorum ossium were extremely limited. Where possible, notes on homologies with nonavian Theropoda and other Archosauromorpha were based on the literature (Gatesy 1990; Meyers 1996; Dilkes 1999; Hutchinson and Gatesy 2000; Hutchinson 2001a–b; Carrano and Hutchinson 2002; Meers 2003). However, no detailed myological characterizations were feasible for Dinornithiformes, Aepyornithiformes, Dromornithidae, Plotopteridae, Phorhusrhacidae, *Aptornis*, *Raphus*, and *Pezophaps*. Some taxa posed challenges of comparability for some myological characters (noted individually), e.g., musculature of the manus and/or some digiti pedis in some ratites and Sphenisciformes, and where digiti pedis (e.g., hallux) were vestigial or absent (e.g., ratites, some Tinamiformes and Pelecaniformes, Gaviiformes, Podicipediformes, most Procellariiformes, *Phoenicopterus*, Turnicidae, and many Charadriiformes).

Technicalities of Examinations

STUDY SKINS AND INTEGUMENTARY CHARACTERS

Reference to skin specimens was of limited but important status in the present analysis, and largely limited to macroscopic, conservative characters possessed of interordinal comparability, e.g., counts of remiges and rectrices, scutellation and webbing of the feet, and elaborations of the integument of the head. Color patterns of definitive or natal plumages, even those shown to have some signal within avian orders (e.g., Jehl 1968, 1971; Livezey 1991, 1995a–b, 1996a–c), were not included in a study of this scale. Finally, a substantial number of microscopic characters of the definitive pennation were included, based largely on critical references (A. C. Chandler 1916; Brom and Visser 1989; Brom 1990; G. Mayr 1996) and essential extensions of sampling using microscopic examinations.

Osteological Study

Study of skeletons was performed where elements were large or articulated by direct examination, whereas a significant proportion of comparative work required the aid of dissecting microscopy. Critical treatises on cranial development include those by W. K. Parker (1866, 1869a, 1879, 1890, 1891a). The literature consulted for osteological characterizations is immense (see annotations in descriptions), with especially critical references being Fürbringer (1888), Boas (1929, 1934), Butendieck and Wissdorf (1982), and Baumel and Witmer (1993).

Myological Study

Myological dissection was reserved primarily for phylogenetically critical or little-known taxa, emphasis being on representatives (preferably exemplar taxa, if available) of families lacking myological description in the literature (Appendix 1). Destructive sampling was minimized by guarded reliance on the literature, notably for comparatively rare taxa such as *Brachypteracias* and *Leptosomus* (Korzun 1988). Intraspecific variation—Rudge and Raikow (1992), Raikow (1993), Raikow et al. (1993), and Kesner (1994)—was noted if potentially influential. In a minority of cases, specimens of primary taxonomic exemplars were not available for myological study, and necessitated dissection of examples of congeners or (rarely) confamilials for coding characters of the musculature (Appendix 1).

For the ratites, direct study was augmented by McGowan (1979, 1982, 1984) and a critique of the same by Vanden Berge (1982). Homology of musculi pelvici, including nomenclature applied to Crocodylia and Theropoda, was updated from that by Tarsitano (1981) by Carrano and Hutchinson (2002: table 1). Recent works (e.g., Harvey et al. 1968; Maurer and Raikow 1981; Swierczewski and Raikow 1981; McKitrick 1991a–b, 1992, pers. comm.) expanded upon the classical literature, e.g., Garrod (1873a–b, 1874a–b, 1875a–b, 1876a–f, 1877a–d, 1878a–b, 1879a–b), Forbes (1880a–c, 1881a–c, 1882a, d, f), Gadow (1882a–b, 1891a–b), and Fürbringer (1888: taf. VIII–XXVI). Qualitative components of semiquantitative "muscle formulae" devised during the 19th century and subsequent refinements (e.g., Hudson 1937, 1948; Hudson and Lanzillotti 1955, 1964; Hudson et al. 1966, 1969, 1972) were recast where feasible and informative. See: Berger (1960a–b), Sibley and Ahlquist (1972: table 2), Raikow (1977a–b), Raikow et al. (1979, 1980, 1993), and Rudge and Raikow (1992) for recent descriptions.

Supplemental Osteological Literature for Characterizations of Taxa

Necessary reliance on the published literature for study and confirmation of direct observation was essential for a study of this magnitude and taxonomic diversity. The following references are noteworthy in this respect, listed by taxonomic group:

- **Basal Archosauromorpha**.—Broom (1913), Romer (1923b), Kälin (1933, 1941), Ewer (1965), Frey (1988), Sereno (1991a), Sereno and Arcucci (1991, 1994), Welman (1995), Meers (2003).
- **Basal Dinosauria**.—Romer (1923a), Rowe (1989), Sereno and Novas (1992), Sereno and Wild (1992), Sereno et al. (1993), Sereno (1994).
- **Ornithischia**.—Galton (1970), Sereno (1991b).
- **Sauropoda**.—A. D. Walker (1964), Welles (1984), Sereno et al. (1994), J. A. Wilson and Sereno (1998).
- **Stem Theropoda**.—Osborn (1912, 1917, 1924), Gilmore (1920, 1924a–b), Stovall and Langston (1950), Colbert and Russell (1969), Ostrom (1969, 1974a, 1976c, 1978, 1990), Osmólska et al. (1972), Barsbold (1974, 1979, 1983), Madsen (1976), Osmólska (1976, 1981, 1985, 1987, 1996), Sues (1977, 1978, 1997), Nicholls and Russell (1985), Currie and Russell (1988), Colbert (1989), Barsbold and Osmólska (1990, 1999), Barsbold et al. (1990), Bonaparte et al. (1990), Osmólska and Barsbold (1990), D. Smith and Galton (1990), Bonaparte (1991), Howse and Milner (1993), Pérez-Moreno et al. (1993, 1994), Zhao and Currie (1993 [1994]), J. M. Clark et al. (1994), Currie and Peng (1994), Currie and Zhao (1994a–b [1993a–b]), Currie et al. (1994 [1993], 2003), Sereno and Novas (1994 [1993]), Currie (1995, 1996, 1997, 2003), Currie et al. (1996), Sereno et al. (1996, 1998), K. Carpenter (1997), Norell and Makovicky (1997, 1999), Norell et al. (1997, 2000), J. D. Harris (1998), Sasso and Signore (1998), Azuma and Currie (2000), Brochu (2000, 2003), Currie and Carpenter (2000), De Klerk et al. (2000), Xu and Wang (2000), Currie and Dong (2001), Coria and Currie (2002), Maryanska et al. (2002), Vickers-Rich et al. (2002), Xu (2002), Xu et al. (2002, 2004), Hurum and Sabath (2003), Hwang et al. (2004).
- ***Archaeopteryx***.—Dames (1884, 1897), Petronievics (1921, 1925, 1927, 1950), Heinroth (1923),

Steiner (1938), Lowe (1944b), de Beer (1954), Heller (1959), Wellnhofer (1974, 1984, 1992, 1993), Howgate (1984), Bühler (1985), L. D. Martin (1985), Elzanowski and Wellnhofer (1993, 1995, 1996), Feduccia (1993), Britt et al. (1998), Elzanowski (1999a–b, 2001, 2002), Elzanowski and Pasko (1999), Ji et al. (2005), G. Mayr et al. (2005).

- **Hesperornithiformes**.—Marsh (1880), F. A. Lucas (1904), Cracraft (1982), L. J. Bryant (1983), L. D. Martin (1984, 1985, 1987, 1991), Bühler et al. (1988), Elzanowski (1991, 1995), Nessov and Prizemlin (1991), Nessov and Yarkow (1993).
- **Tinamiformes**.—W. K. Parker (1862, 1864), Alix (1874), Adolphi (1922), de Villiers (1946), Verheyen (1960a–b), Elzanowski (1987), Saiff (1988), Bertelli et al. (2002).
- **Ratites**.—Owen (1836, 1838, 1839, 1841, 1842, 1844, 1846a–b, 1848a–c, 1849b, 1851, 1852, 1856a–b, 1858a–b, 1866a–b, 1869a–b, 1870a–c, 1871a, 1872, 1873a–b, 1877, 1879, 1882, 1883a–b, 1886), Bianconi (1863), G. Jäger (1865), W. K. Parker (1866, 1888c), Murie (1867), Nathusius (1870, 1871), Mivart (1874, 1877), Gadow (1880, 1885), Beddard (1886a, 1899), Collett (1886), Haast (1886a–b), T. J. Parker (1891, 1892, 1895), Andrews (1894, 1896, 1897, 1904), Last (1894), Pycraft (1900, 1901), Rothschild (1900), Broom (1907), Schulze (1908), Schestakowa (1925), Lowe (1928b, 1930, 1931a, 1935, 1939a, 1942, 1944a), Piiper (1928), Lange (1929), Lamberton (1930), de Beer and Barrington (1934), Wiman (1935, 1937), Steiner (1936, 1946, 1958), Brock (1937), Archey (1941), Lutz (1942), Frank (1954), D. Starck (1955), de Beer (1956), Lang (1956), Friant (1959), Verheyen (1960c–d), H. J. Müller (1961a), Bock (1963a), Meise (1963), Firbas and Zweymüller (1971), Sibley and Frelin (1972), Cracraft (1974), Elzanowski (1976), Frank and Smit (1976), Sauer (1976), Budras and Meier (1981), Saiff (1981, 1982, 1983), Sibley and Ahlquist (1981), Stegmann (1981), Balouet (1984, 1987), McGowan (1984, 1985, 1989), Rosser and George (1984, 1986), C. Müller (1985), Patterson and Rich (1987), Peters (1987), Bledsoe (1988), Bock and Bühler (1988), Elzanowski (1988), Worthy (1988), Kurochkin (1995b), Rich et al. (1995), J. M. Starck (1995), Fuss (1996), W. Müller and Weber (1998), Patak and Baldwin (1998), Worthy and Holdaway (2002).
- **Diatrymiformes**.—Witmer and Rose (1991), Andors (1992).
- **Galliformes**.—W. K. Parker (1862, 1864, 1869a, 1891a), Shufeldt (1881a, 1888b, 1914, 1919a–b, 1920), Beddard (1886b), H. L. Clark (1898), Kulczycki (1901), Gaupp (1905), Pohlman (1921), Bremer (1940a), Berger (1955a), Verheyen (1956a, 1960b), G. A. Clark (1960, 1964a–b), Vuilleumier (1965), S. A. Richards (1968), Vaurie (1968), Amadon (1970), Radu (1975), Crowe (1978), Steadman (1980), Poplin and Mourer-Chauviré (1985), Russell and Joffe (1985); Dyke et al. (2003).
- **Dromornithidae**.—Stirling and Zietz (1900, 1905, 1913), Rich (1979, 1980a, 1991), Rich and Molnar (1996), Field and Boles (1998), Murray and Megirian (1998), Murray and Vickers-Rich (2004).
- **Anhimae**.—Beddard (1886c, 1894), Beddard and Mitchell (1894), Mitchell (1895), Shufeldt (1901a), Verheyen (1956b).
- **Anseres**.—Owen (1875), Shufeldt (1888a, 1913a), W. K. Parker (1890), Pycraft (1906a), Knöpfli (1919), de Beer and Barrington (1934), Verheyen (1953b, 1955a), Woolfenden (1961), S. L. Olson and Feduccia (1980a), Livezey (1986, 1997a), O. Jäger (1990).
- **Procellariiformes**.—Gadow (1883), Shufeldt (1888c, 1907), Pycraft (1899a), Lowe (1925a), Kuroda (1954), Verheyen (1958a), Saiff (1974), Imber (1985).
- **Sphenisciformes**.—Gervais and Alix (1877), Pycraft (1898b), Shufeldt (1901b), Virchow (1931), Lowe (1933), C. W. Parsons (1934), Lanham (1947), Crompton (1953), Verheyen (1958b), Krassovskii (1966), Schreiweis (1972, 1982), Saiff (1976), Giannini and Bertelli (2004).
- **Gaviiformes**.—Shufeldt (1891a, 1892), Pycraft (1899b), Stegmann (1974), Cracraft (1982), Boertmann (1990).
- **Podicipediformes**.—Coues (1868), Shufeldt (1891a, 1892, 1904b), Beddard (1896a), Pycraft (1899b), Rosenberg (1911), Verheyen (1959a), Stegmann (1969, 1974), Cracraft (1982), Bochenski (1994).
- **Pelecaniformes**.—Garrod (1876a, 1878a), Mivart (1878), Forbes (1882a), Shufeldt (1884a, 1888c, 1902a, 1913b), Beddard (1892, 1897b), Pycraft (1898a), Böker (1939), Lanham (1947), Slabý (1951), Verheyen (1960f), Owre (1967), S. L. Olson (1977), Harrison (1978), Saiff (1978), Cracraft (1985), Siegel-Causey (1988, 1989, 1997).
- **Plotopteridae**.—S. L. Olson and Hasegawa (1979, 1985, 1996), S. L. Olson (1980).
- **Ciconiiformes**.—Garrod (1875b, 1877a), Shufeldt (1889a–b, 1901c), Beddard (1896b, 1901a), T. Adams (1955), Bock (1956), Verheyen (1959b), Cracraft (1967a), S. L. Olson (1979).
- **Phoenicopteridae**.—Gadow (1877), Weldon (1883), W. K. Parker (1889b), Shufeldt (1889c, 1901d), Sibley et al. (1969), S. L. Olson and Feduccia (1980b).
- **Balaenicipitidae**.—W. K. Parker (1860, 1861), Reinhardt (1860, 1862), A. D. Bartlett (1861), Giebel (1873), Beddard (1888a), Shufeldt (1901e), Mitchell (1913b), Böhm (1930), Cottam (1957), Cracraft (1985).
- **Scopidae**.—Beddard (1884), Shufeldt (1901e).

- **Falconiformes**.—Shufeldt (1881b, 1886a, 1889d, 1891b–c, 1922), Beddard (1889b, 1902a, 1903a–b), Suschkin (1899a–b, 1905), Pycraft (1902), Compton (1938), Verheyen (1959c), Richardson (1972), S. L. Olson (1982, 1987a), Kemp and Crowe (1990).
- **Cathartidae**.—Shufeldt (1881c, 1883), Cracraft and Rich (1972), Rich (1980b), Rea (1983), Emslie (1988), Seibold and Helbig (1995).
- **Gastornithiformes**.—E. T. Newton (1886), L. D. Martin (1992).
- **Basal Gruiformes**.—A. D. Bartlett (1862), W. K. Parker (1869b), E. Bartlett (1877), Milne-Edwards (1878a), Forbes (1882f), Beddard (1891), Andrews (1899), Mitchell (1901b, 1915), Schaub (1914), Lowe (1924), Verheyen (1957b), Appert (1968, 1985), J. Steinbacher (1968), Stegmann (1978), Weber and Hesse (1995), Livezey (1998b).
- **Grues**.—Giebel (1855), Garrod (1876b), Beddard (1889a, 1890a–b, 1893a, 1902b), Shufeldt (1894a, 1915a–b), Lowe (1928a), Berger (1956a), Verheyen (1957a), Cracraft (1968b, 1969, 1971b, 1973), Macke (1969), Alvarez del Toro (1971), S. L. Olson (1973), Stegmann (1978), Livezey (1998b, 2003).
- **Charadriiformes**.—Owen (1866c), Coues (1868), Garrod (1877b), Forbes (1881b), Shufeldt (1888d, 1893b, 1901f, 1903a), W. K. Parker (1890), Beddard (1896c, 1901d), Mitchell (1905), Lowe (1915b–c, 1916a–b, 1922, 1923, 1925b, 1927, 1931b–d), Clara (1925), Piiper (1928), Boetticher (1934), Wiman and Hessland (1942), Storer (1945, 1952), Maillard (1948), Verheyen (1957c, 1958c–d, 1959d), Bock (1958), Stegmann (1978), Strauch (1978, 1985), Björklund (1994).
- **Pedionomidae**.—Gadow (1891a), Bock and McEvey (1969a), S. L. Olson and Steadman (1981), Livezey (1998b).
- **Turnicidae**.—W. K. Parker (1862, 1864), Nathusius (1882b), Ogilvie-Grant (1889), Lowe (1923), Verheyen (1958e), Livezey (1998b), Rotthowe and Starck (1998).
- **Columbidae**.—Garrod (1874d), Shufeldt (1891d, 1901g), Mitchell (1899), Verheyen (1957d), Stegmann (1959), Cracraft (1971c).
- **Raphidae**.—Strickland and Melville (1848), Owen (1869c, 1871b), E. Newton and Gadow (1893).
- **Pteroclidae**.—W. K. Parker (1862, 1864), Elliot (1878, 1885), Gadow (1882a), Shufeldt (1901h), Bowen (1927), Stegmann (1959), Fjeldså (1976), de Juana (1997).
- **Psittaciformes**.—Giebel (1862), Garrod (1874e), Eudes-Deslongchamps (1879), Fürbringer (1889), Beddard and Parsons (1893), Mivart (1895a–b), D. W. Thompson (1899), Abraham (1901), Shufeldt (1902b), R. Martin (1904), Shufeldt (1918b), Böker (1929), Verheyen (1956e), G. A. Smith (1975), Güntert (1981), de Kock (1987).
- **Caprimulgiformes**.—Garrod (1873d), Shufeldt (1885b, 1886d), Beddard (1886d), W. K. Parker (1889c), H. L. Clark (1894, 1901), Wetmore (1919 [1918]), Lubosch (1929a–b), Verheyen (1956a), Hoff (1966), Cowles (1967), Bühler (1970), S. L. Olson (1987b).
- **Strigiformes**.—Collett (1871), Milne-Edwards (1878b), Shufeldt (1881d, 1889e, 1900a), Beddard (1888b, 1890c), Pycraft (1898c, 1903a, c), Verheyen (1956a), May (1961), A. H. Miller (1965), Hoff (1966), F. N. Lee (1967), Bock and McEvey (1969b), Arredondo (1977).
- **Cuculidae**.—Beddard (1885a, 1898b, 1901b, 1902c), Shufeldt (1886b–c, 1901i), Pycraft (1903d), Larson (1930), Lowe (1943), Berger (1952, 1953a–b, 1954, 1955b, 1960b), Seibel (1988), Hughes (2000).
- **Musophagidae**.—Schalow (1886), Lowe (1943), Verheyen (1956g), Burton (1970), Seibel (1988), Hughes (2000).
- **Opisthocomidae**.—Perrin (1875), Garrod (1879b), Nathusius (1881, 1882b), Gadow (1883), Elliot (1885), Beddard (1889c), Quelch (1890), W. K. Parker (1891b), T. J. Parker (1892), Mitchell (1896), Pycraft (1898d), Shufeldt (1918a), Banzhaf (1929), Böker (1929), Barnikol (1953), C. W. Parsons (1954), Verheyen (1956h), Sibley and Ahlquist (1973), Seibel (1988), Marceliano (1996), Hughes (2000).
- **Apodiformes**.—Shufeldt (1885b, 1886d, 1889f, 1893c, 1902c), W. K. Parker (1889d), Buri (1900), H. L. Clark (1906), Scharnke (1931), Lowe (1939b), Verheyen (1956f), Orr (1963), Cohn (1968), Morioka (1974), Collins (1983), Bleiweiss (1987, 2002).
- **Trogoniformes**.—Forbes (1881c), Verheyen (1956a), Maurer and Raikow (1981).
- **Coliiformes**.—Murie (1872a), Garrod (1876d), Pycraft (1907b), Verheyen (1956d), D. Starck (1960), Schoonees (1963), Rowan (1967), Schifter (1967, 1985), Goldschmid (1972a–d), Berman and Raikow (1982).
- **Coraciiformes**.—Sclater (1865, 1872), Murie (1872b–c, 1873), Forbes (1880a, 1882c), Shufeldt (1884b, 1903b), Seebohm (1890c), Beddard (1893b), Mitchell (1901c), W. DeW. Miller (1912), Desselberger (1930), J. Steinbacher (1937), Lowe (1948), Fourie (1955), Verheyen (1955b), Sibley (1956), Manger Cats-Kuenen (1961), Cracraft (1971d), S. L. Olson (1976), Kemp (1979), Fry (1980), Hammouda and Mokhtar (1980), Kemp and Crowe (1985), Pascotto and Donatelli (2003).
- **Piciformes**.—Sclater (1870), Garrod (1872a), W. K. Parker (1875a), Forbes (1882c), Beddard (1889d, 1896d–e, 1901c), Seebohm (1890b), Shufeldt (1891e, 1900b), Scharnke (1931), Richardson (1942), Lowe (1946), Verheyen (1955c), Bock and Miller (1959), D. Goodwin (1964),

Spring (1965), Fry (1969), S. F. Simpson and Cracraft (1981), S. L. Olson (1983), Raikow and Cracraft (1983), Bock (1999b).

- **Passeriformes**.—Forbes (1879, 1880a–b, 1882d–e), Shufeldt (1882, 1888d, 1889g, 1890), F. A. Lucas (1888, 1894), Seebohm (1890b), Pycraft (1905a–c, 1906b, 1907c), Sonies (1907), Suschkin (1927), Linsdale (1928), Boetticher (1931), Scharnke (1932), Küchler (1936), Stonor (1936, 1937, 1938, 1942), Lowe (1938), Amadon (1950, 1956), Arvey (1951), Beecher (1953), de Kock (1955), Bock (1963b), Morioka (1967), Sibley (1968, 1974), Bock and Morioka (1971), Morlion (1971), S. L. Olson (1971), L. P. Richards and Bock (1973), Raikow (1976, 1977a–b, 1978, 1982, 1987, 1993, 1994), Schodde and McKean (1976), Bock and Morony (1978a), Raikow et al. (1980, 1990, 1993), Bock and Clench (1985), McKitrick (1985a–b, 1986), Rich et al. (1985), J. M. Starck (1993), Raikow and Bledsoe (2000), Birdsley (2002).

Clearly, a century of anatomical literature on most major groups of modern and fossil birds, together with rich anatomical collections, represented a wealth of information and foundation for a modern reappraisal of avian phylogenetics by morphological means. Implementation of modern methods using this vast resource is the substance of the present descriptive work and its companion analytical paper.

Homology—Fundamental Concepts and *A Priori* Diagnosis

The primary conceptual foundation of characters and comprised states in a phylogenetic context is homology, the historical roots of which being within comparative anatomy (Boyden 1943, 1947; Nelson 1978, 1994; Wiley 1981; Patterson 1982; Roth 1984, 1988; Stevens 1984; de Pinna 1991, 1994; Horder 1994; Panchen 1994; G. P. Wagner 1996; S. R. Harris et al. 2003). Despite the lasting relevance of the original concept as articulated by Owen (1843)—one stressing historical integrity *despite* diverse form and function—problems both theoretical and practical remain (Rieppel 1980, 1992, 1993, 1994; Sattler 1984; Roth 1991; McKitrick 1994; Sluys 1996). Nevertheless, primary assessments of homology and congruent nomenclature are essential for definition and description of characters (Cracraft 1967b), a necessity prompting two ancillary revisions of anatomical complexes as a foundation for characterizations in the present study prior to analysis (Zusi and Livezey 2000, 2006).

Theory of homology, modalities evident in both discrete and continuous (metric) traits, and recognition of typical limits of variation about modalities within lineages (Archie 1985; Pimentel and Riggins 1987; Baum 1988; Chappil 1989; Thiele 1993; Crowe 1994; Strait et al. 1996; Rae 1998; Rohlf 1998; Swiderski et al. 1998; Zelditch et al. 2000; Wiens 2000, 2001; Siddall and Jensen 2003) underlies inclusion of multistate and polymorphic characterizations (Lipscomb 1992; B. Goodwin 1994; Steel and Penny 2005). Multistate characterization, however, is sufficiently complex in practice that important variation in theoretical perspectives and implemented protocols exists among systematists (Mabee and Humphries 1993; Forey and Kitching 2000). Moreover, it is predictable that with increasing taxonomic scale of an analysis, numbers of variants observed for (homologous) characters typically will increase, i.e., absent artificial imposition of binary structure (see below), more states are to be expected for a given character subdelimited for Aves than a comparable treatment for a single avian order. This expectation was realized in the present study: one-third of the characters comprised three or more states.

Recognition of "characters" and "parts" of organisms and subsystems is both fundamental and challenging for phylogenetic analysis (Rieppel 1991; Wägele 1994, 1995; Hawkins 2000; McShea and Venit 2001; G. P. Wagner and Laubichler 2001; Zwick 2001) and associated macroevolutionary inferences (K. S. Thompson 1992). As has become standard in comparable works, anatomical features and variation herein were deemed potentially admissable as phylogenetic characters where inferred to be homologous (implicitly or explicitly considered to share genetic bases) and hence possessed of historical signal across taxa (Colless 1985; Rodriguez 1986; Fristrup 2000; Brakefield 2001). Houle (2001: 109) defined characters to be "the units of evolutionary change," the historical tracts of which are employed by phylogeneticists to reconstruct bifurcating networks descriptive of phylogenetic descent among lineages possessing these "units." Such features were not only comparable across taxa, but were considered (and in some cases, demonstrated) to share ontogenetic mechanisms.

Two levels of assessment (Haszprunar 1992, 1998) and practical protocols (Ingilis 1966; Brower and Schawaroch 1996) are employed in inferences of homology (Patterson 1982; G. P. Wagner 1989a–b, 1995), which essentially embody "primary" or prephylogenetic evaluations, and "secondary" or phylogenetic assessments. Primary or pre-analytical assessments that principally emphasize similarity of definitive form derive from criteria of homology proposed by Remane (1952, 1956), which essentially are threefold: (*i*) similarity of position, (*ii*) similarity of definitive form, and (*iii*) continuity of similarity through intermediate forms (taxa or ontogenetic stages). These assessments hold a special philosophical position in that homology is determined independently of effect on phylogenetic inferences and congruence among characters (Haszprunar 1998). The importance of "similarity" in classical diagnosis of homology necessitates a fundamental distinction to be drawn between this usage and the discredited phenetic perspective in which general "similarity" is considered to be directly indicative of phylogenetic relationship among lineages (Wiley 1981).

The third aspect of "primary" assessments appears to pertain to intermediacy through evolutionary relatives, but the wording seems to admit similarity of ontogenetic stages as well (Shubin 1994). Historically, a centrality of form, linked to the concept of the "archetype," was related to homology, in which variation within homologous characters was interpreted as a departure from the archetypical form for a taxon (Young 1993). With the conceptual replacement of static archetypology with modification with decent among lineages, variation of all kinds took on new, often critically important meanings. Fortunately, the relevance of phenotypic hierarchies to historical descent survived the demise of the "archetype."

"Secondary" or phylogenetic affirmations of homology turn on patterns of state-changes in the phylogenetic reconstruction derived from all characters (de Pinna 1991; Hawkins et al. 1997; Haszprunar 1998). In a sense, the "final" stage of the assessment of homology reflects the "reciprocal illumination" that characterizes this process (e.g., Chu 2002). Admittedly, however, "finality" in this inferential context is illusory, in that this reciprocal process of stagewise evaluation of homology is repeated with each new refinement or emendation of characters or analytical approach employed. In that a historical view of homology turns appropriately on common phylogenetic history (Coddington 1988, 1994; Jeffrey et al. 2002) and inferences of this kind (e.g., G. A. Clark 1973), assertions of homology seem implausible absent a phylogenetic context and included transformations of states (de Pinna 1991; Brady 1994). In practice, further refinements of homology occur with the subsequent reanalysis of characters by investigators in light of this or subsequent phylogenetic works.

Fossils: Analytical Perspectives and Limitations

A purportedly special role for fossils derives from the traditional assumption that an *ancient* fossil necessarily represents a *primitive* lineage, one providing unique insights into *plesiomorphic* states of modern, presumably apomorphic descendant lineages (Schaeffer et al. 1972; Brodkorb 1976; S. L. Olson 1985). This assumption now is recognized as faulty (Cracraft 1979, 1980; Coddington 1994; Livezey 1997a), and fossils increasingly are treated simply as the remains of long-dead representatives of extinct terminal lineages having likelihoods of analytical importance comparable to those of modern forms. For example, the discovery of a surviving population of a single species of dromaeosaurid dinosaur would hold substantially more promise for phylogenetic inference of modern Aves—both for analysis of characters and rooting of trees—than a dozen, typically preserved, fossil Tetanurae. Anatomical completeness and phylogenetic position, not the time elapsed since extinction, are the properties critical to phylogenetic inference of fossils.

The appearance that fossils *per se* are uniquely informative for birds has been distorted further by a misinterpretation stemming from the recent spate of new taxa and a misfortune of extinction that resulted in these extinct lineages being more closely related to modern birds than any other extant taxon. However, phylogenetic relationships *within* neognathous Neornithes can be estimated through comparative study of extant representatives alone, deeper inferences being limited substantially by the apomorphies of palaeognathous taxa. A nested series of reasonably preserved fossil Theropoda and deeper outgroups were assumed to provide, in combination, adequate rooting information (Barriel and Tassy 1997, 1998), and to permit inferences among orders or inclusive of both palaeognathous and neognathous Neornithes.

Nevertheless, a minority of investigators persist in the accordance of special analytical properties to fossils. E.g., a practice of alteration of character states of modern clades ("crown" groups), based on states of grades of purported fossil relatives ("stem" taxa) subtending these terminal groups, is perpetuated by some in analyses of higher-order phylogenetic relationships (e.g., G. Mayr 2002a, 2003b, 2004b; G. Mayr and Clarke 2003; G. Mayr et al. 2003). In addition to the assumption of necessary plesiomorphy of fossils, this practice appears to derive from the traditional paleontological view that fossils modally or necessarily represent lineages *directly ancestral* to modern taxa (Howard 1950; E. C. Olson 1981). This perspective contrasts markedly with the predominant neontological view, in which ancestral states are inferred by reconstruction of phylogenetic relationships among (descendent) terminals. The limitations of characterization of fossils resulting from deficiencies of preservation and incompleteness, however, are obvious (Livezey 1998b). P. J. Wagner (2000) extrapolated these limitations to estimate an asymptotic "exhaustion" of morphological characters to be gleaned from fossil taxa, which could be applied as well to any collection of specimens. At least until the present time, however, the apparent "exhaustion" possibly inferred for neontological specimens would be principally a function of study, not genuine potential of the material under examination.

Equally unfounded is the assumption that perceptions of functional importance are directly indicative of homoplasy in phylogenetic reconstructions. A classically entrenched example concerns pelvic refinements of Hesperornithiformes, Podicipedidae, and Gaviidae—initiated by Stolpe (1932, 1935a–b)—and subsequently perpetuated uncritically (e.g., Storer 1960a–b, 1971a–b). A related but more abstract notion asserts that functional dimensions must be known in detail to qualify a character for inclusion in a phylogenetic analysis (Bock 1967, 1977, 1989; Szalay and Bock 1991). This perspective appears to be related to a view of characters as "functional units," a concept of interest in its own right (Schwenk 2001). In a phylogenetic context, these adaptationist biases subsequently have been countered, and function is recognized as one attribute of phylogenetic history (Cracraft 1981b; Schoch 1986; Lauder 1990, 1994; Amundson and Lauder 1994; Knox 1998; Böhning-Gaese and Oberrath 1999; Butler and King 2004).

Recent paleontological discoveries have engendered a new generation of hypotheses for evolution of flight conditional on theropod ancestry (Gauthier and Padian 1985, 1989; Chatterjee 1997; Zhou and Hou 1998; Zhang and Zhou 2000; Gishlick 2001; Zhou and Farlow 2001; Zhang et al. 2002; Chatterjee and Templin 2003), as opposed to speculative scenarios largely predicated on *Archaeopteryx* and related ecofunctional preconceptions (Nopsca 1907, 1923, 1925; Feduccia and Tordoff 1979; Ostrom 1979, 1991; Feduccia 1980, 1993, 1995, 1996, 2001; L. D. Martin 1983a–b, 1991; Wellnhofer 1983; Duncker 1989; Ulinski and Margoliash 1990; Rayner 1991; Speakman 1993; Geist and Feduccia 2000).

A parallel progression characterized hypotheses of origin of feathers and endothermy, in which older schemes assumed a vague, comparatively direct descent from a reptilian scale (Spearman 1966; Maderson 1972; Regal 1975; Brush 1993, 1996) to recent hypotheses in which several fundamental apomorphies are sequenced within Theropoda (Prum 1999; Brush 2000; Schreitzer and Marshall 2001; Xu et al. 2001), predominantly within inferential limits or "phylogenetic brackets" (Witmer 1995a). Such phylogenetic frameworks are essential for reconstruction of the evolution of quintessential attributes (Balouet 1987), complex structures (Atchley and Hall 1991; G. P. Wagner and Altenberg 1996), and broad functional patterns (Holmgren 1933; Feduccia 1973; Dullemeijer 1980; Carroll 1997; Zweers and Vanden Berge 1997a–b; Zweers et al. 1997).

Despite counterexamples (Mabee 1989, 1993, 2000) and deficiencies in the knowledge of developmental mechanisms or genetic determinants of characters (Alberch 1985; Meyer 1999; G. A. Wray 1999), the reasonable assumption of a common ontogeny for homologues persists as a criterion of variable priority (Kraus 1978; Nelson 1978, 1994; Roth 1984, 1988; de Queiroz 1985; Kluge and Strauss 1985; G. P. Wagner 1989a–b, 1994; Wheeler 1990; D. M. Williams et al. 1990; H. N. Bryant 1991, 1997; de Pinna 1994; Mario 1994; Shubin 1994; Meier 1997; G. P. Wagner and Gauthier 1999; S. F. Gilbert and Bolker 2001; Jeffrey et al. 2002). This likelihood has been extended to account for vestigial states (Stone 1998). Unfortunately, avian systematics has been afflicted by an apparent conflict between ontogenetic (Hinchliffe 1977, 1985, 1989; Hinchliffe and Griffiths 1983; Holder 1983; Hinchliffe and Hecht 1984) and paleontological evidence bearing on homology of the manus (Chatterjee 1998b; G. P. Wagner and Gauthier 1999). This disagreement has been interpreted as empirical support both for and against the hypothesis of theropod ancestry for birds (Hecht and Hecht 1994; Burke and Feduccia 1997; Feduccia 1999; Feduccia and Nowicki 2002).

Delimitation and Classes of Characters and States

STANDARD PROTOCOL

Of critical importance to any phylogenetic analysis is the issue of the criteria and protocols for definition of characters and states (Wiley 1981; Pimentel and Riggins 1987; Pogue and Mickevich 1990; Stevens 1991; Pleijel 1995; Wiens 1998a, 2001). In the present analysis, natural variation amenable to assignment to discrete states (e.g., not presenting a continuum of conditions among and/or within taxa) were characterized. Contrary to the generalities inferred by Poe and Wiens (2000), characters were not excluded merely because variation within one or more terminal taxa was observed, but because significant issues of homology were perceived *a priori* by means of delimitation of states or confident allocation of taxa pertained (Salisbury 1999).

Variation within terminal taxa, however, was not irrelevant to characterization. We consciously applied a criterion of scale to the level of detail implicit in characters and states scored for analysis. We sought to encode variation among taxa for a feature showing variation among taxa (historical signatures), but to do so at a maximal level of detail such that the associated variation within taxa ("noise") approached a practical, relative minimum. Accordingly, this criterion, in which level of detail of characterization approximates a maximum of "historical signatures" relative to "noise" (within-taxon variation), may be conceptualized as the precision of focus and level of (practical) magnification employed in microanatomical study. This morphological criterion is analogous to choice of scale or power of magnification (e.g., all nucleotides, positionally constrained nucleotides, codon, restriction fragments, or amino acid equivalents) subjected to the plane of focus by weighting schemes or evolutionary models. An important reflection of proper scale is that states derived therein permit objective, independently repeatable scoring of taxa under consideration, while capturing a maximum of information. For example, myological characters typically are of lesser detail (comparatively gross nature) in light of preservational, condition-related, or malleable character of muscles, whereas comparatively stable details of skeletal elements permit a finer degree of delimitation.

A hierarchy of mutual exclusivity was conceptually requisite for characters and included states, a framework in which relationships among characters and states are considered of primary analytical and logical importance. States are mutually exclusive structural alternatives of characters (H. N. Bryant 1989) diagnosed among the taxa under study. This methodology is not premised on an ontogenetic independence of characters and included states—a developmental improbability under many circumstances (Arthur 1984, 2004; Cheverud 2001; West-Eberhard 2003)—but instead is intended to partition optimally encoded information while minimizing redundancy. Characters potentially can pertain to a number of aspects of a single feature or complex (Hawkins et al. 1997). Characters in turn were hypothesized to be homologous complexes of states—aspects of phenotypes usually possessed of homology at genetic and ontogenetic scales as well as historical identity and resultant potential for phylogenetic signal. In addition to the logical advantages of this perspective, this approach provides analytical advantages as well, including suboptimal treatment of "polymorphism" in search algorithms (Wiens 2000). Given that a number of characters can be devised for a single homologous trait, each comprising two or more mutually exclusive (potentially ordered) alternatives, this approach imposes no practical limits on the empirical foundation for phylogenetic reconstructions.

In order to avoid redundancy among characters, issues of status (presence *vs*. absence) and form were included as states within a single character (where possible) instead of devising multiple, arbitrarily delimited, and often partially redundant, binary characters. The practice of "forced-" or "additive-binary" characterization is not uncommon, especially in somewhat older morphological applications (e.g., Chiappe 1992), and often is included in the concept of "additive binary" characters (Meier 1994). This methodology is considered herein to be prone to at least two analytical errors: (*i*) delimitation, principally unintended and unrecognized, of "empty" combinations of characters and states (actually unobserved or logically impossible on structural or functional bases); and (*ii*) unjustified imposition of implicit ordering of states that instead could be treated more realistically as ordered or unordered (explicitly) if included within a single, multistate character. Nonetheless, despite the justifications for inclusion of multistate characters (Pleijel 1995), there is no protocol presently available that flawlessly serves all philosophical and practical considerations (Stevens 2000).

In studies committed *a priori* to strict dichotomy of characterizations, both classes of error are not infrequent. An example of an error of type (*i*) would attend the separate characterization of status (presence *vs*. absence) and form (e.g., rectangular *vs*. circular) of a single feature. This scheme holds the potential for the implicit definition of half of the four two-character conditions that are illogical; all taxa for which the first character (status) was "absent" and form was scored as anything but "missing" would have resulted in impossible biconditional conditions. If recognized as "missing," the analytical burdens related to such uncertainty are assumed.

The second problem—occult, unjustified differential penalizing of state-changes or ordering—afflicts combinations of states in the two aforementioned hypothetical characters. If the two, binary characters were combined into a single, three-state character—(absent), (present, rectangular), (present, circular)—transitions among the three states might be unordered (transitions between any two different states, i.e., unit penalty) or ordered (zero, one, or two steps, respectively). Alternatively, within the context of two binary characters, ten directed transitions are possible, representing four, four, and two transitions entailing 0, 1, and 2 total steps, respectively; eight of the ten transitions include at least one internally contradictory condition (e.g., structure absent but of circular form).

Avoidance of the aforementioned practice leads to increased numbers of multistate characters (Lipscomb 1992; N. B. Simmons 2001; Siddall and Jensen 2003), a state of affairs that we consider to be a realistic representation of history, but which arguably may expand the character-space examined (M. P. Simmons et al. 2004). Morphological evolution—especially at higher scales of relationships and comparatively ancient (inter)nodes—seldom is limited to binary change and frequently manifests multiple states ramified among two or more lineages. Negative impacts on analytical logistics, however, can be caused by comparatively high proportions of multistate (especially unordered) characters (Lipscomb 1992).

Regardless of complexity of states within characters and ordering, throughout we designed the analytical process on the practical criterion of phylogenetic inference (and underlying theoretical premise of evolutionary change) of maximal (global) parsimony, i.e., we sought the cladistic tree(s) that "explain" variation among taxa using minimal state-changes in the dichotomous tree(s) of characters and taxa included in the ingroup. As this philosophical and practical perspective is the only one refined for morphological data, we adopt this approach while acknowledging its limitations (J. I. Davis et al. 2005) and restrict justification of the choice to an acknowledgment of ongoing controversies (Wiens and Hillis 1996; Haszprunar 1998; Kluge 2005; Steel and Penny 2005).

Weighting of Characters

A compendium of characters to be included in a phylogenetic analysis may seem to be independent of the imposition of ordering or differential weights to characters. To the contrary, however, inferences regarding sequential relationships among states within characters and relative signal predicted *a priori* for characters can influence both the merging and partitioning of states among candidate characters and the likelihood of inclusion of characters posing diverse challenges of coding. Ultimately, characters were coded for taxa using MacClade© (Maddison and Maddison 1992).

A topic of waning popularity—differential weighting of characters (Neff 1986; Wheeler 1986; H. N. Bryant 1989; Chippindale and Wiens 1994)—characters were assigned uniform weight *a priori* in this analysis (but see Neff 1986). However, limited use of weighting *a posteriori* or "successive weighting" or the iterative, increasingly intense weighting of characters based on recursive searches (Farris 1969; J. M. Carpenter 1988; Trueman 1998) may be justified, especially in exploratory contexts.

A comparatively uncommon and subtle use of weighting, also eschewed herein, is the inverse weighting of multistate characters in proportion to the number of states defined (e.g., James et al. 2003). Intended to avoid "artificial" inflation of influence by multistate characters under the criterion of parsimony (especially where variation is problematic), we consider the practice to be faulty for two reasons: (*i*) given that many investigators artificially impose binary structure on characters that others would construe as multistate characters, number of *states per character* is at least in part subjective and exacerbated by a bias for combination of states or division of characters; (*ii*) organization of traits as characters and states thereof is often subjective with respect to numerical parsimony, i.e., one step may correspond to one change regardless of whether the change is within or between characters; and (*iii*) multiple states may reflect magnitude of evolutionary change and potential phylogenetic signal, such that no attempt to down-weight phenotypic richness, especially where subjected to uniform, unbiased definitional protocols, would be justified.

Classes of Variation

Intraspecific Variation and Polymorphism

The evolutionary implications of phenotypic variation within species, although subject to increasingly sophisticated theoretical and empirical study (Lajus et al. 2003; Nijhout and Davidowitz 2003; David et al. 2004; Frankino and Raff 2004), tend to be viewed merely as obstructions to robust phylogenetic hypotheses. The nature of terminal taxa and associated protocols for coding hold implications for frequencies of polymorphic codes, e.g., in the present study variation observed for close relatives of the exemplar taxa was reflected in polymorphic characterizations for that terminal.

Analytical treatment of multiple-state codings as polymorphism *sensu stricto* (N. B. Simmons 2001), as opposed to equation with complete uncertainty, augments information for all but binary characters (Nixon and Davis 1991; Crandall et al. 1994; Wiens 1995, 1999, 2000; Wiens and Servedio 1997), especially where ordering is imposed (Maddison and Maddison 1992; Swofford 1998). Where additional, informative character states occur in closely related taxa but not found in exemplar taxa, this was recorded in associated notes. The corresponding codes for polymorphic states *per se* (e.g., "a/b," "b/c," "a/c," and "a/b/d/f") were explicitly defined in the data matrix. However, for the sake of brevity, polymorphism codings were not listed in character descriptions.

Ordering of States

Intrinsic qualities of characters, including ordering, were assessed prior to analysis and therefore are discussed in this descriptive work. We acted in accordance with the premise that ordering should be intentional, justified, and explicitly indicated. Where characters were treated as ordered, single steps ($s = 1$) are implied by changes between consecutive states (e.g., “a,” “b,” and “c”), with changes of more than one state following accordingly (Slowinski 1993). E.g., for number of steps (s), ordering of states ≡ *ord* {a, b, c} ⇒ s (“a” → “c” ∨ “c” → “a”) = 2. Transitions in states were considered to be commutative—i.e., s (“x” → “y”) = s (“y” → “x”)—which implies that reversals are no more “costly” than apomorphic changes (Hauser and Presch 1991; Slowinski 1993).

An alternative, comparatively uncommon protocol is *irreversibility*, which imposes unidirectionality of change (i.e., *precludes* reversals). Similarly, *Dollo* parsimony—under which an apomorphy is limited to a single instance in the tree and homoplasy to multiple losses (reversals)—imposes a variably pervasive preconception about evolutionary change on the analysis, likely altering set of shortest trees, increasing the minimum tree length, and changing optimizations of other characters. Analytical refinements concerning evolutionary reversibility of characters (Sanderson 1993) and alternatives to strict parsimony in morphological contexts (P. J. Wagner 1998; Lewis 2001) are forthcoming.

Meristic characters (e.g., morphoclines) or continuous morphometric characters (Baum 1988; Thiele 1993; Crowe 1994; Strait et al. 1996; Rae 1998; Swiderski et al. 1998) most commonly were ordered, as were characters comprising states related naturally by structure, e.g., by size or ordinal states concerning linearity, proximity, or pneumaticity. Unordered characters assign single steps to transitions between any pair of different states of a given character. All assignments of steps (s) between states, including noncommutative (asymmetrical) transitions—i.e., s (“a” → “c”) ≠ s (“c” → “a”)—can be represented by step-matrices. Elements of such matrices specify a “cost” or number of steps to each pairwise transition (Ree and Donoghue 1998). Linearly (un)ordered characters are but special cases of a step-matrix, the latter embodying the quantitative paradigm for hypotheses of phylogenetic characteristics of discrete morphological characters. E.g., an unordered, commutative (symmetrical), multistate character corresponds to a step-matrix—entries for rows and columns corresponding to initial and terminal states, respectively)—in which diagonal elements are zero and off-diagonal elements are one. A linearly ordered, symmetrical character comprising five states (“a” through “e”), in which transitions of identity (e.g., “a” → “a”) or “silent” transitions (e.g., “a” → “b” → “a”) are undetected and treated as zero change, corresponds to the following step-matrix of upper-diagonal form:

$$\begin{array}{cc}
 & \begin{array}{ccccc}\mathbf{a} & \mathbf{b} & \mathbf{c} & \mathbf{d} & \mathbf{e}\end{array} \\
\begin{array}{c}\mathbf{a}\\ \mathbf{b}\\ \mathbf{c}\\ \mathbf{d}\\ \mathbf{e}\end{array} & \begin{bmatrix} 0 & 1 & 2 & 3 & 4 \\ & 0 & 1 & 2 & 3 \\ & & 0 & 1 & 2 \\ & & & 0 & 1 \\ & & & & 0 \end{bmatrix}
\end{array}$$

Transitional “penalties” (here given as integral) between states of any discrete character can be specified similarly by step-matrices (Hauser and Presch 1991; Slowinski 1993), and can serve as a valuable tool for interpreting homoplasy (Ree and Donoghue 1998).

Outgroups and Basal Polarities

As with the issue of ordering of states within characters, the selection and use of outgroups may seem more germaine to phylogenetic analysis *sensu* tree searches. However, outgroups are pertinent here both with respect to: (*i*) the expansive impact on taxonomic scale through admission of recently discovered, analytically critical taxa, as well as (*ii*) coding of character states of outgroups with respect to preservation of specimens, published literature, and the related issue of missing data.

Given the advantages of inferring basal polarities by comparison of ingroup taxa with two or more outgroup taxa (Watrous and Wheeler 1981; Maddison et al. 1984; Nixon and Carpenter 1993; Barriel and Tassy 1997, 1998; H. N. Bryant 2001), despite some progress in alternative approaches (Stevens 1980), a suite of outgroups was used to root trees in the present analysis, with ontogenetic evidence employed only in ancillary capacity (Kraus 1978; Nelson 1978; de Queiroz 1985; Kluge and Strauss 1985; Wheeler 1990; H. N. Bryant 1991; de Pinna 1991, 1994; Rieppel 1993; Mabee 2000). The state considered plesiomorphic *a priori* among those observed, typically upon ancillary criteria such as inclusion of taxa established as basal, ontogenetic information, and/or morphoclinal ordination (H. N. Bryant 1991), were assigned state "a." In multistate, ordered characters, states other than the first that are provisionally averred to be plesiomorphic for Neornithes are distinguished in the notes where assignments are considered of interest. It is critical, however, to distinguish such *a priori* judgments from the means of rooting the tree, the latter being based on outgroups (Weston 1994; H. N. Bryant 2001), the former simply being a convention of style having no analytical importance.

It is worthwhile to note that Mesozoic fossils were treated directly as outgroup taxa for purposes of rooting trees, and not as special purveyors of insights into polarities on the grounds of mere antiquity or fossilization. For Aves, it is merely an accident of taphonomy and patterns of extinction that taxa most informative as outgroups (i.e., the Dinosauria) are limited to fossil taxa, the only logical extant alternative being the distantly related Crocodylia (Hedges 1994). Under certain special circumstances of uniformity of rates and relative density of sampling, however, fossil taxa of confident stratigraphy can permit estimates of absolute rates that are not accessible by means of modern terminals (Benton 1995, 1998; Benton and Storrs 1996; Benton and Hitchin 1997). Although rooting with Crocodylia is commonly employed as the sole outgroup in molecular analyses of higher-order Aves (van Tuinen et al. 2000; van Tuinen et al. 2001; van Tuinen and Dyke 2003; Dyke and van Tuinen 2004), it is a practice exacerbated by excessive reliance on the demonstrably weak assumption of "clocklike" rates of evolutionary changes over these enormous expanses of time and diverse evolutionary lineages, which in practice requires substantial "resetting" multiple times within Neornithes alone (Dyke 2003). If for a given sample of genes the crocodylian rooting is, in fact, largely uninformative (i.e., effectively random, unreliable for estimates of initial states in extinct sister-groups of Aves), the resultant tree would effectively represent a phenetic clustering of taxa; in a minority of molecular studies that, like Sibley and Ahquist (1990), placement of Passeriformes as basal among Neornithes (e.g., Waddell et al. 1999), seems a likely cause for uninformative or misleading rooting where insufficiently conservative genes and/or crocodylian outgroups are used for inferences among modern Aves. The enormous span of time between times of divergence of Crocodylomorpha also is conspicuous in phylogenetically framed morphological comparisons (Brochu 1997). In the present study the prospect of rooting solely with crocodylomorphs proved daunting if not outright impossible for reasons of noncomparability; the recently augmented sample of more closely related (fossil) outgroups in a morphological context proved an enormous windfall of data for purposes of rooting.

Accordingly, Mesozoic Theropoda closely related to Aves were used for purposes of rooting as strict outgroups, as opposed to the paleotraditional assumption that fossils are necessarily informative regarding plesiomorphic states by direct ancestry (Brodkorb 1971a, 1976). This simplistic view has been discounted by avian counterexamples for rooting at diverse phylogenetic scales, e.g., fossils *Gastornis*, *Diatryma*, *Presbyornis*, *Enaliornis*, or *Teratornis*. A particularly well-established case is the comparatively greater utility of extant Galliformes, Anhimidae, and Anseranatidae relative to Eocene *Presbyornis* for purposes of interordinal inferences among the Galloanseres (Livezey 1997a). On practical grounds alone, however, most fossil Aves from the early Cenozoic simply are preserved inadequately for purposes of characterizations, most being represented by a small minority of essential skeletal elements (cf. Brodkorb 1964, 1967, 1971a–b; S. L. Olson 1985), and virtually none conserve significant information pertaining to characters of the musculature or integument.

"Missing" Characters and States

Wherever possible, we distinguished two primary classes of "missing" data in descriptions of characters and listing of taxa by states: (*i*) "missing *characters*" *sensu* taxa were deemed "noncomparable" (Maddison 1993; Strong and Lipscomb 1999) or "inapplicable" (D.-C. Lee and Bryant 1999), and (*ii*) unknown or undetermined states, *sensu* a character in one or more taxa could not be compared reliably because of quality of specimens (Nixon and Davis 1991; Platnick et al. 1991; Wilkinson 1995, 2003). The former typically arises because fundamental morphological changes in a given anatomical region preclude confident comparison of states between groups of taxa, thereby preventing confident comparison of homologues. Examples included: (*i*) characters of the pectoral limb in the Dinornithiformes; (*ii*) states were not determined because of a lack of suitable specimens, especially fossils (Kidwell and Holland 2002). Despite the differences between the two classes of uncertainty (Maddison and Maddison 1992; Swofford 1998), both were analyzed as "missing" because both represent similar analytical challenges (Nixon and Davis 1991) and this approach remains the only option available with existing software (Pleijel 1995; Hawkins et al. 1997; Strong and Lipscomb 1999).

Published Provenance of Characters

Important studies that pertained to particular characters were cited under "Notes" to reflect the history and frequency of use of characters. Only a minority of such references refer to variation *identical* to that partitioned by the characters with which the former are noted (e.g., some references are cited under multiple characters). However, all were averred to pertain to the same anatomical features or phylogenetic information derived therefrom, although often based on other taxa or using different states.

Incorporation of characters original to the literature generally entailed both identification of character and states (including both formerly recognized and newly defined), and frequently entailed interpretation of diverse approaches to description and translation of features into formal anatomical nomenclature. Paleontologically derived characters were based in part on monographic classics—e.g., Ostrom (1969, 1974a, 1976a) for *Deinonychus*, Ostrom (1972, 1974b, 1976b) for *Archaeopteryx*, and Ostrom (1978) for *Compsognathus*—and new descriptive treatises—e.g., Welman (1995) for *Euparkeria*, and Brochu (2003), Currie (2003), and Currie et al. (2003) for *Tyrannosaurus*—but most citations refer to works using classical or vernacular nomenclature that we redescribed using formal nomenclature as part of incorporation.

Published Characters Excluded from Analysis

JUSTIFICATION

This work is not intended to serve as a complete compilation of morphological variation in Aves and closely related Theropoda. Characters included herein represent variation that was deemed: (*i*) tractable and describable for the taxa to be analyzed; and (*ii*) if variable within taxa, either a clear modality was discerned or polymorphism of recognized states was inferred. Many forms of variation manifested by taxa not included as exemplars are known and described in publications, but for reasons of taxonomic samples and phylogenetic scale were not admissable for the present analytical purposes. Examples of characters apparently meaningful for more restricted groups of taxa but not considered informative here include: (*i*) many of the characters described by Holdaway (1991: appendix 5.1) for falconiform genera; (*ii*) partially redundant suites of characters by O'Hara (1989) and Bertelli and Giannini (2005: appendix 2) for species-level analyses of Spheniscidae; and (*iii*) virtually all of the subtle osteological characters employed by James et al. (2003: appendices 1–2) and James (2004: appendices 1–2) for passerines. A re-analysis of the data set of K. Lee et al. (1997) by Dyke (2003) could not be included in the synonymies of characters, hence listings in the former must suffice. Similarly, Pereira and Baker (2005) re-analyzed the characters of Strauch (1978), but were not explicitly cited in the character descriptions as no original information was provided.

Characters noted by previous authors may have been excluded for one or more of the following reasons: (*i*) inadequacy of descriptions; or (*ii*) variability presented continua of states, often within taxa, not tractable by coding, including use of polymorphism (as delimited here). In a number of instances, exclusion simply reflected our inability to recognize the variation intended by the authors of the published description(s).

EXCLUDED OSTEOLOGICAL CHARACTERS

Cranium et Ossa Faciei

Duijm (1951) and Elzanowski and Galton (1991: character 1).—angularity of lamina parasphenoidalis relative to ossa maxillare et palatina ("airencephaly"); S. F. Simpson and Cracraft (1981: character 14).—lateromedial (bilateral) compression of calvaria; Dyke et al. (2003: appendix 1, character 21).—margo ventralis foraminis magnum; Cracraft (1986: appendix, character 53), Chatterjee (1991: character 4), Elzanowski and Galton (1991: character 2).—sulcus venus semicircularis; Chu (1998: appendix 1, character 4).—position of crista (linea) nuchalis transversa; Cracraft (1988: series VII, character 3), Cracraft and Mindell (1989: table 1, character 29), Livezey (1991: appendix 1, character 155), Ericson (1996: character 3), and Livezey (1996b: appendix 1, character 7).—externum of basis rostri parasphenoidalis; Maryanska et al. (2002: appendix 1, character 65).—articulatio pterygo-palatina; Sereno (1999: character 141) and Suzuki et al. (2002: character 4).—proportion of ramus dentalis in mandibula; Norell and Clarke (2001: appendix I, character 43), J. A. Clarke (2002: appendix I, character 43), J. A. Clarke and Norell (2002: appendix 2, character 43), and Zhou and Zhang (2002: appendix III, character 43).—proximity of ossa spleniales to symphysis mandibulae; G. Mayr (2003b: appendix I, character 6).—stipes columellae; Cracraft (1982: series 1, character 1) and Cracraft (1988: series X, character 1).—impressio musculi facies lateralis corporis et processus orbitalis quadrati; Xu (2002: suite II, character

15).—fovea ventralis (orbitalis) laterosphenoidale; Cracraft (1988: series V, character 5) and Cracraft and Mindell (1989: table 1, character 16).—"anterior wall of the *middle-ear cavity* thickened and cancellous."

Livezey (1998b: appendix A, character 79).—impressiones cranii origiorum tendinorum ossificantes musculorum mandibulae; Maryanska et al. (2002: appendix 1, character 76).—relative height of processus retroarticularis; Chatterjee (1991: character 6).—axis majoris cavitas cranii ossium basioccipitale, basisphenoidale, et parasphenoidale; Elzanowski (1991: table 3) and Elzanowski and Galton (1991: character 17).—situs post-temporalis foraminis ramus occipitalis arteria ophthalmici externa; Livezey (1998b: appendix A, character 20).—bilaterally broad processus rostralis (premaxillare) ossis nasale; Holtz (2000 [1998]: appendix I, character 95), citing in turn Makovicky and Norell (1998).—foramina nervorum cranii fossae acoustica interna; Chatterjee (1991: character 3) and Chatterjee (1999: appendix II, character 4).—fossa cerebelli, caudal extension to position ventral to os supraoccipitale within cavum cranii; G. Mayr (2004b: appendix 1, character 14).—processus paroccipitalis, caudal curvature at terminus; Chu (1998: appendix 1, characters 12–13).—foramina nn. trochlearis et ophthalmici in incisura nervus optici of os laterosphenoidale; Sereno and Novas (1992: appendix, character 4) and Coria and Currie (2002: appendix 1, character 1).—sizes of dorsalmost of two fenestrae diagnostic of "Diapsida" (cf. Chiappe et al. 1998; Hou et al. 1999a) delimited largely by cruciate os postorbitale; Brochu (2003).—os sphenethmoidale; Xu (2002: suite I, character 29).—processus mandibularis quadrati, facies articularis pterygoidea in *Sinornithosaurus*; Sereno et al. (1994, 1996), Holtz (2000 [1998]: appendix I, character 48), Holtz (2000 [1998]: appendix 2, character 48), and Rauhut (2003: character 41, fig. 12).—processus jugalis (ventralis) postorbitale; Marceliano (1996), Xu and Norell (2004: supplement, character 208).—os angulare relative to cavitas glenoidalis mandibulae.

Sereno (1999: character 138) and Suzuki et al. (2002: character 1).—processus frontalis premaxillaris; Xu (2002: suite I, character 20).—cavitas ventralis ossis premaxillare of *Sinornithosaurus*, a similar condition in ceratosaurians (Rowe and Gauthier 1990); Sereno et al. (1998: footnote 22, character 11).—sutura maxillaropremaxillaris; J. M. Clark et al. (1994), Chu (1998: appendix 1, character 46), Norell and Clarke (2001: appendix I, character 16, part), J. A. Clarke (2002: appendix I, character 16, part), J. A. Clarke and Norell (2002: appendix 2, character 16, part), Zhou and Zhang (2002: appendix III, character 16, part), and G. Mayr (2004b: appendix 1, character 6).—synostosis (sutura) palatinomaxillaris, lamella dorsalis palatini; G. Mayr (2004a: appendix 1, character 11) and G. Mayr and Ericson (2004: appendix I, character 14).—terminus caudalis vomeris; Sereno et al. (1996: footnote 45, character 32), Holtz (2000 [1998]: appendix I, character 14), Holtz (2000 [1998]: appendix 2, character 14), Maryanska et al. (2002: appendix 1, character 3), and Maryanska et al. (2002: appendix 1, character 9), concerning relative length of rostrum; Cracraft (1986: appendix, character 41) and Witmer and Martin (1987: character 7).—junctura vomeromaxillaris; Chu (1998: appendix 1, character 59), citing Strauch (1978)—os prearticulare; Chu (1998: appendix 1, character 60).—junctura prearticulo-splenialis; Hughes (2000: appendix 2, character 38), possibly determinable for therizinosaurid *Erlicosaurus* (J. M. Clark et al. 1994).—fossa cranii caudalis (os exoccipitale), fovea ganglii vagoglossopharyngealis (foramen n. vagi), rostrocaudal position relative to ostium of canalis ophthalmic externi; Prum (1988: character 5) and J. A. Wilson and Sereno (1998: appendix, character 76).—junctura (articulatio) jugo-ectopterygoidea.

Hughes (2000: appendix 2, character 35).—margo caudalis of lamina basiparasphenoidalis ("crista basilaris transversa") and ostium canalis carotici; Livezey (1991: appendix 1, character 156).—relative diameters of foramina nervorum maxillomandibularis et opticum; Chu (1998: appendix 1, character 25).—confluence of sulci nervorum olfactorii orbitae; Hughes (2000: appendix 2, character 10).—ventral attenuation of processus orbitalis lacrimalis; Sereno (1999: character 18), Norell et al. (2000: appendix 1, character 15).—"basisphenoidal recess"; Prum (1988: character 25).—"prominent ridge" between orbita; Livezey (1996a: appendix 1, character 3) and Chu (1998: appendix 1, characters 37–38).—terminus rostralis aperturae nasi.

Elzanowski and Galton (1991: character 11).—"foramen venae cerebralis mediae replaced by recessus"; Xu et al. (2002: supplement, character 23).—presence of fossae (formina) pneumatica along rima fossae antorbitalis; Siegel-Causey (1997: table I, character 2), Maryanska et al. (2002: appendix 1, characters 63, 67, and 89), Suzuki et al. (2002: character 14), Xu (2002: suite I, characters 36, 38, and 58).—variation in foramen nervi cranialis V by Saiff (1974, 1976, 1978, 1981, 1982, 1983, 1988) and summarized by Siegel-Causey (1997: table I, character 3) and Chu (1998: appendix 1, character 48).—lateromedial curvature of os palatinum, lamina choanalis dorsalis, margo medialis, processus choanalis; Cracraft (1974: cranial character 2, part), Cracraft and Mindell (1989: table 1, character 24), Elzanowski (1995: character N9), and Ericson (1997: table 1, character 8).—articulatio palatino-rostroparasphenoidalis; Elzanowski (1995: 39).—ostium rostralis choanae ossea palatina; Elzanowski and Wellnhofer (1996: fig. 11) and Xu (2002: suite I, character 46).—

facies articularis quadratica pterygoidei; Elzanowski (1991: table 3), Elzanowski and Galton (1991: character 15), and Elzanowski (1995: character Nb'5).—"suprarecessal compartment"; Technau (1936), Harrison and Walker (1976a–b: figs. 1 and 3), and Bourdon et al. (2005: appendix 1, characters 8 and 11).—bulbus nasomaxillaris (**new term**) et sinus antorbitalis.

Sereno et al. (1996: footnote 45), Holtz (2000 [1998]: appendix I, character 52), and Holtz (2000 [1998]: appendix 2, character 52).—rostral bulbosity of os postorbitale; Chu (1998: appendix 1, character 15).—foramen ophthalmicum internum, sella turcica; Maryanska et al. (2002: appendix 1, character 1).—ratio between preorbital and "basal" skull lengths; Bakker et al. (1988) and Holtz (1994a: appendix 1, characters 63 and 103), concerning cuneus occipitalis between crista nuchalis transversa et foramen magnum; G. Mayr (2002b: appendix 1, character 7).—dorsoventral extent of processus paroccipitalis (ossa exoccipitale et parasphenoidale) relative to cranium; Livezey (1997a: appendix 1, character 6; *corrigenda*, Livezey 1998a), Hughes (2000: appendix 2, characters 33–34).—crista basilaris transversa parasphenoidalis; Livezey (1997a: appendix 1, character 30; *corrigenda*, Livezey 1998a), Livezey (1998b: appendix A, character 21), and related feature by Chu (1998: appendix 1, character 42).—facies dorsalis of os premaxillare, corpus ossis premaxillare, at terminus rostralis of apertura nasi ossea; J. D. Harris (1998: appendix 2, character 16), Azuma and Currie (2000: appendix 1, character 98), and Currie and Carpenter (2000: appendix 1, character 20).—length of corpus ossis quadrati; G. Mayr (2002a: legend fig. 9, node 3, character 1).—planum sagittalis mandibulae.

Shufeldt (1901d: 300), Ericson (1997: table 1, character 11; table 2, character 9), and Chu (1998: appendix 1, character 45).—situs dorsoventralis of os maxillare, processus palatus relative to junctura jugomaxillaris; Maryanska et al. (2002: appendix 1, character 20).—situs dorsoventralis of apertura nasalis relative to os maxillare, and related character by Xu (2002: suite I, character 41); Elzanowski (1991: table 3), Elzanowski and Galton (1991: character 16).—extension of crista (linea) nuchalis transversa onto os squamosum, processus zygomaticus; Currie and Zhao (1994b [1993b]), Zhao and Currie (1993 [1994]), and Xu (2002: suite I, character 27).—processus caudolateralis of os parietale; Livezey (1998b: appendix A, character 36).—concavitas ventralis palatini, pars lateralis et lamina choanalis ventralis; Xu (2002: suite I, character 31).—sulcus medialis pterygoidei; Chu (1998: appendix 1, character 56).—lateromedial expansion os dentale, pars dorsalis at margo dorsalis of os spleniale in Laridae; Norell et al. (2000: appendix 1, character 4).—canalis osseus rami maxillaris n. cranii V; Maryanska et al. (2002: appendix 1, character 5).—relative rostrocaudal length of os premaxillare; Livezey (1998b: appendix A, character 38).—rostral terminus vomeris relative to apertura nasi ossea; G. Mayr et al. (2003: appendix 1, characters 20 and 22).—forma mandibulae.

Xu (2002: suite I, character 34).—carina rostralis on facies medialis of sulcus dentorum premaxillares; Xu (2002: suite I, character 32).—foramina ventral to dentes dentalis; Sanz et al. (1997: footnote 29, character *v*).—margo ventralis fenestrae caudalis mandibulae; Chu (1998: appendix 1, character 63) and Hughes (2000: appendix 2, character 56).—pars rostralis corporis et cornua ossis (cartilaginis) paraglossum (entoglossum), Maryanska et al. (2002: appendix 1, character 53).—"depression in the periotic region"; Elzanowski (1995: 43) and Rotthowe and Starck (1998: appendix, character 9).—ephemeral presence of sutura intersupraoccipitalis (Kurochkin 1995b), Currie and Carpenter (2000: appendix 1, character 19).—"preorbital bar" of "suborbital process"; Elzanowski (1995: character ?PG'4).—processus caudalis ossis maxillare; Technau (1936); Harrison and Walker (1976b: figs. 1 and 3); Bourdon et al. (2005: appendix 1, characters 8 and 11).—bulbus nasomaxillaris (**new term**) et sinus antorbitalis; Cracraft (1985: character 3); Bourdon et al. (2005: appendix 1, character 2); Bourdon (2006: supplement, character 94). Disputed by: G. Mayr (2003b: character 3); Bourdon et al. (2005: appendix 1, character 2).—microapertura nasi ossea (**new term**); Bourdon et al. (2005: appendix 1, characters 6–7).—forma ossis palatini; Bourdon et al. (2005: appendix 1, character 30).—forma pila otica.

Bourdon et al. (2005: appendix 1, characters 2–3), Shufeldt (1888d: figs. 1 and 3), Bourdon et al. (2005: appendix 1, character 3).—apertura nasi (nasalis) ossea; Duijm (1951), Bourdon et al. (2005: appendix 1, character 20).—os parasphenoidale (ventral perspective), lamina parasphenoidalis (basisphenoidalis); Cracraft (1985: character 15), Bourdon et al. (2005: appendix 1, character 28).—recessus (cavitas) tympanicum(as), foramen efferens nervi maxillomandibularis, ostium recessi tympanici rostrali, situs relativum; Bourdon (2006: appendix 1, character 32).—ossa otica, fossa parabasalis, atrium (processus) metoticus, foramen (sulcus) n. glossopharyngealis; Bourdon et al. (2005: appendix 1, character 23), Bourdon (2006: supplement, character 77).—ossa otica, fossa parabasalis, atrium (processus) metoticus, foramen (sulcus) arteria ophthalmica externa; Bourdon et al. (2005: appendix 1, character 24).—ossa otica, pila otica, pronounced caudoventral orientation, associated with lateral orientation of cotyla quadratica otici; Cracraft (1985: fig. 2), Elzanowski and Galton (1991: fig. 4D), Bourdon et al. (2005: appendix 1, character 30).—os quadratum, processus orbitalis; Bourdon (2006: supplement, character

10).—frons, rostrum maxillae, regio proximodorsalis, expansion as planar, triangular facies.

Columna Vertebralis

Hughes (2000: appendix 2, character 127).—shape of facies articularis of zygapophysis caudalis axialis; Makovicky (1995) and Rauhut (2003: character 94).—"large groove excavated into posterior base of axis," possibly in reference to lacuna interzygapophysialis caudalis; Dyke and Gulas (2002: appendix 1, character 37).—"groove on caudal surface of hypapophysis" of vertebrae cervicales in galliforms; Payne and Risley (1976: character 15).—"posteriormost [cervical vertebra] with lateral vertebral canal" among Ardeidae; Sereno (1991a: appendix, ingroup-clades character 21) and Holtz (2000 [1998]: appendix I, character 164).—heterogeneity of corpus lengths in vertebrae cervicales communis; J. D. Harris (1998: appendix 2, character 82) and Currie and Carpenter (2000: appendix 1, character 67).—"aliform process" of extremitas dorsalis of costae cervicales; Rauhut (2003: character 98), pertaining to essentially invariant "broad ridge from the diapophyses to the ventral rim of the posterior end of the vertebral centra"; Payne and Risley (1976: character 29).—synostosis iliosynsacralis; Novas (1994 [1993]: appendix, character 1).—presacral elements; Livezey (1998b: appendix A, characters 275–278).—crista spinosa.

Skeleton Pectoralis

Bourdon et al. (2005: appendix 1, characters 40–41).—extremitas proximalis humeri, impressio insertii m. latissimus dorsi, situs relative to margines dorsalis et ventralis; Fürbringer (1888: plate III), Kurochkin (1995b: table 1, character 7), and Livezey (1998b: appendix A, character 175).—lateromedial thickness of corpus scapulae, margo ventralis; Cracraft (1982: series 3, character 5), Gauthier (1986: 14), Livezey (1986: appendix 1, character 50), Livezey (1996a: appendix 1, character 49), Livezey (1997a: appendix 1, character 77; *corrigenda*, Livezey 1998a), Chu (1998: appendix 1, character 83), Norell and Clarke (2001: appendix I, character 90), J. A. Clarke and Norell (2002: appendix 2, character 90), and Zhou and Zhang (2002: appendix III, characters 90–91).—pneumaticitas coracoidei; Livezey (1998b: appendix A, character 210).—incisura cristae bicipitale humeri; Chu (1998: appendix 1, character 94).—crista deltopectoralis relative to impressio insertii m. deltoideus major humeri; Bledsoe (1988: appendix, character 16).—widths of extremitates relative to corpus proprius humeri; Sanz and Buscalioni (1992: character 5).—diameters of femur and ulna.

Bledsoe (1988: appendix, character 22).—impressio ligamentosus (possibly sulcus nervi radialis humeri), refuted by K. Lee et al. (1997: appendix 2); G. Mayr and Clarke (2003: appendix A, character 78) and G. Mayr (2004a: appendix 1, character 41).—impressio m. scapulohumeralis cranialis; Bledsoe (1988: appendix, character 20), Novas (1996: appendix, character 9, part), Novas (1997: appendix, character 9, part), and Novas and Puerta (1997).—distinctness of condylae dorsalis et ventralis humeri; Kurochkin (1995b: table 1, character 13) and Ericson (1997: table 1, character 61).—lateral flattening of facies ventralis ulnae; Norell and Clarke (2001: appendix I, character 132), J. A. Clarke and Norell (2002: appendix 2, character 132), and Zhou and Zhang (2002: appendix III, character 132).—relative proportions of margo caudalis condyli and facies articularis of trochlea carpalis ulnae; G. Mayr (2004c: appendix I, character 18).—relative size of cotyla ventralis ulnae; Vazquez (1992).—articulatio ulnocarpo-metacarpalis ventralis; Livezey (1986: appendix 1, character 49), Livezey (1996b: appendix 1, character 27), calcar ossis radiocarpalis (Rand 1954: fig. 1D), Chatterjee (1999: appendix II, character 62).—enlargement of os carpi ulnare; Ji et al. (2001).—"semilunate carpal" and "os radiale"; Chatterjee (1999: appendix II, character 60), Maryanska et al. (2002: appendix 1, character 141).—"angling" of os metacarpale alulare; G. Mayr (2004a: appendix 1, character 46).—relative length of phalanx proximalis digiti II manus; Ostrom (1969) and Xu (2002: suite II, character 37).—phalanx tertius digiti III manus; Novas (1994 [1993]: appendix, character 43) and Ji et al. (2001).—phalanges digitorum of Dromaeosauridae; Bourdon (2006: supplement, character 29).—corpus humeri, craniocaudal curvature; Bourdon (2006: appendix 1, character 58).—extremitas proximalis humeri, crista deltopectoralis, ambitus distalis (%) corporis; Bourdon (2006: supplement, character 60).—extremitas proximalis humeri, impressiones mm. latissimi dorsi, extent distal to crista deltopectoralis; Bourdon et al. (2005: appendix 1, character 36); Bourdon (2006: supplement, character 61).

Skeleton Pelvicus

Cracraft (1974: 503, character 18), Gauthier (1986: text character 77), Kurochkin (1995b: table 1, character 20), Novas (1996: appendix, characters 48–49), K. Lee et al. (1997: appendix 1, character 21), Novas (1997: appendix, characters 49–50), Novas and Puerta (1997), Sues (1997: appendix I, character 36), Livezey (1998b: appendix A, character 262), Xu et al. (1999a: character 42), and Zhou and Zhang (2002: appendix III, character 161).—orientation and form of margin of acetabulum; Andors (1992: table 2, character 39).—fenestra(e) ischiadica; Livezey (1998b: appendix A, character 291).—junctura mediocaudalis iliosynsacrum; J. D. Harris (1998: appendix 2, character 104), Currie and Carpenter (2000: appendix 1, character 83), and Holtz (2000 [1998]: appendix I, characters 297–298).—forma marginalis alae postacetabularis ilii; Zhou and Zhang (2002: appendix III, character 156).—axes majores corporalium ossium ischii et pubici; Andors (1992: table 1, character 1).—diameter and length of corpus femoris; Murray and Vickers-Rich (2004: table 9, character 12).—facies medialis, concavitas corporis femoris; Chu (1998: appendix 1, character 111).—situs mediolateralis of linea intermuscularis caudalis relative to pars distalis of crista trochantericus femoris; Livezey (1986: appendix 1, character 61) and Livezey (1989: table 1, character 61).—torsion of corpus tibiotarsi.

Butendieck (1980: 116, fig. 55), Rowe and Gauthier (1990), Holtz (1994a: appendix 1, character 8), Kurochkin (1995b: table 1, character 26), and Holtz (2000 [1998]: appendix I, character 345).—foramen nutricium cristae fibularis tibiotarsi; J. D. Harris (1998: appendix 2, character 129).—“sulcus [a. nutriciae] at base of crista tibiofibularis”; Novas (1992: character 5) and Novas (1994 [1993]: appendix, character 5).—“tibia with lateral longitudinal groove”; Livezey (1986: appendix 1, character 67) and Livezey (1995c: appendix II, character 35).—“external ligamental prominence” of epicondylus lateralis tibiotarsi; Kurochkin (1995b: table 1, character 28).—situs proximodistalis epicondyli medialis relative et marginis proximalis condyli medialis tibiotarsi; Holtz (2000 [1998]: appendix I, character 376).—facies dorsalis of os metatarsale II; G. Mayr (2004c: appendix I, character 40).—spina plantaris, rima medialis trochlearis metatarsale II; Bledsoe (1988: appendix, character 78), Kurochkin (1995b: table 1, character 31), K. Lee et al. (1997: appendix 2), Hughes (2000: appendix 2, character 71) after Seibel (1988: character TM 20), and J. A. Clarke and Norell (2002: appendix 2, character 201).—rimae medialis et lateralis of trochlea metatarsale III; Sanz and Buscalioni (1992: “excluded” characters 2–4).—details of hallux; Gauthier (1986: text character 51) and Xu et al. (1999a: character 79).—synostosis ossis metacarpale I; Cracraft (1988: series VIII, character 10); G. Mayr (1999b: fig. 11); Azuma and Currie (2000: appendix I, character 83).

EXCLUDED MYOLOGICAL CHARACTERS

Musculi Membri Thoracici

McKitrick (1991b: character 5).—m. pectoralis, pars sternobrachialis, margines medioventralis origii; Maurer and Raikow (1981: table 2, character 6).—m. pectoralis propatagialis, insertio; Maurer and Raikow (1981: table 2, character 4).—m. rhomboideus profundus, origo; Maurer and Raikow (1981: table 2, character 10).—m. deltoideus major, tendo origii et ancora tendinis scapulae; Hudson et al. (1969), Bentz and Zusi (1982), and Strauch (1985: table 3, character H8).—trochlea humero-ulnaris; Maurer and Raikow (1981: table 2, character 20).—m. extensor (meta)carpi ulnaris, origo; Maurer and Raikow (1981: table 2, characters 11–12).—mm. deltoidea relative to m. supracoracoideus, tendo insertii, situs insertiorum; Raikow (1978: table 2).—m. flexor digitorum profundus, width of corpus; Hudson and Lanzillotti (1964), Hudson et al. (1969), and Strauch (1985: table 3, character H10).—m. flexor digitorum profundus, sesamoideum tendinis insertii phalangis proximalis digiti (II) majoris; Cracraft (1988: series XV, character 12).—mm. extensor (meta)carpi radialis et deltoideus propatagialis, pars cranialis, tendines insertiorum; Goodge (1972: 70).—m. flexor (meta)carpi ulnaris, tendines insertii; Maurer and Raikow (1981: table 2, character 23).—m. ectepicondylo-ulnaris, origo.

Musculi Membri Pelvici

Goodge (1972: 71).—m. iliotibialis cranialis, origo; Swierczewski and Raikow (1981: character 2) and Raikow (1985a: table 3, character 5).—m. iliotibialis cranialis, origo; Swierczewski and Raikow (1981: character 3).—m. iliotibialis cranialis, insertio(nes), Swierczewski and Raikow (1981: character 4).—m. iliotibialis cranialis, insertio m. femorotibialis internus; Swierczewski and Raikow (1981: character 6).—m. iliotibialis lateralis, partes (pre-, post-)acetabularis; Raikow (1994: table 2, character 2).—m. iliotibialis lateralis, pars postacetabularis, origo, situs craniocaudalis; Raikow (1987: table 1, character 3).—m. iliotibialis lateralis, pars postacetabularis, insertio; Swierczewski and Raikow (1981: character 7).—m. iliotibialis lateralis, partes acetabularis et postacetabularis; Raikow (1987: table 1, character 1) and Raikow (1994: table 2, character 1), regarding m. iliotibialis lateralis, hiatus acetabularis; Swierczewski and Raikow (1981: character 10), origo m. iliofibularis, extent on ala postacetabularis ilii; Raikow (1994: table 2, character 3).—m. iliotrochantericus caudalis, corpus (“belly”); Raikow (1987: table 1, character 4).—m. iliotrochantericus caudalis, fasciculi superficiales; Raikow (1987: table 1, character 6).—mm. iliotrochantericus cranialis et medius, union of corpora (“bellies”); Raikow (1987: table 1, character 5) and Raikow (1994: table 2, character 4).—mm. iliotrochantericus cranialis et medius, corpora et tendines insertii; Schulin (1987: table 1), McKitrick (1991b: character 6), and Livezey (1997a: appendix 1, character 119; *corrigenda*, Livezey 1998a).—mm. iliotrochantericus cranialis et caudalis, fusion; Bentz (1979: table 2), Zusi and Bentz (1984: 44), G. Mayr and Clarke (2003: appendix A, character 124), and Dyke and van Tuinen (2004: appendix 1, character 93).—m. iliotrochantericus medius; Raikow (1987: table 1, character 7).—m. iliofemoralis internus; Raikow (1985a: table 2, character 2).—mm. femorotibialis lateralis (externus) et intermedius; Cracraft (1988: series XIV, character 2).—m. flexor cruris lateralis; Raikow (1985a: table 2, character 4).—m. flexor cruris lateralis, origo(iones), Raikow (1994: table 2, character 5).—m. flexor cruris lateralis, aponeurosis caudalis origii; Raikow (1994: table 2, character 7).—m. flexor cruris lateralis, raphus; Raikow (1994: table 2, character 6).—m. flexor cruris lateralis (semimembranosus), pars accessoria, insertio; McKitrick (1986), Raikow (1987), and Vanden Berge and Zweers (1993: 219, annotation 108).—m. flexor cruris lateralis (semimembranosus), partes pelvica et accessoria, vinculum; Raikow (1985a: table 2, character 9).—m. iliofemoralis internus, origo; Raikow (1994: table 2, character 8).—m. flexor cruris lateralis (semimembranosus), pars pelvica, lobus tibialis; Maurer and Raikow (1981: table 2, character 34).—m. flexor cruris lateralis, pars pelvica, tendo accessoria (femoris) at insertio m. caudofemoralis; Raikow (1994: table 2, character 11).—m. caudofemoralis, corpus, sectio femoralis; Raikow (1994: table 2, character 10).—m. caudofemoralis, tendo origii; Raikow (1994: table 2, character 13).—insertio, situs relative to that of m. pubo-caudalis internus; Raikow (1985a: table 2, character 6).—m. obturatorius lateralis, pars dorsalis, origo, inclusion of margo ventralis of foramen ilioischiadica; Raikow (1985a: table 2, character 7).—m. obturatorius lateralis, pars dorsalis, insertio; Maurer and Raikow (1981: table 2, character 38), Swierczewski and Raikow (1981: characters 18–19), Raikow (1994: table 2, character 8).—m. obturatorius medialis, corpus; Raikow (1994: table 2, character 14).—m. pubo-ischio-femoralis, pars cranialis (lateralis), situs relative to m. flexor cruris lateralis; Raikow (1987: table 1, character 9) and Raikow (1994: table 2, character 15).—m. pubo-ischio-femoralis, pars caudalis, origo; McKitrick (1991a: appendix 1, character 20) and McKitrick (1992: appendix 1, character 20).—m. pubo-ischio-femoralis, pars accessoria.

Raikow (1994: table 2, character 16).—m. fibularis longus, aponeurosis origii; Swierczewski and Raikow (1981: character 24).—m. fibularis longus, tendo insertii, ramus tendinis metatarsale IV cum insertio phalangis proungualis digiti IV pedis; Kurochkin (1968) and Vanden Berge and Zweers (1993: annotation 117).—m. fibularis brevis, caput fibulare; Raikow (1976, 1978) and Vanden Berge and Zweers (1993: annotation 117).—m. fibularis brevis, caput tibiale; Raikow (1994: table 2, character 23).—m. gastrocnemius, pars intermedia, length distal to tendo m. flexor cruris lateralis; Hudson et al. (1969) and Strauch (1985: table 3, character H14).—m. gastrocnemius, pars medialis (interna), extension to facies cranialis generis; Schulin (1987: table 1).—m. gastrocnemius, partes lateralis, intermedia, et medialis, corpora *vs.* tendines; Maurer and Raikow (1981: table 2, character 40) and McKitrick (1985a).—m. gastrocnemius, pars medialis (interna), origo; Raikow (1994: table 2, character 18).—m. gastrocnemius, pars medialis (interna), corpus; Raikow (1994: table 2, character 19).—m. gastrocnemius, pars medialis (interna), corpus; Raikow (1987: table 1, character 14).—m. gastrocnemius, tendo(ines) insertii(iorum), forma *sensu* expansion relative to underlying tendines flexores; Raikow (1987: table 1, character 11).—m. gastrocnemius, pars lateralis, extent relative to underlying mm. flexores laterales; Hudson et al. (1969) and Strauch (1985: table 3, character H16).—m. gastrocnemius, pars intermedia; Raikow (1987: table 1; character 13).—m. gastrocnemius, pars medialis, with respect to margo cranialis of corpus; Hudson et al. (1969), Strauch (1985: table 3, character H15), Raikow (1987: table 1, character 12), and G. Mayr and Clarke (2003: appendix A, character 129).—m. gastrocnemius, pars supramedialis; Vanden Berge (1970), Vanden Berge and Zweers (1993: annotation 119), Raikow (1994: table 2, character 17).—m. plantaris, tendo insertii, union and ossification.

Raikow (1987: table 1, character 10).—m. flexor digitorum longus, corpus, symmetry; Swierczewski and Raikow (1981: character 21).—m. flexor digitorum longus, bifurcatio primus (proximalis) tendinis, situs proximodistalis; Zusi and Bentz (1984: 43).—m. flexor digitorum longus, insertiones tendinorum phalangiorum unguales; Swierczewski and Raikow (1981: character 34).—m. flexor perforans et perforatus digiti III, caput craniale; Raikow (1985a: table 2, character 10).—m. flexor perforans et perforatus digiti III, corpus; Raikow (1987: table 1, character 22).—m. flexor hallucis longus; Raikow (1987: table 1, character 17).—m. flexor hallucis longus, caput intermediale; Raikow (1985a: table 2, character 12).—m. flexor hallucis longus, caput intermediale, histologica; Raikow (1985a: table 2, character 13).—m. flexor hallucis longus, caput mediale; Maurer and Raikow (1981) and G. Mayr (2004c: appendix I, character 54).—m. flexor hallucis longus, tendo insertii; Raikow (1994: table 2, character 24).—m. flexor hallucis longus, tendo insertii ossificans; Raikow (1987: table 1, character 20).—m. flexor hallucis brevis, origo; Raikow (1985a: table 2, character 14) and Raikow (1987: table 1, character 19).—m. flexor digitorum longus, caput femoris; Quinn and Baumel (1990) and Vanden Berge and Zweers (1993: 223, annotation 124).—m. flexor digitorum longus, area tuberculata tendinis et plicae vaginae tendinis; Swierczewski and Raikow (1981: character 40).—m. extensor proprius digiti III.

McKitrick (1991a: appendix 1, character 11), McKitrick (1992: appendix 1, character 11).—ansa m. iliofibularis, elongation of rami (**new term**); McKitrick (1991a: appendix 1, character 31), McKitrick (1992: appendix 1, character 31).—m. ambiens, divisio corporis longitudinalis; Schreiweis (1982), Schulin (1987: table 1).—m. ambiens, insertio on aponeurosis (popliteus) mm. flexores perforati digiti II–IV (whichever present) in fossa poplitea femoris; Swierczewski and Raikow (1981: character 8), Zusi and Bentz (1984: 43), Prum (1988: character 19), McKitrick (1991a: appendix 1, character 8), McKitrick (1992: appendix 1, character 8), Livezey (1997a: table 4), G. Mayr and Clarke (2003: appendix A, character 117), Dyke and van Tuinen (2004: appendix 1, character 86).—m. femorotibialis lateralis (externus), caput distale (pars distalis); Swierczewski and Raikow (1981: character 14).—m. flexor cruris medialis, origo(iones); Swierczewski and Raikow (1981: character 13), Raikow (1994: table 2, character 12).—m. caudofemoralis, pars caudalis, tendo insertii; Goodge (1972), Schreiweis (1982), Raikow (1985a: table 3, character 6).—m. ischiofemoralis (m. ischiotrochantericus of Crocodylia; Bentz (1979: table 2), Maurer and Raikow (1981: table 2, character 37), Swierczewski and Raikow (1981: character 17), Raikow (1985a: table 2, character 5), McKitrick (1991a: appendix 1, character 22), McKitrick (1992: appendix 1, character 22), Hutchinson (2001b: table 1).—m. obturatorius lateralis (m. pubo-ischio-femoralis externus pars 1 of Crocodylia; Hutchinson (2001b: table 1).—pars dorsalis; Schreiweis (1982), McKitrick (1991a: appendix 1, character 26), McKitrick (1992: appendix 1, character 26), Livezey (1997a: table 4), G. Mayr and Clarke (2003: appendix A, character 122), Dyke and van Tuinen (2004: appendix 1, character 91).—m. obturatorius lateralis et medialis (mm. pubo-ischio-femoralis externus partes 1 et 2 of Crocodylia; Hutchinson (2001b: table 1).—distal union; Maurer and Raikow (1981: table 2, characters 35–36), McKitrick (1991a: appendix 1, character 21), McKitrick (1992: appendix 1, character 21).—m. pubo-ischio-femoralis, pars medialis, divisio partorum; Swierczewski and Raikow (1981: character 22), Schulin (1987: table 1), Prum (1988: character 2), Livezey (1997a: table 4).—m. extensor digitorum longus, retinaculum tendineum digiti IV; Swierczewski and Raikow (1981: character 25).—m. fibularis brevis, retinaculum m. fibularis (**new term**); Schulin (1987: table 1), Livezey (1997a: table 4).—m. gastrocnemius, pars intermedia, union with tendines mm. flexores crurales partes lateralis et medialis; m. gastrocnemius, pars medialis (interna), caput quartus (**new term**); McKitrick (1991a: appendix 1, character 36) and McKitrick (1992: appendix 1, character 36).—m. gastrocnemius, tendo insertii, status ossificationis hypotarsi; McKitrick (1991a: appendix 1, character 46), McKitrick (1992: appendix 1, character 46), Livezey (1997a: table 4).—m. flexor perforans et perforatus digiti II, capita, numerus modalis; McKitrick (1991a: appendix 1, character 47), McKitrick (1992: appendix 1, character 47), G. Mayr and Clarke (2003: appendix A, character 132), Dyke and van Tuinen (2004: appendix 1, character 99).—m. flexor perforans et perforatus digiti II, origo ansae iliofibularis; Schulin (1987: table 1).—m. flexor perforans et perforatus digitus II, perforatio accessoria (**new term**) m. flexor digitus longus; Schulin (1987: table 1), Livezey (1997a: table 4).—m. flexor perforatus digiti II, caput laterale; Swierczewski and Raikow (1981: characters 26 and 28), Raikow (1985a: table 2, character 11), Schulin (1987: table 1), Livezey (1997a: table 4).—m. flexor perforatus digiti II, perforatio tendinis, numerus tendinorum flexores; Swierczewski and Raikow (1981: character 30).—m. flexor perforatus digiti III, forma capitis; Swierczewski and Raikow (1981: character 29).—m. flexor perforatus digiti III, tendines origii. Hudson et al. (1969); Schulin (1987: table 1).—m. flexor perforans et perforatus digiti III, caput (distale) fibulare (**new term**); Swierczewski and Raikow (1981: character 31), McKitrick (1985a: fig. 15), Schulin (1987: table 1), Cracraft (1988: series XIV, character 3) with respect to “absence of a vinculum connecting the flexors of digit IV” in many falconiforms; Raikow (1987: table 1, character 16); Livezey (1997a: table 4).—m. flexor perforatus digiti IV, tendines insertii; Gadow (1893), George and Berger (1966), S. F. Simpson and Cracraft (1981), Raikow (1985a), G. Mayr et al. (2003: appendix 1, character 84).—m. flexor hallucis longus, tendines insertiorum digiti II–IV pedis; Maurer and Raikow (1981: table 2, character 56).—m. extensor hallucis longus, tendo hallucis; Schulin (1987: table 1).—m. flexor hallucis brevis, numerus capitorum modalis. Swierczewski and Raikow (1981: character 38), McKitrick (1991a: appendix 1, character 59), McKitrick (1992: appendix 1, character 59).—m. flexor hallucis brevis, tendines insertii; Schulin (1987: table 1), Livezey (1997a: appendix 1, character 123; *corrigenda*, Livezey 1998a).—m. flexor hallucis brevis, tendo m. flexor hallicus longus, perforatio tendinis; Holmes (1963), Hudson et al. (1972: 248), Maurer and Raikow (1981: table 2, character 49), Berman and Raikow (1982), Schreiweis (1982).—m. extensor proprius digiti III; Schulin (1987: table 1), McKitrick (1991a: appendix 1, character 61), McKitrick (1992: appendix 1, character 61), Livezey (1997a: table 4).—m. extensor hallucis longus, partes majores, numerus modalis; McKitrick (1991a: appendix 1, character 62); McKitrick (1992: appendix 1, character 62); G. Mayr and Clarke (2003: appendix A, character 139).—m. extensor hallucis longus, pars (caput) accessoria; Schulin (1987: table 1), Livezey (1997a: table 4).—m. abductor digiti II, origo, caput metatarsale I; Swierczewski and Raikow (1981: character 42), Vanden Berge and

Zweers (1993: 224, annotation 130).—m. abductor digiti IV, retinaculum trochlea IV tarsometatarsi; Gadow and Selenka (1891), Hudson (1937), Schreiweis (1982).—m. adductor digiti IV.

Excluded Miscellaneous Characters

Published characters of the integumentum of other less-intensively studied anatomical systems that were neither associated with included characters nor profitably confirmed were: Pycraft (1910), Prum (1988: character 12), Raikow (1994: table 2, characters 31–32, 36), and Livezey (1996b, 1997b: appendix 1, characters 1–3).—rostrum maxillae; Livezey (1998b: appendix A, character 404).—situs depressionis nasalis; Cracraft (1985: character 21), Raikow (1994: table 2, character 20).—externum aperturae nasi; Livezey (1998b: appendix A, character 384).—coloration of depressio nasalis; Griffiths (1994a–b: appendix II) and Dyke and van Tuinen (2004: appendix 1, characters 109–110).—cartilagines tracheobronchiales "typus A"; Livezey (1986: appendix 1, character 5).

DESCRIPTIONS OF CHARACTERS

Organization and Format of Character Descriptions

A typical format for a character and included states employed in this paper is as follows:

0000. Character (by anatomical features in order of decreasing inclusivity or scale), specific aspect partitioned by states (ordering, if multistate):
a. first state, default (presumptive) basal polarity;
b. second state;
c. third state;
x. noncomparable (taxa so considered).
Note.—Prior analytical characterizations, associated literature, and commentary regarding assessments, analytical issues, and exceptional taxa.

The concept of presumptive "basal polarities" is deserving of more-detailed discussion. In this study, assignment of the first state ("a") as default basal polarity, and specification of others where required by ordering, is a stylistic convenience lacking analytical implications. Whereas rooting with a hypothetical ancestor—vector of presumptive basal polarities (H. N. Bryant 1997)—imposes significant analytical influence, mere proposal of *a priori* polarity for a character carries no analytical implications (e.g., PAUP does not root by first states of characters by default). In some cases, annotations regarding *a priori* judgments of polarities in combination with references to states scored for fossils and hypothetical "stem groups" (e.g., G. Mayr 2002a, 2004b, d) can further confuse matters and detract from the algorithmic fact that in the absence of a hypothetical ancestor or other imposition of basal polarities, the mere practice of listing the condition deemed *a priori* to be plesiomorphic as the first state for members of the ingroup purely represents a consistency of style. If actual outgroups (fossil or modern) are provided, the subsequent analysis will root the most parsimonious tree(s) with the states scored for the outgroup taxa, and do so regardless of any extra-analytical assessments or assumptions. Finally, basal polarities are of local relevance: once undergoing transformation, descendent lineages use the immediately preceding state for rooting.

Anatomical Nomenclature

Dedication to formal anatomical nomenclature in descriptions of characters is but one expression of a growing recognition of the importance or semantic precision in phylogenetics (e.g., Baumel et al. 1979, 1993; Komárek 1979; Butendieck 1980; Butendieck and Wissdorf 1982; Komárek et al. 1982a–b; Mareckǿvá et al. 2001). The primary source followed here was *Nomina Anatomica Avium* (second edition; Baumel et al. 1993)—especially Baumel and Raikow (1993), Baumel and Witmer (1993), G. A. Clark (1993a–b), and Vanden Berge and Zweers (1993)—with revisions indicated. Nomenclatural refinements were the subject of ancillary works (Zusi and Livezey 2000, 2006; Livezey and Zusi 2001), many additional terms are emended as "**new term**." Arthrological characters are listed with those for related osteological elements. Use of Latin terms for anatomical features considered to be homologous (e.g., "foramen magnum") paralleled the emphasis conferred upon binomial taxa, intentionally setting them apart from associated narratives. However, in this work, anatomical usages (unlike taxomonic citations) were not set in italics.

Myological nomenclature indisputably has undergone significant refinement virtually throughout the musculature of birds. Important synonyms are listed by Vanden Berge and Zweers (1993), but equivalent terms for the especially antiquated and (infrequently) misinterpreted nomenclature of Shufeldt (1890) were given most completely by Berger (1954, 1960a–b).

In addition to use of formal nomenclature for descriptions of characters *per se* and groupings thereof, it also was extended significantly to descriptions of characters—including *classes* of states (e.g., status, forma, et situs)—and in a limited way to descriptions of observed states. Examples include: *ancora* for "anchor" or "attachment"; *jugum* for "ridge"; *basis* for "base"; *torus* or *tumulus* for "bulge" or "mound," respectively; *situs* for "site"; *fragmentum* for "splint"; *vestigium* for "vestige"; *amplexus* for "clasp"; *latus* for "side"; and *numerus modalis* for "modal number." Finally, descriptions of states for some characters may include informal English terms of Latin origin, e.g., cruciate for "T- or X-shaped"; cuneate for "wedge-shaped"; bifurcate for "forked" or "Y-shaped"; and flabellate for "fan-shaped."

Arthrologia et Osteologia

Note.—For general avian osteology, variably narrow taxonomically, see: Nitzsch (1811); Owen (1843, 1849a); Marshall (1872a–b); A. Newton (1893, 1894, 1895, 1896); Beddard (1898a); Pycraft (1910); Portmann (1938, 1955, 1963); Tordoff (1954); Bellairs and Jenkin (1960); Pocock (1966); Ballmann (1969a–b, 1979); Baumel (1979a–b); Schummer (1992); Baumel and Raikow (1993); Baumel and Witmer (1993).

For developmental osteology, see: Schenk (1897); Kallius (1905); Rex (1905, 1911, 1914, 1924); Schaub (1908, 1912, 1914); Waterston and Geddes (1909); E. M. Williams (1909); Steiner (1922, 1923, 1934); Schestakowa (1927, 1928); Schinz and Zangerl (1937a); D. Starck (1941, 1979, 1982, 1989); Montagna (1945); Saunders (1948); Slabý (1951, 1959); Burckhardt (1954); Becker (1959); Seichert and Rechter (1972); Stork (1972); Sedinger (1986); Schroeter and Tosney (1991a–b); J. M. Starck (1993).

HISTOLOGIA OSSIUM

0001. Os spongiosum, status generalis:

a. absent; **b.** present.

Note.—Os spongiosum—also known as "trabecular" or "cancellous" bone—can occur throughout the mature skeleton, and during early ontogeny invests the calvaria (diplöe), columna vertebralis, and skeleton appendiculare. Os spongiosum is replaced progressively with corpora adiposa and diverticulae pneumaticae, which include cellulae pneumaticae. **Os medullare** is a special, physiologically convertible form of os spongiosum that serves as a supplementary source of minerals (especially calcium) to the camera calcifera during reproduction by females, notably for deposition of the testa ("egg shell"). Although data currently available are too meager for formal analysis, evidence is consistent with the origin of modern birds from traditionally recognized Theropoda (Schweitzer et al. 2005). Histological study by Ricqlès et al. (2001, 2003) indicates that *Confuciusornis* and perhaps allied basal avialians (e.g., *Archaeopteryx*) possessed growth rates similar to massive Neornithes (e.g., Tinamiformes). See: R. Winkler (1979); Baumel and Witmer (1993: annotation 6).

0002. Ossa pneumatica (skeleton axiale et/aut appendiculare), typically evidenced by foramina et/aut pori pneumatica, status et forma (**ordered**):

a. absent;

b. present, of limited anatomical distribution;

c. present, of comparatively wide anatomical distribution, and "simple" (camerate) form;

d. present, encompassing all three major skeletal regions (below), and "complex" (camellate) form, including presence of presumptively plesiomorphic complex of "Haversian canals";

e. present, encompassing all three major skeletal regions (below), and "complex" (camellate) form, but excluding presence of presumptively plesiomorphic complex of "Haversian canals."

Note.—Assumptions concerning pneumatization of bones are numerous (King 1966). Verheyen (1953a) considered cranial pneumaticity in Neornithes. Zavattari and Cellini (1956) contrasted palaeognathous and neognathous taxa on the basis of histologia ossium, notably "complex Haversian systema canaliculae." Recently, Britt (1993) reviewed evidence for ossa pneumatica postcraniales in Dinosauria. See also: Menzbeir (1887); Duncker (1971); Meister (1962); Hogg (1984a–b); Britt (1993); Britt et al. (1998); Cubo et al. (2001). Details of ossa pneumatica are known only for *Gallus* (Hogg 1984b); nevertheless, several generalizations are evident for birds: (*i*) saccus cervicalis invests vertebrae cervicales et thoracicae, et costae vertebrales; (*ii*) saccus clavicularis effects pneumaticae sterni, costae sternales, ossa cinguli membri thoracici, et ossa membri thoracicae; (*iii*) saccus abdominalis aerates ossa pelvici, synsacri, et membri pelvici; and (*iv*) saccus thoracicus is related to diverticula intrathoracica.

0003. Skeleton appendiculare, ossa longa, cinguli anulares (**new term**), status:

a. present; **b.** absent.

Note.—New term refers to "growth rings" in periphery of cross sections of long bones, indicative of regularly variable periods of heterogeneous, protracted growth. See: Hogg (1980, 1982); Kooyman

(1991); Chinsamy et al. (1994, 1998); Castanet et al. (1996, 2000); Chinsamy and Elzanowski (2001); Ricqlès et al. (2001).

0004. Skeleton appendiculare, ossa longa, systema canalorum Haversii (**new term**), forma (**ordered**):

a. complex; **b.** semicomplex;

c. irregular.

Note.—See: Zavattari and Cellini (1956).

0005. Skeleton appendiculare, ossa longa, densitas et status histologica ossium (**ordered**):

a. high, primary pachyostosis scaling with body mass;

b. low, nonpachyostotic, aerodynamic;

c. moderate, secondary pachyostosis associated with graviportality, burgeoned body mass, and (typically) secondary flightlessness.

Note.—Pachyostosis also approached by Plotopteridae and some Alcidae. See: G. Mayr (2004b: appendix 1, character 50).

Skeleton Axiale

Cranium

Note.—Important contributions to knowledge of the anatomy of the cranium of Mesozoic Theropoda include: Currie (1985) for the theropod *Stenonychosaurus*; A. D. Walker (1984) and Elzanowski and Wellnhofer (1996) for *Archaeopteryx*; Currie and Zhao (1994b [1993b]) for Troödontidae, notably regarding pneumatization; Chure and Madsen (1998) for ?*Stokesosaurus*; Makovicky and Norell (1998) for Ornithomimosauria, notably homologies of foramina basicranii; Larsson et al. (2000) pertaining to enlargement of the "forebrain" among nonavian Theropoda. Also, three enantiornithine taxa (*Iberomesornis*, *Concornis*, *Eoalulavis*) are represented only by postcranial elements, and hence are included implicitly among taxa for which cranial characters are of undetermined state. A critical paper for coding Hesperornithiformes was that by Galton and Martin (2002) on *Enaliornis*. Essential material for Dromornithidae was summarized and preliminarily analyzed by Murray and Vickers-Rich (2004). The dissertation by J. A. Clarke (2002, 2004) on *Ichthyornis* is the premier study of this taxon.

The literature concerning the homologies, development, elemental composition, and pneumatization of the avian skull (and vertebral corollaries) is comparatively vast. Important references include: Barkow (1829); Gegenbaur (1871, 1873); Magnus (1871); W. K. Parker (1875b, 1879); Nathusius (1882a); Wunderlich (1886 [1884]); Baur (1889); Gaupp (1894, 1899, 1905); C. Hill (1900); Beecker (1903); Lurje (1906); Sonies (1907); Neumann (1914); Watt (1917); Weidenreich (1923); Dabelow (1925, 1929); de Beer (1926, 1937); Kesteven (1926a–c, 1941, 1942); Lange (1929); Lubosch (1929a–b); Möller (1930, 1931, 1932, 1969a–c); Lüdicke (1933, 1940); Erdmann (1940); Fisher (1944); McDowell (1948, 1978); Van der Klaauw (1948, 1951, 1952, 1963, 1966); Duijm (1951); Barnikol (1952); Wedin (1953); Lang (1956); Webb (1957); Bellairs (1958); Engelbrecht (1958); Bock (1960a–b, 1964, 1966, 1999a); Simonetta (1960a); May (1961); Warter (1965); Schumacher and Wolff (1966a–b); D. Starck (1969); Toerien (1971, 1972); Bühler (1972, 1981, 1985, 1987); Schumacher et al. (1972); Kurzanov (1976); Hogg (1978, 1983); Smit and Frank (1979); R. Winkler (1979); Elzanowski (1981, 1985); Jenni (1981); Whetstone (1983); R. Johnson (1984); A. D. Walker (1984); Vorster (1989); Weber (1990, 1993, 1996); Witmer (1990, 1995b, 1997, 2001); Bock and Andors (1992); Emerson and Bramble (1993); Hanken and Hall (1993); Møller and Cuervo (1998); Murray and Megirian (1998); Posso and Donatelli (2001); Bout (2003).

Calvaria Cranii

0006. Platycalvaria (**new term**)—dorsum cranii conspicuously flattened—status:

a. absent, associated with bilateral width being less than dorsoventral depth;

b. present, associated with bilateral width exceeding dorsoventral depth.

Note.—See: Cracraft (1985: character 12); Siegel-Causey (1988: character 10); Siegel-Causey (1997: table I, character 11).

0007. Megacalvaria (**new term**)—generalized, relative cranial enlargement, an external manifestation of correspondingly enlarged endocranium—reflected by comparatively caudal fossa temporalis on calvaria cranii, status:

a. absent, "encephalization-quotient" typically less than 2.5;

b. present, moderate to extensive, "encephalization-quotient" typically greater than 2.5.

Note.—See: Gauthier (1986: unindexed synapomorphy of Avialae); Elzanowski and Galton (1991: character 10); Holtz (1994a: appendix 1, character 75); Azuma and Currie (2000: appendix 1, character 14); Holtz (2000 [1998]: appendix I, character 82); Rauhut (2003: character 63). Enlargement of the brain in general, and the forebrain in particular, was explored among theropods by Russell (1972), Osmólska (1976), Hopson (1977, 1979, 1980), Currie and Zhao (1994b [1993b]), Currie (1995), Larsson et al. (2000), and Dominguez Alonso et al. (2005).

0008. Cranium, pars rostralis (cf. "forebrain"), forma:

a. small and narrow;

b. enlarged and trianguloid.

Note.—See: Pérez-Moreno et al. (1994: legend for fig. 3, character 6), in terms of "skull narrow and shallow, with elongated facial part"; Vickers-Rich et al. (2002), concerning *Avimimus*; Rauhut (2003: character 64).

0009. Pneumaticas cranii (**new term**)—cranial pneumatization, especially basis cranii, ossa basisphenoidales, as substantiated by ossa spongiosum of calvaria (planum transversus) and features of externum (e.g., fonticulae, fenestrae, et foramina) and (typically) ventral expansion—status (**ordered**):

a. limited; **b.** moderate;

c. substantial.

Note.—Romer (1956: 951) listed pneumatization of the skull as a uniting character for Archosaurian reptiles. Published treatments generally emphasize a more-narrow apomorphy, specifically a "pronounced ventral expansion and pneumatization of os basisphenoidale." See: R. Winkler (1979), in review of "pneumatisation" of skulls of Neornithes; Bakker et al. (1988); Elzanowski and Galton (1991: character 4); Russell and Dong (1994a [1993a]: table 2, character 10); Russell and Dong (1994b [1993b]: troödontid character 2); Holtz (1994a: appendix 1, character 115); Chiappe et al. (1996: appendix 1, character 83), with respect to "basicranial fontanelle on the ventral surface of the basisphenoid"; Sereno et al. (1996: footnote 45, character 52); Sues (1997: appendix 1, character 9), with respect to "expanded and pneumatized parabasisphenoid"; J. D. Harris (1998: appendix 2, character 23), with respect to pneumatic foramina in "basisphenoid recess"; Xu et al. (1999a: character 15); Azuma and Currie (2000: appendix 1, character 13); Currie and Carpenter (2000: appendix 1, character 23); Holtz (2000 [1998]: appendix I, character 88), with respect to pneumatization of the "periotic region"; Maryanska et al. (2002: appendix 1, characters 27 and 49).

0010. Fossa musculorum temporalium, extent on ossa postorbitale (where present) et frontale (facies dorsales) relative to orbita, magnitudo:

a. limited extension onto facies dorsales of ossa postorbitales (where present) et frontales;

b. extends to much of os postorbitale (where present), processus frontalis, and rostrad on os frontale at least to level of orbita, margo caudalis;

x. noncomparable by absence of os postorbitale (Neornithes).

Note.—Regarding nomenclature of fossae, see: Zusi (1962); Siegel-Causey (1988: characters 1–2); Chu (1998: appendix 1, character 19); Zusi and Livezey (2000). Fossa primarily positioned on ossa frontales, parietales, et possibly postorbitales in nonavialian taxa, whereas in Aves it principally involves ossa squamosi et parietales. See: Bas (1955a–b, 1957); Sereno et al. (1993: legend for fig. 3a); Novas (1994 [1993]: appendix, character 8); Currie (1995: appendix, character 9); Xu et al. (1999b: character 88); Hughes (2000: appendix 2, character 1); Xu et al. (2000: supplement, character 68); Maryanska et al. (2002: appendix 1, character 29), regarding extent of "fossa supratemporalis" on ossa frontales; Xu et al. (2002a: supplement, character 4, part); G. Mayr (2003a: appendix I, character 16); G. Mayr (2003b: appendix I, character 17).

0011. Rostrum faciei, forma *sensu* elongation and compression of cranium and rostrum maxillae, and sectio transversus coronae (**unordered**):

a. "oreinirostral" (i.e., strongly bilaterally compressed) and variously elongate rostrocaudally, with dorsoventrally deep subtriangular paracoronal cross section;

b. "elongate-platyrostral" (i.e., dorsoventrally compressed) and rostrocaudally elongate, with obtuse triangular paracoronal cross section;

c. "truncate-platyrostral" (i.e., dorsoventrally compressed) and rostrocaudally truncate, with acutely triangular paracoronal cross section.

Note.—See: Holtz (1994a); Holtz (2000 [1998]: appendix I, character 1); Sereno (2001: table 2, character 39), as synapomorphic of Aves; Xu (2002: suite II, character 1) regarding depth of the "snout" rostral to apertura nasi in Mesozoic Theropoda.

Lamina externa (externum) cranii

0012. Regio postorbitalis, principally ossa frontales et parietales, forma *sensu* dorsoventral height relative to regio interorbitalis:

a. subequal in height;

b. distinctly lower and sloping caudoventrad.

Note.—See: Holtz (1994a: appendix 1, character 14); Rauhut (2003: character 44).

0013. Regio ossium frontales et parietales (frons), pronounced thickening produced by *multi-layered* cellulae pneumaticae (os spongiosum), status:

a. absent, including thickening caused by undirected, densely spiculate bone;

b. present.

Note.—See: Bühler (1972) regarding *Sandwichkonstuktionen*.

0014. Depressio frontalis, status:

a. present, variably detectable at some point on midline of ossa frontales;

b. absent, both from planum interorbitalis and calvaria, resulting in region being variably convex.

Note.—See: Shufeldt (1902a: fig. 1); Harrison and Walker (1976b: pl. 1, figs. C and D); Ericson (1997: table 1, character 4; table 2, character 2); Livezey (1998b: appendix A, character 70); Ji et al. (2001), regarding unnamed dromaeosaurid NGMC 91-A; Bourdon et al. (2005: appendix 1, character 10). Can be complicated by variation in conformation and conspicuousness of sulci glandulae nasales.

0015. Fossa supratemporalis (**new term**), margo rostralis, forma:

a. straight or slightly sinusoidal;

b. distinctly sinusoidal (with associated foveola) and extending onto processus postorbitalis;

x. noncomparable (Neornithes).

Note.—See: Currie (1995: appendix, character 3); Xu et al. (1999b: character 83); Xu et al. (2000: supplement, character 63); Xu et al. (2002a: supplement, character 171). Synonymy of "supratemporal fossa" of Xu et al. (2002b) with fossa musculorum temporalium of Zusi and Livezey (2000) only approximate given different ossa cranii composing solum fossae.

0016. Fossa musculorum temporalium, extension medially to closely approach on midline (typically of comparatively great depth), status:

a. absent; **b.** present.

Note.—See: Zusi (1962, 1975); S. F. Simpson and Cracraft (1981: character 13); Cracraft (1982: series 1, character 2); Cracraft (1985: character 47); Siegel-Causey (1988: characters 1–3); Chu (1998: appendix 1, characters 1–2, 19); Zusi and Livezey (2000); Bourdon et al. (2005: appendix 1, character 13).

0017. Frons, crista pneumatica frontalis (**new term**), status:

a. absent; **b.** present.

Note.—See: J. M. Clark et al. (2001); Maryanska et al. (2002: appendix 1, character 2), regarding "longitudinal pneumatized crestlike prominence."

0018. Meatus acusticus externus, extension relative to features of ossa postorbitale et squamosum, forma:

a. extends to pila intertemporalis (**new term**)—"intertemporal bar"—of ossa postorbitale et squamosum;

b. extends to processus ventralis paraquadraticus (**new term**)—ventral process"—of os squamosum and lateral extension of processus paroccipitalis beyond os quadratum, processus (caput) oticus;

x. noncomparable (Neornithes).

Note.—In Neornithes, meatus bordered by: (*i*) os parasphenoidale, ala parasphenoidalis; (*ii*) os exoccipitale, processus paroccipitalis; et (*iii*) os quadratum, crista tympanica. See: Houde (1988: table 27, character 17); Currie (1995: appendix, character 13); Xu et al. (1999b: character 92); Xu et al. (2000: supplement, character 72). Apparently related to Chiappe and Calvo (1994: appendix I, character 1), Chiappe et al. (1996: appendix 1, character 81), and Chatterjee (1999: appendix II, character 25), in turn inspired by Witmer (1990: 371, character 5), who referred to "extension of the caudal tympanic recess into the caudal portion of the basicranium."

0019. Lamina parasphenoidalis, ala parasphenoidalis, tectum tympanicum parasphenoidalis (**new term**), characterized in part by dorsolateral, subtriangular fossa musculorum, enclosing the recessi tympanici et cotylae quadratici squamosum et otici, status:

a. absent; **b.** present.

Note.—See: Bourdon et al. (2005: appendix 1, character 28), in reference to a "bony ring" in same region, distinct from anulus tympanicus by interruption by hiatus subtympanicus.

0020. Fossa glandulae nasalis (wholly or principally facies dorsalis ossis frontale), frequently including fenestrae penetrating ventrad into orbita, status et forma:

a. absent; **b.** rudimentary; **c.** distinct.

Note.—See: Sibley and Ahlquist (1972: table 1), who contrasted Gaviidae (large fossa glandulae nasalis) with Podicipedidae (sine fossa); Cracraft (1985: character 6); Cracraft (1988: series VIII, character 1); Livezey (1996a: appendix 1, character 9); Chu (1998: appendix 1, characters 20–21); G. Mayr (2003a: appendix I, character 17); G. Mayr and Clarke (2003: appendix A, character 25); G. Mayr (2004a: appendix 1, character 14); G. Mayr (2004b: appendix 1, character 18); Bourdon et al. (2005: appendix 1, character 12); Bourdon (2006: supplement, character 85).

Occiput (regio occipitalis calvarii)

Note.—Preliminary examination of juvenile Neornithes indicates that regiones of the occiput ventral to the fonticulae occipitales (or homologous loci) comprise a juxtaposed complex of facies caudalis of os epioticum et os exoccipitale. During ontogeny, externum of the former is covered by a ventral expansion of the overlying ossa exoccipitales, and the latter reinforced at least marginally by ventral growth of ossa supraoccipitales (in most or all modern taxa, the last pair of elements having undergone prior synostosis medialis). Survey of available juvenile skeletons suggests that palaeognathous taxa undergo external obfuscation of ossa otica at a later ontogenetic stage than most or all neognathous birds.

0021. Condylus occipitalis (caudal perspective, planum transversus occipitalis), forma modalis:

a. essentially circular;

b. distinctly bilobate or reniform, lobae partitioned by incisura mediana condyli, lateromedially elongate.

Note.—Juvenile specimens, notably of ratites, confirm that the condylus includes bilateral, dorsal contributions by ossa exoccipitales and a single, medial, ventral contribution by the os basioccipitale.

Sole monographic survey by Goebloed (1958) is critical, but omitted many taxonomic groups and we disagreed concerning the admittedly difficult Columbiformes. Significant intraspecific variation, and conspicuousness of medial sulcus confounds assessment of general shape of condylus. See: Houde (1988: table 27, character 10); Livezey (1997a: appendix 1, character 1; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, character 86); Dyke (2001b: appendix 1, character 1); Coria and Currie (2002: appendix 1, character 15), regarding shape in Tyrannosauridae; G. Mayr and Ericson (2004: appendix I, character 19).

0022. Condylus occipitalis, collum condyli occipitalis (**new term**), status et forma (**ordered**):

a. absent, essentially sessile condylus of less than hemiglobular form;

b. rudimentary, basis condylaris subcylindrical with diameter equal to or slightly less than that of condylus proprius;

c. present, condylus comparatively prominent, and variably subpedicellate or (sub)umbelliform with basis having (often slightly) smaller diameter than condylus proprius, aspect subglobular.

Note.—See: Makovicky and Sues (1998: appendix 1, character 21); Holtz (2000 [1998]: appendix I, character 103); Norell et al. (2001: appendix 1, character 58); J. M. Clark et al. (2002a: appendix 2.2, character 57); Coria and Currie (2002: appendix 1, character 6), regarding cavitates pneumaticae in collum among Tyrannosauridae; Vickers-Rich et al. (2002), concerning *Avimimus*; Xu (2002: suite II, character 98); Xu et al. (2002a: supplement, character 43); Hwang et al. (2004: supplement, character 56); Xu and Norell (2004: supplement, character 56).

0023. Condylus occipitalis, fossa subcondylaris (ventral perspective), status et forma (**unordered**):

a. absent;

b. present, distinct, hemicircular sulcus bounding rostral half of basis externa cranii that surrounds condylus;

c. present, fovea immediately rostral to condylus and of equal diameter.

Note.—State “a” includes a diversity of other, ill-defined concavitates laminae basioccipitalis rostral to condylus occipitalis. See: Livezey (1998b: appendix A, character 85).

0024. Condylus occipitalis, rostrocaudal position relative to os exoccipitale, processus paroccipitalis, forma:

a. rostral; **b.** approximately equal or caudal.

Note.—See: G. Mayr (2003a: appendix I, character 14); G. Mayr (2004a: appendix 1, character 19).

0025. Condylus occipitalis et foramen magnum, angulus (lateral perspective) between planae foraminis et basis cranii—e.g., lamina parasphenoidalis (basitemporalis) et especially palatum osseum—i.e., comparative dorsoventral position of articulatio craniovertebralis, forma:

a. articulatio comparatively ventral, angulus “sharp,” sur(supra)diagonal (> 45°), often approaching perpendicularity;

b. articulatio comparatively dorsal, angulus “shallow,” subdiagonal (< 45°), often approaching coplanarity.

Note.—See: S. F. Simpson and Cracraft (1981: character 5); Coria and Currie (2002: appendix 1, character 7). Some Scolopacidae manifest extreme apomorphy in which foramen magnum is oriented subperpendicularly ventrad to basis cranii (e.g., *Scolopax*). Worthy and Holdaway (2002: 117) confirmed comparatively ventral position of articulatio craniovertebralis in ratites, including Dinornithiformes.

0026. Foramen magnum, pronounced ventrorostral shift placing occiput co-planar with palatum osseum, with associated changes in relative positions of lamina basiparasphenoidalis, foramen magnum, and basis cranii interna, status:

a. absent; **b.** present.

Note.—Exemplars did not include most extreme examples of apomorphy, a geometric condition related to “airencephaly,” e.g., comparatively derived Scolopacidae such as *Gallinago* and *Scolopax*. See: Romer (1956: 951) regarding planum occipitalis et geometrica articulatio condyli occipitalis.

0027. Foramen magnum, forma modalis *sensu* lobation:

a. unilobate, circular, oblong, or elliptical;

b. distinctly bilobate, with dorsal, lesser lobus having rounded margo dorsalis.

Note.—Significant intrageneric variation, and apomorphic condition occurs in some avian genera not included among exemplar taxa.

0028. Foramen magnum (caudal perspective), forma:

a. subcircular, slightly wider than tall;

b. oval, taller than wide.

Note.—See: Makovicky and Sues (1998); Norell et al. (2000: appendix 1, character 14); Norell et al. (2001: appendix 1, character 57); J. M. Clark et al. (2002a: appendix 2.2, character 56); Vickers-Rich et al. (2002), concerning *Avimimus*; Xu (2002: suite II, character 97); Hwang et al. (2004: supplement, character 55); Xu and Norell (2004: supplement, character 55).

0029. Foramen magnum, diameter relative to that of condylus occipitalis:

a. former no greater than latter;

b. former greater than latter.

Note.—See: Maryanska et al. (2002: appendix 1, character 47).

0030. Caudoventral deflection occipitalis (relative to planum normal to palatum osseum), forma:

a. caudad; **b.** ventrocaudad.

Note.—See: Holtz (1994a: appendix 1, character 74); Sues (1997: appendix 1, character 13); Currie and Carpenter (2000: appendix 1, character 25); Holtz (2000 [1998]: appendix I, character 101).

0031. Prominentia cerebellaris, marked, abrupt caudal extension—extending caudad to crista (linea) nuchalis transversa—and conformation as smooth, rounded, subglobular bulla lacking distinguishable linea aut carina medialis, status:

a. absent; **b.** present.

Note.—See: Chu (1998: appendix 1, character 3).

0032. Crista (linea) nuchalis sagittalis (principally ossa parietales), status et forma (**ordered**):

a. absent or obsolete, eminentia limited to jugum lateralis dorsal to fenestra supratemporalis;

b. present, low or moderately developed;

c. present, prominent.

Note.—Primarily a feature of ossa parietales, but may involve to lesser degree ossa supraoccipitales (to which feature attributed for *Carnotaurus*). See: Currie (1985); Bonaparte (1991); Currie and Zhao (1994a [1993a]); Holtz (1994a: appendix 1, character 14); Russell and Dong (1994a [1993a]: table 2, character 8); Forster et al. (1998: supplement, character 10); Livezey (1998b: appendix A, character 89), originally conceived to differentiate the two species of *Aptornis*; Xu et al. (1999a: character 8); Xu et al. (1999b: character 10); Holtz (2000 [1998]: appendix I, character 84); Xu et al. (2000: supplement, character 8); Norell et al. (2001: appendix 1, character 48); J. M. Clark et al. (2002a: appendix 2.2, character 47); Coria and Currie (2002: appendix 1, character 12); Maryanska et al. (2002: appendix 1, character 28); Vickers-Rich et al. (2002), concerning *Avimimus*; Xu (2002: suite II, character 90); Xu et al. (2002a: supplement, character 35); Hwang et al. (2004: supplement, character 46); Xu and Norell (2004: supplement, character 46).

0033. Crista (linea) nuchalis transversa (largely ossa supraoccipitales), status:

a. present and pronounced;

b. indistinct or absent.

Note.—See: Gauthier (1986); Holtz (1994a: appendix 1, character 24), ambiguous concerning crista intended; Forster et al. (1998: supplement, character 20); Xu et al. (1999b: character 18); Holtz (2000 [1998]: appendix I, character 83); Maryanska et al. (2002: appendix 1, character 44); Vickers-Rich et al. (2002), concerning *Avimimus*.

0034. Crista (linea) nuchalis transversa, caudal deviation on midline of cranium onto caudally prominent, rounded, ventrally concave, lamina medialis nuchalis (**new term**), status:

a. absent; **b.** present.

Note.—See: Owre (1967: figs. 45–46), effecting articulatio supraoccipitalo-nuchalis (**new term**).

0035. Cristae laminae externae cranii—elongate, concave, triangular lamina bordered by cristae (*i*) nuchalis transvera, (*ii*) nuchalis lateralis, (*iii*) otica dorsalis, et (*iv*) post zygomatica, status:

a. absent; **b.** present.

Note.—"Nuchalis transversa" is synonymous with "occipital" and "crest C" of Zusi and Storer (1969) and "occipitalis" of Dullemeijer (1951a–b). "Nuchalis lateralis" is synonymous with "crest B" of Zusi and Storer (1969) and "occipitalis" of Bas (1954). "Otica dorsalis" is synonymous with "dorsalis" of Butendieck and Wissdorf (1982), "praeglenoidea" of Weber (1996), "crest D" of Zusi and Storer (1969), and "c.26" of Bas (1954). "Temporalis ventralis" is synonymous with "temporalis" of Bas (1954).

See: Siegel-Causey (1988: character 6), regarding "second postorbital (temporal) process"; Chu (1998: appendix 1, character 10)—area muscularis aspera on paries caudalis orbitae of os laterosphenoidale; Livezey (1998b: appendix A, character 80), pertaining to fossa musculorum temporalium.

0036. Lamina externae cranii—broad, concave, triangular lamina bordered by cristae (*i*) nuchalis lateralis, (*ii*) otica dorsalis, et (*iii*) m. depressor mandibulae, status:

a. absent; **b.** present.

Note.—"Crista m. depressor mandibulae" is synonymous with "crest A" of Zusi and Storer (1969) and "limiting crest" of Dullemeijer (1951a–b).

See: Siegel-Causey (1988: character 6), regarding "second postorbital (temporal) process"; Chu (1998: appendix 1, character 10)—area muscularis aspera on paries caudalis orbitae of os laterosphenoidale; Livezey (1998b: appendix A, character 80), regarding fossa musculorum temporalium.

0037. Recessus basisphenoidalis, ostium caudalis basisphenoidalis, subdivision (lobation), status et forma modalis:

a. present, ostium undivided, unilobate;

b. present, ostium divided, subdivided by a thin osseus spicule, bilobate;

c. absent.

Note.—In reference to "posterior opening of basisphenoid recess."

See: Norell et al. (2001: appendix 1, character 13); J. M. Clark et al. (2002a: appendix 2.2, character 10); Vickers-Rich et al. (2002), concerning *Avimimus*; Xu (2002: suite II, character 239); Xu et al. (2002a: supplement, character 184); Hwang et al. (2004: supplement, character 10); Xu and Norell (2004: supplement, character 10).

Cavum Cranii

0038. Fossa cranii rostralis, fossa tecti mesencephali, and canalis semicircularis anterior, forma:

a. triangular;

b. approximately linearly aligned, the axis of alignment almost perpendicular to planum of palate.

Note.—Forma defined here as the relative geometric relationship of their respective midpoints (lateral perspective, planum parasagittalis).

0039. Fossa cranii rostralis (internal perspective), forma:

a. comparatively narrow lateromedially, essentially ovate, with rostrolateral paries not markedly convex;

b. comparatively broad lateromedially, distinctly kidney-shaped, with rostrolateral paries markedly convex.

Note.—Derived state related to comparatively voluminous encephalon and its rostral extension parallel to axis majoris vertebralis dorsal to orbita.

0040. Fossa cranii rostralis, caudal expansion lateral to canalis semicircularis (anterior) rostralis (**new term**), status:

a. absent, fossa rostral;

b. present, fossa caudal.

0041. Fossa cranii rostralis, foramen nervorum olfactorii, status:

a. absent, n. olfactorii passing internally within the interorbital region of skull, medial to paries medialis orbitae and paries dorsalis orbitae, and ventral to os frontale;

b. present, n. olfactorii passing at least in part lateral to paries medialis orbitae.

Note.—With respect to foramen nervorum olfactorii, we follow the implication by Baumel and Witmer (1993) in restricting the term to foramina in paries caudalis orbitae (i.e., accommodating passage of n. olfactorii from fossa cranii rostralis into orbita); this foramen is continued rostrally by sulcus n. olfactorii in many taxa. See: Zusi (1975); Chatterjee (1991: character 2); Chatterjee (1999: appendix II, character 3).

0042. Fossa cranii rostralis, fossa bulbi olfactorii, forma *sensu* proximity to cavum nasi, regio olfactoria (**ordered**):

a. cavum significantly rostral to fossa bulbi;

b. cavum closely approaching but not contiguous with fossa bulbi;

c. cavum rostrocaudally contiguous (remains rostrocaudally partitioned) with fossa bulbi;

d. cavum extending substantially caudad so as to be positioned partially dorsal to fossa bulbi.

Note.—Nonexemplary genera of Sphenisciformes approach state "a."

0043. Fossa cranii media, fossa tecti mesencephali (fossa ganglii trigemini or membrane-covered spatium directly ventral), canalis nervus maxillomandibularis, proportion of canalis to which fossa cranii media is ventral, forma (**ordered**):

a. caudal one-third; **b.** middle one-third;

c. rostral one-third.

Note.—Provisional *a priori* basal polarity is state "b."

0044. Fossa cranii media, fossa tecti mesencephali (fossa ganglii trigemini or membrane-covered spatium directly ventral to it; dissection required), canalis nervus maxillomandibularis, length between crista marginalis tecti caudalis (**new term**) and foramen nervus maxillomandibularis relative to diameter of latter foramen:

a. long, exceeding (usually markedly) diameter;

b. short, approximating diameter.

0045. Fossa cranii media, fossa tecti mesencephali (fossa ganglii trigemini or membrane-covered spatium directly ventral), canalis nervus maxillomandibularis, conformation of osseus passage internal to foramen nervus maxillomandibularis and to crista tecti caudalis (**unordered**):

a. sulcus, without foramen in crista tecti caudalis, including those in which osseus arcus (see below) was indicated but incomplete;

b. sulcus, with passage enclosed dorsally by complete osseus arcus, forming in crista tecti caudalis;

c. cuniculus, passage enclosed dorsally for at least one-half its length.

0046. Fossa cranii media, fossa tecti mesencephali (fossa ganglii trigemini or membrane-covered spatium directly ventral), canalis nervus maxillomandibularis, foramen nervus maxillomandibularis to foramen nervi ophthalmici, situs externus:

a. adjacent but narrowly partitioned by pila ossea, or confluent;

b. well separated by lamina ossea.

Note.—See: Saiff (1974, 1976, 1978, 1980, 1981, 1982, 1983, 1988); J. D. Harris (1998: appendix 2, character 26); Azuma and Currie (2000: appendix 1, character 16); Currie and Carpenter (2000: appendix 1, character 28); Norell et al. (2000: appendix 1, character 12); Bourdon et al. 2005: appendix 1, character 29), regarding rostrocaudal situs relative to that of recessus tympanicus rostralis. Baumel and Witmer (1993) list foramina involved under os laterosphenoidale, and although these pertain to externum cranii, character listed here as the evaluations were facilitated by internal examination.

0047. Foramen nervi maxillomandibularis, division by osseus partition into separate foramina for nervi maxillaris et mandibularis, status:

a. absent; **b.** present.

Note.—Character determinable from externum cranii. Intraspecific variation in *Alectoris* and *Goura*.

Baumel and Witmer (1993: 81) erroneously listed *Tyto*, *Buteo*, and *Cathartes* as apomorphic in this feature.

0048. Foramen nervi maxillomandibularis, situs rostrocaudalis relative to os parasphenoidale, lamina parasphenoidalis, ala parasphenoidalis, or homologous lamina (if present):

a. rostral;

b. caudal, coincident with prominently developed ala parasphenoidalis and hiatus subtympanicus.

Note.—See: Kühne and Lewis (1985); Elzanowski (1991: table 3) and Elzanowski and Galton (1991: character 9); Hughes (2000: appendix 2, characters 39–40).

0049. Fossa cranii media, fossa tecti mesencephali, situs relative to fossa cranii rostralis and associated orientation of separating crista tentorialis:

a. ventral or caudoventral, crista obliquely sloping relative to planum palatum;

b. essentially caudal, crista almost perpendicular to planum palatum.

Note.—See: Portmann and Stingelin (1961) and R. Pearson (1972) regarding orientation of subparts of brain in *Phalacrocorax*; Siegel-Causey (1988: characters 27–28) regarding foramina trigeminales proötica in *Phalacrocorax*; Chu (1998: appendix 1, character 8) regarding Laridae.

0050. Fossa cranii media, fossa tecti mesencephali, crista tentorialis, extreme medial prominence, associated with solum of fossa cranii rostralis as discoid, dorsally concave lamina, status:

a. absent; **b.** present.

Note.—The solum indicated ends abruptly at the comparatively large foramen ganglii trigemini, the latter marking the caudal terminus of a reduced fossa tecti mesencephali, and has the appearance of being compressed ventrad against the canalis semicircularis anterior.

0051. Fossa cranii media, fossa tecti mesencephali, crista tentorialis, lateromedial depth (**ordered**):

a. small, crista almost indistinguishable;

b. medium, distinct, variably shaped, but not prominent;

c. large, shelflike, deeper in middle than at rostral or caudal ends.

Note.—Provisional basal polarity is state "b."

0052. Fossa cranii media, fossa tecti mesencephali, crista tentorialis, junctura with fossa cerebelli, crista marginalis cerebelli, position relative to canalis semicircularis anterior:

a. along rostro-dorsal margo of canalis;

b. dorsal to canalis, with distinct segment of crista marginalis between canalis and junctura cristae.

0053. Fossa cranii media, fossa tecti mesencephali et fossa (chiasma) opticus (**new term**), linea cerebralis optici (**new term**), status (**ordered**):

a. absent or rudimentary, crista tentorialis separated from planum medialis by significant expanse of smooth bone;

b. moderately distinct, defining variably conformed boundary between fossae cranii rostalis et media (or to margo rostromedialis ossis where paries caudales orbitae deficient), typically appearing as rostral continuation of crista tentorialis;

c. prominent, forming substantial osseus crista or lamina dorsal to fossa opticus.

Note.—Distinction of states "a" and "c" problematic in some taxa. See: Stephan (1979), regarding Spheniscidae.

0054. Fossa cranii caudalis, foramen magnum, prominent, bilateral, rostromedially oriented tuberculae on margines laterales foraminis, status:

a. absent; **b.** present.

Note.—Determinable from externum through foramen magnum. Evidently represent extreme homologues of variably roughened facets in other taxa, the function of which is unknown; apparently without formal name.

0055. Fossa cranii caudalis, foramen magnum, margo ellipticalis, orientation of axis majoris ellipsoidalis relative to axes dorsoventralis et lateromedialis, forma:

a. aligned with latter, foramen subcircular;

b. aligned with former, foramen taller than wide.

Note.—See: Makovicky and Sues (1998: appendix 1, character 20); Holtz (2000 [1998]: appendix I, character 102); Xu et al. (2002a: supplement, character 42).

0056. Fossa cranii media, fossa tecti mesencephali, caudal expansion lateral to canalis semicircularis anterior, status:

a. absent; **b.** present.

0057. Fossa cerebelli, crista marginalis cerebelli, planum transversus cristae—perpendicular to planum transversus ossis parasphenoidale, ostium pharyngeale et os basioccipitale, fossa subcondylaris—relative to area enclosed by canalis semicircularis anterior, situs rostrocaudalis (**ordered**):

a. rostral; **b.** coincident; **c.** caudal.

0058. Fossa cerebelli, sulcus venus semicircularis, osseus medial lamina, status:

a. present, sulcus enclosed at least at junctura with crista tecti caudalis;

b. absent, but sulcus may be narrow or constricted at junctura with crista tecti caudalis.

Note.—See: Chatterjee (1999: entry 10), in reference to "sinus canal" between ossa epioticum et supraoccipitale.

0059. Fossa cerebelli, sulcus venus semicircularis, inclusion of dorsolateral portion on solum of fossa cranii rostralis, status:

a. absent; **b.** present.

0060. Fossa cerebelli, vertex (junctura) cristae marginalis cerebelli (**new term**), marginis tecti caudalis et tentorialis, forma:

a. simple intersection of cristae without prominent tubercular development;

b. prominent, triangular-based, typically blunt tuberculum or eminentia immediately rostro-dorsal to canalis semicircularis anterior, and visible through foramen magnum of intact crania.

Note.—State "b" approached in *Fregata*, Sulidae, *Pelecanus*, and *Balaeniceps*.

0061. Tuberculum pineale, status:

a. absent;

b. present, extending ventrad to cristae internae.

Note.—This feature is a variably prominent, triangular eminentia on the calvaria interna at the intersection of crista frontalis interna et crista marginalis cerebelli, positioned in proximity to the glandula pinealis (Tilney and Warren 1919). Other variation in cristae vallecularis et frontalis interna, although suggestive, did not sustain discrete coding of states.

Ossa Cranii, I

Os Basioccipitale

Note.—Examination of suitably prepared, juvenile specimens suggests that during early ontogeny, bilaterally paired ossa basioccipitales synostotically unite to form the definitive, apparently single lamina. Dorsal os supraoccipitale, like ventral counterpart os basioccipitale, is considered to be singular, as opposed to bilaterally paired (Romer 1956). See: Simonetta (1957, 1960a–b, 1963, 1968) for review of general cranial architecture.

0062. Os basioccipitale, fovea ganglii vagoglossopharyngealis, foramina externa, numerus modalis:

a. one, gangliae nervorum cranii IX and X sharing common foramen;

b. two, gangliae nervorum cranii IX and X having separate foramina.

Note.—A single fovea ganglii vago-glossopharyngealis is located in the sutura opisthotico-basioccipitalis of basis cranii interna, fossa cranii caudalis. Variation in Aves corresponds to foramina efferentes basis cranii externa, and evidently serves as synapomorphy for Neognathae. Problematic relationship with character compiled by Saiff (1988: table 1) as "separate IX foramen," compiled largely from previous ordinal studies (Saiff 1974, 1976, 1978, 1980, 1981, 1982, 1983, 1988).

See: Cracraft (1988: series VII, character 4); Cracraft and Mindell (1989: table 1, character 30) regarding foramina in (basi)parasphenoidal plate for "carotid/stapedial arteries, lateral head vein, and the hyomandibular branch of nerve VII, with a large foramen for nerves IX and X along its posterior margin"; Elzanowski (1991: table 3); Elzanowski and Galton (1991: character 8); Elzanowski (1995: 43–44, character unindexed); Ericson (1996: character 4); Sereno et al. (1996: footnote 45, character 40); Rotthowe and Starck (1998: appendix, character 6); Bourdon et al. (2005: appendix 1, characters 23–24).

Os(sa) Basioccipitale et/aut Basisphenoidale

0063. Os(sa) basioccipitale et/aut basisphenoidale, tuberculum basilare ("basal tubera"), separation by incisura intertubercularis basilares (**new term**) from limitus caudoventralis suturarum opisthotico-exoccipitalis et opisthotico-basisphenoidalis, status:

a. absent; **b.** present.

Note.—Homology of basal tubera of stem Theropoda with tuberculum basilare of Aves generally accepted (Baumel and Witmer 1993: annotation 83). See: J. D. Harris (1998: appendix 2, character 25); Azuma and Currie (2000: appendix 1, character 11, part); Currie and Carpenter (2000: appendix 1, character 27), in reference to "basisphenoid separated from basal tubera by notch"; Holtz (2000 [1998]: appendix I, character 99).

0064. Os(sa) basioccipitale et/aut basisphenoidale, tuberculum basilare, definitive composition:

a. includes both elements, which remain undivided;

b. includes both elements, divided by lateral, longitudinal sulcus into pars medialis tuberculae (**new term**) ossis basioccipitale, and pars lateralis tuberculae (**new term**) ossis basisphenoidale.

Note.—Bilateral tuberculae at the rostrolateral vertices of os basioccipitale, composed of os basioccipitale alone, are encased during development by os basisphenoidale, a trend reflected in definite states (Pycraft 1902; Saiff 1974; Witmer 1990). Tuberculum basilare (also known as the "basal tuber")—distinct and caudal to processes basipterygoidei—serves primarily as tuberculum insertii m. rectus capitis dorsalis (Baumel and Witmer 1993: annotation 83).

See: Sereno and Novas (1992: appendix, character 9); Sereno et al. (1994: footnote 12); Sereno et al. (1996: footnote 45, character 44); J. D. Harris (1998: appendix 2, character 22), regarding "basioccipital participates in basal tubera"; Azuma and Currie (2000: appendix 1, character 11, part); Currie and Carpenter (2000: appendix 1, character 24); Holtz (2000 [1998]: appendix I, character 96); Maryanska et al. (2002: appendix 1, character 48), termed "basal tubera"; Rauhut (2003: character 55).

0065. Os(sa) basioccipitale et/aut basisphenoidale, tuberculum basilare ("basal tuber"), prominence (depth):

a. moderately prominent;

b. very prominent, widely separated.

Note.—See Norell et al. (2000: appendix 1, character 16); Maryanska et al. (2002: appendix 1, character 48), termed "basal tubera"; Vickers-Rich et al. (2002), concerning *Avimimus*.

0066. Os(sa) basioccipitale et/aut basisphenoidale, tuberculum basilare ("basal tuber"), incisura intertubercularis (**new term**), forma:

a. broad, parabolic—"U-shaped";

b. narrow, chevroniform—"V-shaped";

x. noncomparable (Neornithes).

Note.—Character manifested inordinate variation and precluded confident assignments of Neornithes in manner comparable to nonavian Theropoda; similar problems were encountered in attempts to expand conformational characters of some authors—e.g., Harrison and Walker (1976b: pl. i, fig. b) and Bourdon et al. (2005: appendix 1, character 27) for Neornithes.

See: Norell et al. (2000: appendix 1, character 17); Xu (2002: suite II, character 14), regarding "incisure between basal tubera"; Hwang et al. (2004: supplement, character 222); Makovicky and Norell (2004: character 222); Xu and Norell (2004: supplement, character 222), including position with respect to condylus occipitalis and angulus intertubercularis.

0067. Os(sa) basioccipitale et/aut basisphenoidale, tuberculae basilares ("basal tubers"), intertubercular distance relative to width of condylus occipitalis:

a. former greater than latter;

b. former less than latter.

Note.—See: Elzanowski (1991: table 3); Elzanowski and Galton (1991: character 5); Azuma and Currie (2000: appendix 1, character 12); Holtz (2000 [1998]: appendix I, character 97); Currie et al. (2003: appendix, character 4).

0068. Os(sa) basioccipitale et/aut basisphenoidale, tuberculum basilare ("basal tuber"), expanse of os basisphenoidale between tuberculae basilares et processes basipterygoidei, length relative to width:

a. approximately equal;

b. length approximately 1.5 times width.

Note.—See: Rauhut (2003: character 56).

Os Exoccipitale

Fossa parabasalis: Foramina vascularia et nervosa

Saiff (1974, 1976, 1978, 1980, 1981, 1982, 1983, 1988)—summary of characters provided in Saiff (1988: table 1)—demonstrated that variation in diverse foramina were of potential phylogenetic importance. Most of the venae arteriae et nervi passing through these foramina were associated with anterior ostia through paries caudalis orbitae or the basicranium (especially dorsal to lamina basisphenoidalis). Some passed through the cranium interna whereas others passed laterally through fossa parabasalis (including "metotic process" *sensu* Saiff), and most or all penetrate the cranium caudally through the occiput (ossa supraoccipitale et exoccipitale). "Metotic process," herein referred to as paries caudalis et ventralis of fossa parabasalis, was defined by Saiff (1974: 216) as: "The ossified first metotic cartilage which forms lateral to the hypoglossal foramina and constitutes the floor and most of the posterior wall of the recessus scalae tympani [cavum tympanicum]." In a survey of these structures in Falconiformes, Saiff (pers. comm.) figured the processus metoticus as a pila ossea at margo caudalis recessi tympanici.

Characters pertaining to canalis (sulcus) carotis cerebralis, canalis (sulcus) arteria ophthalmicus externus et nn. abducentis, oculomotorii, maxillomandibularis, opthalmici, et trochlearis as variably manifest in paries caudalis orbitae, cavum tympanicum, et/aut occiput (Saiff 1974, 1976, 1978, 1980, 1981, 1982, 1983, 1988); Bourdon et al. (2005: appendix 1, characters 29, 33–34); Bourdon (2006: supplement, characters 77–78).

0069. Os exoccipitale, fossa parabasalis, status:

a. absent; **b.** present.

Note.—Deemed synonymous with "deep lateral depression in otic region of braincase." See: Baur (1889); J. M. Clark et al. (1994); Holtz (1994a: appendix 1, character 64); Sues (1997: appendix 1, character 12); Makovicky and Sues (1998: appendix 1, character 16); Holtz (2000 [1998]: character I, character 89); Hwang et al. (2004: supplement, character 8).

0070. Os exoccipitale, fossa parabasalis, ostium canalis (afferens) carotici, foramen (foramina) for arteriae carotis communis, numerus modalis:

a. two foramina, arteriae enter separately;

b. single foramen, arteriae enter together.

Note.—Familial summary presented by Saiff (1988: table 1), under "carotid canal," compiled largely from previous ordinal studies Saiff (1974, 1976, 1978, 1980, 1981, 1982, 1983, 1988). See: Cracraft (1988: series VII, character 4); Cracraft (1988: 353) also contrasted *Balaeniceps* with typical Pelecaniformes in part by the former possessing " . . . a single foramen or notch for the carotid and stapedial arteries (*Balaeniceps* has separate foramina, which seems to be primitive)"; Cracraft and Mindell (1989: table 1, characters 18, 26, and 30), last regarding foramina in basiparasphenoidal plate for "carotid/stapedial arteries, lateral head vein, and the hymomandibular branch of nerve VII, with a large foramen for nerves IX and X along its posterior margin" (p. 347); Elzanowski (1991: table 3); Elzanowski and Galton (1991: character 7); Elzanowski (1995: character Nb'2); Ericson (1996); Siegel-Causey (1997: table I, character 6), regarding foramina in (basi)parasphenoidal plate for "carotid/stapedial arteries, lateral head vein, and the hymomandibular branch of nerve VII, with a large foramen for nerves IX and X along its posterior margin" (p. 347); J. D. Harris (1998: appendix 2, character 27), with respect to "pneumatic openings associated with internal carotid artery"; Azuma and Currie (2000: appendix 1, character 15), also with respect to "internal carotid"; Currie and Carpenter (2000: appendix 1, character 29), concerning "internal carotid artery, pneumatized opening"; Holtz (2000 [1998]: appendix I, character 91), citing Makovicky and Sues (1998); Cracraft and Clarke (2001); G. Mayr and Clarke (2003: appendix A, character 26), who associated this complex with convexity of lamina basiparasphenoidalis and its angulus with rostrum parasphenoidale.

0071. Os exoccipitale, fossa parabasalis, foramen internum nervi facialis (nervus cranii VII), et foramen internum nervi vestibulocochlearis (nervus cranii VIII), sitae relativa cranioventrales:

a. former ventral to latter;

b. former cranioventral to latter.

Note.—See: Holtz (2000 [1998]: appendix I, character 94), citing in turn Makovicky and Norell (1998); Hughes (2000: appendix 2, character 30).

0072. Os exoccipitale, fossa parabasalis, foramina efferentes nervorum cranii X–XII—nn. vagus, accessorius, et hypoglossus, respectively—fovea foraminis, status (**new term**):

a. fovea present, exitus recessed, foramen within orbiculate fovea foraminis;

b. fovea absent, exitus superficial, perforata in externum.

Note.—Internal avian counterpart to fossa parabasalis is fovea ganglii vagoglossopharyngealis. See: Norell et al. (2001: appendix 1, character 15); J. M. Clark et al. (2002a: appendix 2.2, character 19); Vickers-Rich et al. (2002), concerning *Avimimus*; Xu (2002: suite II, character 240); Xu et al. (2002a: supplement, character 185); Hwang et al. (2004: supplement, character 19); Xu and Norell (2004: supplement, character 19).

0073. Os exoccipitale, fossa parabasalis, foramina nervi cranii X (n. vagus) et XI (n. accessorius), situs relative to foramina nervus cranii XII (n. hypoglossus), foramen v. jugularis, et condylus occipitalis:

a. nervi vagus et accessorius exit laterad through common foramen with venus jugularis;

b. nervi vagus et accessorius exit caudolaterad through foramen separated from that (those) for n. hypoglossus et v. jugularis by pila metotica between rima lateralis ossis basioccipitale and basis processi paroccipitalis.

Note.—See: Xu et al. (2002b); Rauhut (2003: character 60).

0074. Os exoccipitale (lamina externa cranii, occiput), foramen magnum, incisura foraminis, status et forma (**unordered**):

a. absent or indistinct;

b. present, positioned at dorsoventral midpoint of margines laterales;

c. present, positioned at dorsolateral vertices of foramen.

0075. Os exoccipitale (lamina externa cranii, occiput), foramen magnum, marked dorsal intrusion by condylus occipitalis (ossa basioccipitale et exoccipitales, processes condylares) into margo ventralis foraminis at midline, effecting inverted cordiform outline of foramen (caudal perspective), status:

a. absent; **b.** present.

Os Supraoccipitale

Note.—Some juvenile specimens (e.g., *Eudocimus ruber*; CM 15946) retain variably distinct fissurae dorsales ossium supraoccipitalia that are suggestive of suturae intersupraoccipitales (**new term**), whereas this element generally is considered to derive from a single, median primordium.

0076. Os supraoccipitale, facies nuchalis (facies articularis ossis nuchale, where present), relative to that of condylus occipitalis—composed of os basioccipitale medioventrally and exoccipitales dorsolaterally—situs rostrocaudalis:

a. caudal; **b.** rostral or equal.

Note.—See: Dullemeijer (1951a–c); Siegel-Causey (1988: character 35).

0077. Os supraoccipitale, foramen dorsomediana—cf. foramen (ostium)—status et situs (**ordered**):

a. absent, foramina bilaterally symmetrical within regiones occipitales;

b. present, foramina approaching or unified—foramen dorsomediana (**new term**)—often within margo dorsalis foraminis magnum;

c. present, distinctly dorsal, often proximate to crista nuchalis transversa.

Note.—See: Beddard (1898a: 314), as "median supra-occipital foramen"; Bourdon et al. (2005: appendix 1, characters 18–19).

0078. Os supraoccipitale, fonticulus occipitalis (typically closed by membrana *in vivo*, may admit vena occipitalis externa peripherally), status definitivum:

a. absent; **b.** present.

Note.—May be widespread embryonically and concealed by adulthood, and some taxa (especially massive species) show developmental variation in size and (rarely) presence of fonticulus in older individuals (e.g., *Cnemiornis*, some *Grus*). Ostia v. occipitalis externa extended rostrad (internally) as v. semicircularis and sinus petrosus caudalis.

See: Strauch (1978: character 18), reanalyzed by Björklund (1994) and Chu (1995); Strauch (1985: character 6); Livezey (1986: appendix 1, character 9); Livezey (1989: table 1, character 9); Andors (1992: table 2, character 9); Ericson (1997: table 1, character 1; table 2, character 1); Livezey (1997a: appendix 1, character 5; *corrigenda*, Livezey 1998a); Chu (1998: appendix 1, character 9); Livezey (1998b: appendix A, character 87); Dyke (2001b: appendix 1, character 5); G. Mayr and Clarke (2003: appendix A, character 27); G. Mayr (2004a: appendix 1, character 15); G. Mayr and Ericson (2004: appendix I, character 17).

0079. Os supraoccipitale, foramen efferens vena occipitalis externa, status et situs:

a. present, bilateral;

b. absent, venae occipitales interna et externa confluent and exiting cavum cranii as unified vena occipitalis communis through intervallum atlantico-occipitalis.

Note.—See: Bourdon et al. (2005: appendix 1, character 19); Bourdon (2006: supplement, character 97).

Os Postorbitale

0080. Os postorbitale, status:

a. present, typically united by sutura with os jugale, thereby contributing to typical "diapsid temporal configuration";

b. absent, expunging aspect of "diapsid temporal configuration" through associated confluence of two fenestrae temporales with orbita and absence of arcus temporalis.

Note.—See: Cracraft (1986: appendix, character 59); Cracraft (1988: series I, character 8); Chatterjee (1991: characters 8 and 12); J. M. Clark et al. (1994); Chatterjee (1995: character 2); Chiappe et al. (1996: appendix 1, character 93); Hou et al. (1996: character 6); Sanz et al. (1997: footnote 29, character *iv*); Chatterjee (1999: appendix II, characters 2 and 10, part); Hou et al. (1999a); Chiappe (2001a: appendix 1, character 13); Ji et al. (2001), regarding unnamed dromaeosaurid NGMC 91-A; Chiappe (2002: appendix 20.2, character 13); Chiappe and Lacasa-Ruiz (2002), regarding *Noguerornis*; Vickers-Rich et al. (2002), concerning *Avimimus*; Xu et al. (2003), confirming a "triradiate" os postorbitale in *Microraptor*.

0081. Os postorbitale, processus postorbitalis, relative to fenestra subtemporalis et os quadratum (lateral perspective), forma:

a. processus postorbitalis parallels os quadratum, fenestra subtemporalis rectangular;

b. processus postorbitalis or os jugale contact os quadratojugale to constrict fenestra subtemporalis;

x. noncomparable by absence of os postorbitale (Neornithes).

Note.—See: Norell et al. (2001: appendix 1, character 10); J. M. Clark et al. (2002a: appendix 2.2, character 5); Xu (2002: suite II, character 59), regarding constriction of fenestra by ossa postorbitale et quadratojugale; Hwang et al. (2004: supplement, character 5); Xu and Norell (2004: supplement, character 5).

0082. Os postorbitale, processus frontalis, intrusion into orbita, status:

a. absent; **b.** present;

x. noncomparable by absence of os postorbitale (Neornithes).

Note.—See: Norell et al. (2001: appendix 1, character 9); J. M. Clark et al. (2002a: appendix 2.2, character 3); Vickers-Rich et al. (2002); Xu (2002: suite II, character 58); Xu et al. (2002a: supplement, character 174); Hwang et al. (2004: supplement, character 3); Xu and Norell (2004: supplement, character 3).

0083. Os postorbitale, processus frontalis, gradus transitus from margo dorsalis orbitae:

a. smooth;

b. abrupt, sharply demarcated from margo orbitalis;

x. noncomparable by absence of os postorbitale (Neornithes).

Note.—See: Currie (1995); Norell et al. (2001: appendix 1, character 45); J. M. Clark et al. (2002a: appendix 2.2, character 45); Vickers-Rich et al. (2002), concerning *Avimimus*; Xu (2002: suite II, character 229); Hwang et al. (2004: supplement, character 44); Xu and Norell (2004: supplement, character 44).

0084. Os postorbitale, processus frontalis, orientation and profile of margo dorsalis as delimited by suturae (lateral perspective), forma:

a. straight, margo dorsalis linear, element perpendicular or cruciate ("T-shaped");

b. curved rostrodorsad, margo dorsalis concave, element subperpendicular (*distorted* "T-shaped");

x. noncomparable by absence of os postorbitale (Neornithes).

Note.—See: J. M. Clark et al. (1994); Currie (1995: appendix, character 10); Xu et al. (1999b: character 89); Holtz (2000 [1998]: appendix I, character 54); Xu et al. (2000: supplement, character 69); Ji et al. (2001), regarding unnamed dromaeosaurid NGMC 91-A; Norell et al. (2001: appendix 1, character 47); J. M. Clark et al. (2002a: appendix 2.2, character 4); Maryanska et al. (2002: appendix 1, character 23), regarding "T-shaped" or "frontal process [of os postorbitale] upturned at about 90 degrees"; Xu (2002: suite II, character 248); Hwang et al. (2004: supplement, character 4); Xu and Norell (2004: supplement, character 4).

0085. Os postorbitale, processus frontalis, eminentia postorbitales (**new term**), status:
a. absent; **b.** present;
x. noncomparable by absence of os postorbitale (Neornithes).
Note.—See: Russell and Dong (1994a–b [1993a–b]); Holtz (2000 [1998]: appendix I, character 47).

0086. Os postorbitale, processus (ventralis) jugalis (**new term**), angulus rostralis (**new term**), status:
a. absent, processus monotonically tapering ventrad;
b. present, processus with small, triangular, rostrally directed "spur" evidently indicative of margo ventralis oculae;
x. noncomparable by absence of os postorbitale (Neornithes).
Note.—See: Sereno et al. (1996: footnote 45); J. D. Harris (1998: appendix 2, character 9); Currie and Carpenter (2000: appendix 1, character 12), regarding "suborbital flange"; Holtz (2000 [1998]: appendix I, character 53); Rauhut (2003: character 40).

0087. Os postorbitale, processus (ventralis) jugalis (**new term**), status:
a. absent; **b.** present;
x. noncomparable by absence of os postorbitale (Neornithes).
Note.—See: Sereno et al. (1996: footnote 45, character 49).

0088. Os postorbitale, processus (ventralis) jugalis (**new term**), ventral extent relative to margo ventralis of orbita, situs dorsoventralis:
a. dorsal; **b.** ventral;
x. noncomparable by absence of os postorbitale (Neornithes).
Note.—See: J. D. Harris (1998: appendix 2, character 7); Azuma and Currie (2000: appendix 1, character 89); Currie and Carpenter (2000: appendix 1, character 10); Holtz (2000 [1998]: appendix I, character 49); Xu et al. (2002a: supplement, character 3).

0089. Os postorbitale (lateral perspective), processus (ventralis) jugalis (**new term**), forma:
a. essentially straight;
b. curves craniodorsally with margo dorsalis concave;
x. noncomparable by absence of os postorbitale (Neornithes).
Note.—See: Ericson (1997: table 2, character 4); Xu et al. (2002a: supplement, character 193), in relation to shape of "anterior [frontal] process."

Os Orbitosphenoidale

0090. Os orbitosphenoidale, status definitivum:
a. present and distinguishable;
b. absent or indistinguishable, accompanied by expansion of os laterosphenoidale to become major latero-rostral component of calvaria, especially paries caudalis of the orbita.
Note.—See: Russell and Dong (1994a [1993a]: table 2, character 9); Holtz (2000 [1998]: appendix I, character 85). Where not discernable, an occult vestigium of os orbitosphenoidale may persist, obscured by the mediodorsal synostosis of os laterosphenoidale with os orbitosphenoidale early in ontogeny (Jollie 1957). Seldom discernable in adult Neornithes, Baumel and Witmer (1993: annotation 88) state that os laterosphenoidale (orbitosphenoidale of Jollie 1957) forms much of the ventral part of paries caudalis orbitalis, extending laterally from the septum interorbitalis (where perforated by nervi cranii II, III, IV, and VI) to the fossa musculorum temporalium, processus postorbitalis, and cavitas tympanicus. De Beer (1937) inferred os orbitosphenoidale to be absent in *Apteryx*, all ossification of the ethmoid region of the skull being derived solely by os mesethmoidale. Synonymy of os laterosphenoidale with os orbitosphenoidale unusual in that two primordia are distinguished in early embryogenesis (Jollie 1957; Goodrich 1958; H. J. Müller 1963; Hogg 1978), both uniting by synostosis with os mesethmoidale.

Os Laterosphenoidale (Pleurosphenoidale)

Note.—Variably prominent impressiones musculorum characterize the externum cranii, especially ossa laterosphenoidale, squamosum, frontale, et parietale. Much of the phylogenetically meaningful variation is manifested only through myological dissections (Zusi and Livezey 2000), and accordingly are treated herein under the respective musculi. Features so treated include impressio origii m. pseudotemporalis superficialis (**new term**), impressio origii m. cucullaris capitus, membrana temporalis (**new term**), et impressio origii m. adductor mandibulae externus, pars coronoideus (**new term**).

Of special interest is the status and extent of the fossa subtemporalis, a feature that, if present, is situated ventrad or caudal to fossa musculorum temporalium and rostral to fossa m. depressor mandibulae (Zusi and Livezey 2000). Prominent impressiones characteristic of some taxa—e.g., Gaviiformes, many Procellariiformes, Sphenisciformes, Podicipediformes—were treated elsewhere (Dullemeijer 1951a–c, 1952; Davids 1952; Den Boer 1953a–b; Bas 1954, 1955a–b; Burggraaf 1954; Burggraaf and Fuchs 1954, 1955; A. Fuchs 1954a–b, 1955; Fujioka 1963; Van der Klaauw 1963). See: Cracraft (1982: series 1, character 2); Cracraft (1985: character 48), pertaining to semihorizontal surface dorsal to cotyla articularis quadrati; Cracraft (1988: series X, character 2), as uniting loons, grebes, and penguins; Coria and Currie (2002: appendix 1, character 8), termed "temporal fossa" of Tyrannosauridae. Variation detected in "tuberculum pseudotemporale," attributed by Baumel and Witmer (1993) to some finches, was not pertinent to higher-level relationships of Aves.

0091. Ossa laterosphenoidale et frontale, facies orbitalis, impressio glandulae nasalis, status et forma (**ordered**):

a. absent or obsolete; **b.** present, distinct;

c. present, prominent.

Note.—This feature of ventrum orbitae co-occurs with fossa glandulae nasalis on facies dorsalis facialis in some taxa. In some taxa assigned "prominence" there occur osseous enclosures accommodating the glandulae in rostrodorsum orbitae.

See: Technau (1936); Siegel-Causey (1990); Bourdon et al. (2005: appendix 1, character 39); Bourdon (2006: supplement, character 98).

0092. Os laterosphenoidale, facies orbitalis, processus postorbitalis, incorporation of os frontale in processus proprius, status:

a. present, processus primarily or entirely derived from os frontale;

b. absent or limited to minor dorsal flange at base of processus;

x. noncomparable by absence of processus postorbitalis (*Apteryx*, *Phodilus*, *Strix*, *Steatornis*, *Nyctibius*, Podargidae, Aegothelidae) or lack of juveniles (*Phalacrocorax*).

Note.—Tinamiformes are variable, in some genera os frontale composes entire facies lateralis processi, with os laterosphenoidale comprising facies medialis and apex processi. Many taxa indeterminate because assessment requires juvenile specimens, including especially critical Anhingidae. Superficially similar feature in Strigiformes, and involvement of os squamosum in the processus significant in some Anseriformes.

See: H. J. Müller (1963); Houde (1988: table 27, character 18); Chatterjee (1991, 1999: character 12).

0093. Os laterosphenoidale, facies orbitalis, processus postorbitalis, status (**unordered**):

a. prominent;

b. reduced to small tuberculum; **c.** absent.

Note.—Baumel and Witmer (1993: 71) stated that os squamosum contributes to processus in "some galliforms," but we see no evidence of this involvement in the processus proprius. Os laterosphenoidale composes much or all of the processus among Aves, and the basis processi is close or adjacent to the sutura laterospheno-squamosa in many avian taxa.

See: Cracraft (1985: character 16); Siegel-Causey (1988: characters 5–6); Chatterjee (1991, 1999: character 12); Ericson (1997: table 1, character 2); Siegel-Causey (1997: table I, character 13).

0094. Os laterosphenoidale, facies orbitalis, processus postorbitalis, ventral extent (lateral view) relative to cotyla quadratica otici et squamosi (**unordered**):

a. dorsal; **b.** approximately equal;

c. distinctly ventral;

x. noncomparable, processus lacking (*Apteryx*, Phalacrocoracidae).

Note.—Processus includes variable contributions from ossa frontalis et squamosum in some groups (coded separately). See: Livezey (1998b: appendix A, character 74); Hughes (2000: appendix 2, character 5), who attributed processus to os squamosum in Cuculiformes.

0095. Os laterosphenoidale, facies orbitalis, processus postorbitalis, orientation relative to margo dorsalis (lateral view) orbitae (**ordered**):

a. diagonal to perpendicular, angulus 45°–90°;

b. obliquely rostral, angulus subdiagonal (< 45°);

x. noncomparable, processus lacking (*Apteryx*, Anhingidae, Phalacrocoracidae).

Note.—Processus includes variable contributions from ossa frontalis et squamosum in some groups (coded separately).

0096. Os laterosphenoidale, facies orbitalis, processus postorbitalis (if present), lateromedially broad and rostrocaudally compressed, forming variably extensive, rostrally concave, paries caudalis orbitae, status:

a. absent; **b.** present;

x. noncomparable, processus lacking (*Apteryx*, Phalacrocoracidae).

Note.—See: G. Mayr et al. (2003: appendix 1, character 11); G. Mayr (2004d: appendix I, character 4); G. Mayr (2005a: appendix 1, character 4).

0097. Os laterosphenoidale, facies orbitalis, processus postorbitalis (if present), tendines et/aut aponeuroses ossificantes from terminus processi toward arcus jugalis, status:

a. absent; **b.** present;

x. noncomparable, processus lacking (*Apteryx*, Phalacrocoracidae).

Note.—See: Prum (1988: character 1), regarding variation in the "post-orbital ligament" among Rhamphastoidea; G. Mayr (2004d: appendix I, character 4); G. Mayr (2005a: appendix 1, character 4).

0098. Os laterosphenoidale, facies orbitalis, processus postorbitalis (if present), synostosis distalis of aponeuroses ossificantes with os squamosum, processus zygomaticus, status (**ordered**):

a. absent;

b. present, synostosis confined to apex processi;

c. present, synostosis along margo caudoventralis processi;

x. noncomparable, processus lacking (*Apteryx*, Phalacrocoracidae).

Note.—The processus postorbitalis of Anseriformes, termed the "processus sphenotemporalis" by Dzerzhinsky (1982, 1995), assumes an extended role as ancora origii musculorum arising from the processus zygomaticus or homologous locus on os squamosum (Zusi and Livezey 2000). Typical waterfowl (Anseranatidae and Anatidae) resemble Anhimidae but aponeuroses fail to ossify; this confounding factor may also pertain to Megapodiidae and Numididae. See: Holdaway (1991: appendix 5.1, character 15); Weber (1996); Ericson (1997: table 1, character 3); K. Lee et al. (1997: appendix 1, character 53); Livezey (1997a: appendix 1, character 8; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, character 75); Rotthowe and Starck (1998: appendix, character 19); detailed description by Zusi and Livezey (2000); Dyke et al. (2003: appendix 1, character 19).

0099. Os laterosphenoidale, facies orbitalis, processus postorbitalis (if present), synostosis with os exoccipitale, closely caudal to processus zygomaticus, by rostrocaudally oriented, densely ossified arcus parameaticus (**new term**) possessing ventrally directed tuberculum at approximate midpoint, status:

a. absent; **b.** present.

Note.—Possible homology with other unions between processus zygomaticus et processus postorbitalis, many distinctly aponeurotic in nature (e.g., Galliformes), not ascertained by dissection.

0100. Os laterosphenoidale, facies tecti mesencephali, sulcus nervus ophthalmici, dorsal closure by osseus lamina, status principalis:

a. present, closure by variably extensive pons separated from foramen n. ophthalmici by sulcus or forming a cuniculus continuous from foramen n. ophthalmici for a significant distance caudomediad;

b. absent, sulcus completely exposed (open) from foramen inward or closure limited to short arcus on facies internum foraminis n. ophthalmici.

Note.—Basal polarity problematic *a priori*.

0101. Ossa laterosphenoidale et proötica, facies lateralis, fonticulus laterospheno-proötica (**new term**), status:

a. absent;

b. present, a distinct fonticulus dorsocaudal to foramen nervi maxillomandibularis and at least approximating latter in diameter.

Note.—As in other fonticulae, this is closed by membrana *in vivo*. Not to be confused with foramina associated with nervus maxillomandibularis or recessus tympanicus dorsalis. See: Chu (1998: appendix 1, characters 11 and 14), ostia reversed.

0102. Ossa laterosphenoidale et/aut proöticum, facies tecti mesencephali, fossa ganglii trigemini, ostium externum ganglii trigemini, situs relative to foramen vena cerebralis medialis:

a. through common foramen with ganglii trigemini;

b. through separate foramen rostrodorsal to ostium externum ganglii trigemini.

Note.—See: Rauhut (2003: character 61). Apomorphic state (separate foramen) occurs in two adjacent positions (Barsbold 1977; Currie 1985): in sutura proötica-laterosphenoidalis (e.g., *Dromaeosaurus*) or entirely enclosed within adjacent part of os laterosphenoidale (e.g., *Troödon*, Oviraptorosauria).

Os Basisphenoidale

0103. Os basisphenoidale, facies cerebralis, sella turcica, angulus with respect to solum cranii, approximated by axis majoris sellae aut dorsum sellae:

a. essentially perpendicular to the planum of rostrum parasphenoidalis, enclosing a vertically oriented fossa hypophysialis;

b. defining a shallow, acute angulus with the planum of rostrum parasphenoidalis, approaching horizontality, with solum fossae hypophysialis well caudoventral to the cranial margin of dorsum sellae.

Os Parasphenoidale

0104. Os parasphenoidale, rostrum parasphenoidale, status generalis et pneumaticus:

a. rostrum absent, homologue a thin osseous platus, ventrum of which often with sulcus longitudinalis;

b. rostrum present, subconical, and pneumatic.

Note.—Rostal portion of rostrum parasphenoidale forms basis of "cultriform process" (Romer 1956). See: Osmólska et al. (1972); Barsbold (1974); J. M. Clark et al. (1994); Holtz (1994a: appendix 1, character 60); Pérez-Moreno et al. (1994: legend for fig. 3, character 11); Russell and Dong (1994b [1993a]: troödontid character 1); Sues (1997: appendix 1, character 8); Forster et al. (1998: supplement, character 18); Xu et al. (1999a: character 14); Xu et al. (1999b: character 16); Holtz (2000 [1998]: appendix I, character 98); Norell et al. (2000: appendix 1, character 8); Xu et al. (2000: supplement, character 12); Norell et al. (2001: appendix 1, character 19); J. M. Clark et al. (2002a: appendix 2.2, character 11); Maryanska et al. (2002: appendix 1, character 51); Vickers-Rich et al. (2002), concerning *Avimimus*; Xu (2002: suite II, character 64); Xu et al. (2002a: supplement, character 9); Rauhut (2003: character 62); Hwang et al. (2004: supplement, character 11); Xu and Norell (2004: supplement, character 11).

0105. Os parasphenoidale, rostrum parasphenoidale, facies ventralis, angulus rostralis, forma:

a. horizontal or rostrodorsal;

b. rostroventral.

Note.—See: Ericson (1997: table 2, character 6); Maryanska et al. (2002: appendix 1, character 52).

0106. Os parasphenoidale, rostrum parasphenoidale—extension caudad to include lamina basisphenoidalis, facies ventralis—medial carina parasphenoidalis (**new term**) defined by depressiones bilaterales, status:

a. absent; **b.** present.

Note.—Similar, perhaps homologous, in part, with "cultriform process" of nonavian Reptilia, described by Romer (1956: 65) as "a slender rostrum of dermal bone, . . . V-shaped in section, extends forward beneath the anterior part of the braincase between the interpterygoid vacuities." See: Shufeldt (1902a: pls. ii and vi); Bourdon et al. (2005: appendix 1, character 37); Bourdon (2006: supplement, character 103).

0107. Os parasphenoidale, rostrum parasphenoidale, terminus of semicylindrical portion, rostral extent relative to those of orbita et septum nasi osseum, forma:

a. former caudal to margo rostralis orbitae;

b. former well rostral to orbita and contributing to margo ventralis of septum nasi osseum.

Note.—Cranial extent of rostrum parasphenoidale, treated here, evidently unassociated with form, including status of "cultriform process."

Processus basipterygoideus

Note.—Composition considered to include os(sa) parasphenoidale et/aut basisphenoidale.

0108. Processus basipterygoideus, status definitivum (**ordered**):

a. absent;

b. present, contributing to articulatio pterygobasipterygoidea (pterygo-rostroparasphenoidalis);

c. vestigial and nonfunctional, including where processus functional in early ontogeny but secondarily, chondroclastically reduced.

Note.—Incomplete representation of developmental series likely resulted in underestimation of secondary reductions. Outgroup and ontogenetic information (Goldschmid 1972a–d; D. Starck 1989; Weber 1993; Zusi and Livezey 2006) indicate processus plesiomorphic for Neornithes, subsequent retention and parallel reduction being complex. Present in early developmental stages but lost in adults in some taxa (e.g., Spheniscidae). We reject the controversial hypothesis that the comparatively rostral processes of Galloanseres—"processus rostropterygoideus" (Baumel and Raikow 1993: annotation 27)—are not homologous with the processes basipterygoidea of other Neornithes (Gaupp 1902; Böhm 1930; Stresemann 1934; D. Starck 1940; Hofer 1945; Cracraft 1988; Weber 1993; Dzerzhinsky 1995; Ericson 1996; J. A. Clarke 2004). J. A. Clarke (2004: appendix 1, characters 19–20) distinguished the two elemental (palatal and cranial) counterparts—tuberculum ossis pterygoideum (processus "basipterygoideus") from tuberculum ossis basi(para)sphenoidale (processus "basisphenoidalis"). Positional information represented by the variation is included with respect to situs of articulation of basipterygoideus.

See: Ligon (1967: table 1); Ostrom (1969, 1978); Cracraft (1974: cranial character 4); S. L. Olson and Feduccia (1980a: table 1, character 6); Cracraft (1981a: 694); Cracraft (1986: appendix, characters 44–45); Livezey (1986: appendix 1, character 20); Witmer and Martin (1987: character 8); Cracraft (1988: series V, character 2); Cracraft (1988: series VII, character 2); Houde (1988: table 27, character 7); Cracraft and Mindell (1989: table 1, characters 13 and 28); Livezey (1989: table 1, character 20); Holdaway (1991: appendix 5.1, character 18); Andors (1992: table 2, character 12); Weber (1993: table 1); Russell and Dong (1994a [1993a]: table 2, character 11, part); Sereno et al. (1994: footnote 12); Elzanowski (1995: character N'10); Elzanowski and Wellnhofer (1996: 86); Ericson (1996: character 2); Sereno et al. (1996: footnote 45, character 41); Ericson (1997: table 1, character 7); Livezey (1997a: appendix 1, character 7; *corrigenda*, Livezey 1998a); Sues (1997: appendix 1, character 10); J. D. Harris (1998: appendix 2, character 28); Livezey (1998b: appendix A, character 76); Makovicky and Sues (1998: appendix 1, character 15); Rotthowe and Starck (1998: appendix, character 24); Xu et al. (1999a: character 16); Currie and Carpenter (2000: appendix 1, character 30); Holtz (2000 [1998]: appendix 2, character 30); Cracraft and Clarke 2001: appendix 2, character 33); Currie and Chen (2001); Norell and Clarke (2001: appendix I, characters 19 [basisphenoid plate], 20 [processus], 21 [position], and 22 [orientation]), treated similarly by J. A. Clarke (2002: appendix I, character 19), J. A. Clarke and Norell (2002: appendix 2, character 19), and J. A. Clarke (2004: appendix 1, character 19); Norell et al. (2001: appendix 1, character 21); J. M. Clark et al. (2002a: appendix 2.2, character 13); J. A. Clarke (2002); Maryanska et al. (2002: appendix 1, characters 58 [typus rostralis], and 56 and 69 [situs articularis]; G. Mayr (2002a: appendix 1, character 1), with respect to Caprimulgiformes; Vickers-Rich et al. (2002), concerning *Avimimus*; Xu (2002: suite I, character 30; suite II, character 66); Xu et al. (2002a: supplement, characters 10–12), respectively orientation, prominence, and solidity; Xu et al. (2002b); Zhou and Zhang (2002: appendix III, character 19 [forma caudalis processi, citing os basisphenoidale], 20 [typus rostralis], 21–22 [articulatio]); G. Mayr (2003a: appendix I, character 13); G. Mayr (2003b: appendix I, character 5); G. Mayr and Clarke (2003: appendix A, characters 23–24); Dyke and van Tuinen (2004: appendix 1, character 16); G. Mayr (2004a: appendix 1, characters 12–13); G. Mayr (2004b: appendix 1, character 12); G. Mayr and Ericson (2004: appendix I, character 15); Hwang et al. (2004: supplement, character 13); Xu and Norell (2004: supplement, character 13); Ji et al. (2005: supplement, part I, character 19); G. Mayr (2005b: appendix A, character 1).

0109. Processus basipterygoideus, situs relative to axis majoris ossis pterygoidei (**ordered**):

a. caudal one-third; **b.** middle one-third;

c. rostral one-third;

d. extremely rostral, approximately at terminus rostralis pterygoidei.

Note.—Position of processus primary rationale for discounted view that comparatively rostral processus basipterygoideus of Galloanseres is not homologous to those of other Neornithes (see above). See: J. A. Clarke (2004: appendix 1, character 21); Ji et al. (2005: supplement, part I, character 21).

0110. Processus basipterygoideus, separation of processes by incisura from margo caudoventralis suturae exoccipto-parasphenoidalis et synchondrosis basispheno-parasphenoidalis, status:

a. absent; **b.** present.

Note.—Evidently refers to the external topography of synchondrosis basispheno-opisthotico-exoccipitalis (**new term**) and associated elemental composition of processes, at least among Aves. Bilateral tuberculae at the rostrolateral vertices of os basisphenoidale, composed of os basisphenoidale alone, are enclosed during development by os parasphenoidale, lamina parasphenoidalis, a trend reflected in definitive states (Pycraft 1902; Saiff 1974; Witmer 1990).

See: Sereno and Novas (1992: appendix, character 9); Sereno et al. (1994: footnote 12); Sereno et al. (1996: footnote 45, character 44); J. D. Harris (1998: appendix 2, character 25); Azuma and Currie (2000: appendix 1, character 11); Currie and Carpenter (2000: appendix 1, character 24); Holtz (2000 [1998]: appendix I, characters 96 and 99).

0111. Processus basipterygoideus, basis processi, forma:

a. subsessile; **b.** pedicellate.

Note.—See (many confounded with concavitas faciei articularis): Livezey (1986: appendix 1, character 20); Andors (1992: table 2, character 13); Livezey (1997a: appendix 1, character 7; *corrigenda*, Livezey 1998a); Sues (1997); Makovicky and Sues (1998); J. A. Clarke (2002: appendix I, character 20); Maryanska et al. (2002: appendix 1, character 58), in reference to basal Theropoda through avialians; Vickers-Rich et al. (2002), concerning *Avimimus*; Xu (2002: suite II, character 241); Zhou and Zhang (2002: appendix III, character 23), regarding *Jeholornis*; G. Mayr and Clarke (2003: appendix A, character 24); Rauhut (2003: character 58); J. A. Clarke (2004: appendix 1, character 20); G. Mayr (2004a: appendix 1, character 13); Ji et al. (2005: supplement, part I, character 20).

0112. Processus basipterygoideus, principal orientation with respect to rostrum parasphenoidale, forma:

a. rostroventral; **b.** lateroventral;

c. ventrolateral.

Note.—See: Norell et al. (2001: appendix 1, character 20); J. M. Clark et al. (2002a: appendix 2.2, character 12); Vickers-Rich et al. (2002), concerning *Avimimus*; Xu (2002: suite II, character 65); J. A. Clarke (2004: appendix 1, character 22); Hwang et al. (2004: supplement, character 12); Xu and Norell (2004: supplement, character 12); Ji et al. (2005: supplement, part I, character 22).

0113. Processus basipterygoideus, facies articularis pterygobasipterygoideus, *primary* dorsoventral component of orientation of planum faciei, forma:

a. *ventro*lateral; **b.** *dorso*lateral.

See: J. A. Clarke (2004: appendix 1, character 22).

0114. Processus basipterygoideus, corpus processi, forma interna:

a. solid; **b.** hollow.

Note.—See: Norell et al. (2001: appendix 1, character 22); J. M. Clark et al. (2002a: appendix 2.2, character 14); Xu (2002: suite II, character 67); Hwang et al. (2004: supplement, character 14); Xu and Norell (2004: supplement, character 14).

0115. Processus basipterygoideus, recessus dorsolateralis processi basipterygoidei (**new term**), status definitivum:

a. absent; **b.** present.

Note.—See: Norell et al. (2001: appendix 1, character 16); J. M. Clark et al. (2002a: appendix 2.2, character 15); Vickers-Rich et al. (2002), for *Avimimus*; Xu (2002: suite II, character 241); Xu et al. (2002a: supplement, character 186); Hwang et al. (2004: supplement, character 15); Xu and Norell (2004: supplement, character 15).

Lamina parasphenoidalis (basisphenoidalis)

0116. Os parasphenoidale, lamina parasphenoidalis (basisphenoidalis), rostral portion extensive and completely free of overlying bone (presumed to be os basisphenoidale), and underlying a dorsal spatium, status:

a. absent; **b.** present.

Note.—See: Payne and Risley (1976: character 13), regarding status of "basitemporal ridge" of Ardeidae.

0117. Os parasphenoidale, lamina parasphenoidalis (basisphenoidalis), forma:

a. flat, laminar, and neither distinctly pneumatic nor broad;

b. rounded, "inflated," and broad.

Note.—See: Cracraft (1988); Ericson (1996); Cracraft and Clarke (2001: appendix 2, character 34); Dyke et al. (2003: appendix 1, character 7). Another feature in this region, averred to be interdependent from the present character by Ericson (1996), but considered distinct by Cracraft (1988), is a depressio with enclosed foramina neurovascularia (Cracraft and Clarke 2001: appendix 2, character 35); G. Mayr (2004a: appendix 1, character 16); G. Mayr (2004b: appendix 1, character 15); Bourdon et al. (2005: appendix 1, character 25).

0118. Os parasphenoidale, lamina parasphenoidalis, ala parasphenoidalis, continuity as broad, slightly concave, sloping planum with os exoccipitale, processus paroccipitalis, and demarcated medially by conspicuous carina from lamina basiparasphenoidalis, status:

a. absent; **b.** present.

Note.—See: D. W. Thompson (1899).

0119. Os parasphenoidale, lamina parasphenoidalis, ala parasphenoidalis ("os aliparasphenoidale"), covering recessus tympanicus rostralis, status:

a. absent; **b.** present.

Note.—See: Chatterjee (1991: character 13), but excluded by Chatterjee (1999: entry 11); Chiappe (1999); Cracraft and Clarke (2001: appendix 2, character 13), in terms of "ala parasphenoidalis is inflated by the rostral tympanic diverticulum" and credited to revision of Cracraft (1986) by Witmer (1990: 372, characters 7 and 17).

0120. Os parasphenoidale, ala parasphenoidalis, fossa parabasalis, crista fossae parabasalis, status et forma (**ordered**):

a. absent, resulting in hiatus subtympanicus;

b. present, pons incomplete or fibriform;

c. present, pons comparatively robust but not cristate or lateromedially compressed;

d. present, prominent, lateromedially compressed crista.

Note.—May include components of os exoccipitale. See: Elzanowski (1991: table 3), Elzanowski and Galton (1991: character 6), and Elzanowski (1995: character Nb'1), with respect to "spheno-occipital jugamentum"; Livezey (1997a: appendix 1, character 2; *corrigenda*, Livezey 1998a); Chu (1998: appendix 1, character 6), regarding larids; Hughes (2000: appendix 2, character 36), in reference to "barlike process between ostium canalis carotici and lamina basiparasphenoidalis"; Dyke (2001b: appendix 1, character 2).

0121. Os parasphenoidale, processus lateralis parasphenoidalis, anulus tympanicus, status:

a. absent; **b.** present.

Note.—This circular osseus enclosure of meatus acusticus externa (lateral view), which includes dense, moderate, lateral extension of os parasphenoidale, is not considered homologous with osseus enclosures of meatus in other Neornithes (e.g., Strigiformes, Caprimulgiformes). See: Livezey (1997a: appendix 1, character 4; *corrigenda*, Livezey 1998a).

0122. Os parasphenoidale, lamina parasphenoidalis, ala parasphenoidalis, processus lateralis parasphenoidalis, status et forma (**ordered**):

a. obsolete; **b.** moderately developed;

c. prominent;

x. noncomparable (Caprimulgiformes exclusive of Steatornithidae).

Note.—Involved in lateral of two tuberculae basilares et articulationes mandibulosphenoidales—termed "lateral basitemporal process" by Bock (1960b)—typically positioned at terminus rostralis pontis aut jugamentae. See: S. F. Simpson and Cracraft (1981: character 15), regarding reduction or loss of "basitemporal processes" in "Picoidea"; Strauch (1985: character 4), for assessment of Alcidae; Chu (1998: appendix 1, character 17), for larids; Livezey (1998b: appendix A, character 77), regarding Gruiformes; Bourdon et al. (2005: appendix 1, characters 25–26).

0123. Os parasphenoidale, lamina parasphenoidalis, tuberculum basilare, processus medialis parasphenoidalis, status:

a. absent or obsolete; **b.** present, distinct.

Note.—Apparently involved in medial of two possible articulationes mandibulosphenoidales—termed "medial basitemporal process" by Bock (1960b)—*contra* implication of nomenclatural list by Baumel and Witmer (1993). Tuberculum basilare, typically derived from os basioccipitale et/aut basisphenoidae, may correspond instead with crista transversa basilaris. See: K. Lee et al. (1997: appendix 1, character 56); Livezey (1998b: appendix A, character 78); Hughes (2000: appendix 2, character 43); G. Mayr and Clarke (2003: appendix A, character 30), with whom we differed regarding taxonomic assignments; Dyke and van Tuinen (2004: appendix 1, character 18); G. Mayr (2004a: appendix 1, character 18), who included Procellaridae and Oceanitidae as apomorphic.

0124. Os parasphenoidale, lamina parasphenoidalis, canalis caroticus cranialis, ossification caudal to lateral divergence of ramus palatinus and arteria sphenoidea, forma (**ordered**):

a. complete, canalis forming entire, osseus tuba;

b. incomplete, canalis forming irregularly ossified, partly open tuba;

c. lacking, canalis not indicated by ossified remains in this portion.

Note.—If "canalis" restricted to ossified structures, state "c" reverts to "absent." See: Saiff (1974, 1976, 1978, 1988); Chu (1998: appendix 1, character 16); Bourdon et al. (2005: appendix 1, characters 33–34).

0125. Os parasphenoidale, lamina parasphenoidalis, foramen(ina) aut sulcoid ostium for arteria sphenoidea, rami palatinus et sphenomaxillaris, numerus modalis:

a. two distinct foramina;

b. one distinct foramen;

c. one elongate sulcus, enclosing ostia efferens caudalis et afferens rostralis for arteria carotis cerebralis;

x. noncomparable (*Diomedea*, *Fregata*, *Scopus, Sula*).

Note.—Nomina (Baumel et al. 1993) evidently considers this opening or openings under singular term "foramen orbitale" (p. 427). Rostrum parasphenoidale, canalis orbitalis transmits ramus carotis, arteria sphenoidea.

0126. Os parasphenoidale, tuba auditiva (pharyngotympanica) communis, facies rostroventralis, forma definitivum (**ordered**):

a. ostia widely separated and poorly delimited, completely membranous (open for entire length in fossils or prepared neoskeletal specimens);

b. ostia moderately separated, canalis enclosed, completely osseous;

c. ostia closely approach axis medialis cranii, partly membranous or wholly osseous.

Note.—Bilateral tubae converge mediorostrad from ostia tympanica along margines rostrolaterales of lamina parasphenoidalis to form tuba communis and ostium pharyngeale at vertex of basis rostri parasphenoidalis. Evidently also equivalent to "naked, canal, or tunnel" formation of "eustachian tube" of Saiff (1988: table 1), compiled largely from previous ordinal studies (Saiff 1974, 1976, 1978, 1981, 1982, 1983, 1988).

See: H. J. Müller (1961a), regarding ontogeny of ratites; Cracraft (1974); Harrison and Walker (1976b, pl. i, fig. b); Cracraft (1985: character 15); Cracraft (1986: appendix, characters 56–58); Cracraft (1988: series IV, character 4; series V, character 7; series VI, character 7); Siegel-Causey (1988: character 25); Cracraft and Mindell (1989: table 1, character 4); Elzanowski (1995: character Nb'3); Siegel-Causey (1997: table I, character 7), in reference to "bony eustachian tubes"; Rotthowe and Starck (1998: appendix, characters 5 and 12); J. A. Clarke and Chiappe (2001: character 59); Cracraft and Clarke (2001: appendix 2, characters 11–12); Norell and Clarke (2001: appendix I, characters 27–28), proximity of ostia and ossification, respectively, of "eustachian tubes"; J. A. Clarke (2002: characters 27–28); J. A. Clarke and Norell (2002: appendix 2, characters 27–28); Zhou and Zhang (2002: appendix III, characters 27 [number and orientation] and 28 [ossification]); G. Mayr and Clarke (2003: appendix A, characters 28–29), treating ossification and ostium(a) medialis(es) for tubae bilaterales, respectively; J. A. Clarke (2004: appendix 1, characters 27–28); Dyke and van Tuinen (2004: appendix 1, character 17); Bourdon et al. (2005: appendix 1, character 27); Ji et al. (2005: supplement, part I, characters 27–28).

0127. Os parasphenoidale, tuba auditiva, ostium tympanicum, lateral delimitation by depressio subostium auditivum (**new term**), status:

a. absent; **b.** present.

Note.—See: Makovicky and Sues (1998: appendix 1, character 16); Holtz (2000 [1998]: appendix I, character 89); Xu et al. (2002a: supplement, character 5); G. Mayr (2004a: appendix 1, character 17).

Processus paroccipitalis

Note.—Processus paroccipitalis—synonymous with processus paroticus, ala post-tympanica, processus occipitalis lateralis, processus opithoticus, and processus exoccipitalis—is a complexus comprising three otic elements—ossa opisthoticum (medially), metoticum (laterally), and exoccipitale (caudolaterally)—with variable contributions from os parasphenoidale.

0128. Processus paroccipitalis, extension processi into variably complete enclosure of caudal, lateral, and/or ventral aspects of meatus acusticus externus, so as to typically obscure os quadratum dorsal to processus mandibularis (caudal perspective), status et forma (**unordered**):

a. absent, or at most represented by narrow ventrolateral rimming;

b. present, a variably extensive cubiculum, attaining an extreme level of rostral development in *Cyanoramphus* wherein the lamina reaches the processus zygomaticus;

c. present, a bilobate, rostrally concave lamina;

d. present, a rounded, rostrally concave lamina including a laterally broad, ventral floor that is entire or encloses narrow incisura;

e. present, an angular, rostrally concave lamina, in extreme cases including narrow, ventral union with cranium and forming lateromedially compressed capsula;

x. noncomparable by position of processus oticus quadrati (Pelecaniformes, *Balaeniceps*).

Note.—Evidently derived from elaborations of os exoccipitale; lesser contributions of ossa opisthotica (medially), metotica (laterally), and possibly parasphenoidale (ventrally) and os squamosum (dorsally). Caudal, dorsal, and ventral components of the enclosures may correspond ontogenetically to the alae caudalis, dorsalis, et ventralis of ala tympanica.

See: D. W. Thompson (1899), regarding parrots; Andors (1992: table 2, character 8); Livezey (1997a: appendix 1, character 3; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, characters 83 and 88); Hughes (2000: appendix 2, characters 31–32), regarding possibly related characters; J. A. Clarke and Chiappe (2001: character 71); Dyke (2001b: appendix 1, character 3); Xu et al. (2002a: supplement, characters 44–45).

0129. Processus paroccipitalis, pronounced ventral enlargement and lateral broadening processi, with margo lateralis of processus rounded or truncate, forming continuous and curving with margo dorsalis of processus zygomaticus, and defining margo lateralis of meatus acusticus externus, status:

a. present; **b.** absent.

Note.—See: Rotthowe and Starck (1998: appendix, character 28); G. Mayr et al. (2003: appendix 1, character 13).

0130. Processus paroccipitalis et lamina parasphenoidalis, margo(ines) ventrolateralis, forma:

a. separated by incisura marginalis, facies ventralis of processus paroccipitalis comparatively proximate to fossa parabasalis;

b. comparatively extensive laterocaudad and without incisura marginalis, resulting in caudolateral expanse of lamina between processus paroccipitalis and fossa parabasalis and comparatively deep solum ventralis of ostium recessi pneumatici rostralis.

Note.—Hemiprocnidae and Apodidae variably intermediate.

0131. Processus paroccipitalis, margo dorsalis processi, forma:

a. straight;

b. manifesting apparent rostrolateral torsion distad;

x. noncomparable (Neornithes).

Note.—See: Currie (1995); Holtz (2000 [1998]: appendix I, character 87), who delimited caudal, dorsal, and ventral "twists"; Norell et al. (2001: appendix 1, character 61); J. M. Clark et al. (2002a: appendix 2.2, character 60); Vickers-Rich et al. (2002), concerning *Avimimus*; Xu (2002: suite II, character 243); Xu et al. (2002a: supplement, character 188), who discriminated "straight" from "rostrolaterally twisting of the dorsal margins" of the processus; Hwang et al. (2004: supplement, character 59); Xu and Norell (2004: supplement, character 59).

0132. Processus paroccipitalis, terminalis processi, forma *sensu* orientation (**ordered**):

a. laterally or dorsally inflected;

b. ventrolaterally deflected to variable, moderate degree;

c. strongly ventrolateral, terminus entirely ventral to foramen magnum;

d. essentially caudal.

Note.—Anhimidae, Anseranatidae, and Dromornithiformes were oriented strictly diagonally to planum transversum cranii, and *Anseranas* and Dromornithiformes were also similar in laminar aspect; Anatidae were slightly more dorsal in orientation.

See: Davids (1952); Colbert and Russell (1969); L. P. Richards and Bock (1973); R. Johnson (1984); Cracraft (1985: character 17); Paul (1988); Witmer (1990); Currie and Zhao (1994a–b [1993a–b]); Currie (1995: appendix, character 14); Livezey (1997a: appendix 1, character 8, fig. 8); Forster et al. (1998: supplement, character 17); J. D. Harris (1998: appendix 2, character 24); Xu et al. (1999b: character 15); Azuma and Currie (2000: appendix 1, character 41); Currie and Carpenter (2000: appendix 1, character 26); Xu et al. (2000: supplement, character 11); Norell et al. (2001: appendix 1, character 60); J. M. Clark et al. (2002a: appendix 2.2, character 59); Maryanska et al. (2002: appendix 1, character 45); Xu (2002: suite II, character 100); Currie et al. (2003: appendix, character 13); G. Mayr (2003a: character 14); Rauhut (2003: character 52); Hwang et al. (2004: supplement, character 58); Xu and Norell (2004: supplement, character 58); Bourdon et al. (2005: appendix 1, character 21).

0133. Processus paroccipitalis, basis processi, margo ventralis, situs dorsoventralis relative to condylus occipitalis:

a. dorsal or parallel to margo dorsalis condylae;

b. ventral or parallel to midpoint condylae.

Note.—See: Rauhut (2003: character 54).

0134. Processus paroccipitalis, caudal elongation and prominent lateromedial compression and terminus distalis processi, status et forma (**unordered**):

a. neither present;

b. both present, without distinct lateral orientation;

c. both present, with distinct lateral orientation.

Note.—See: Cracraft (1985: character 17); Bourdon et al. (2005: appendix 1, character 22).

0135. Processus paroccipitalis, terminus distalis, margines dorsalis et ventralis, forma:

a. elongate, margines approximately parallel;

b. truncate, margines broadly separated, terminus convex.

Note.—See: Bakker et al. (1988); Holtz (1994a: appendix 1, character 68); K. Lee et al. (1997: appendix 1, character 53); Makovicky and Sues (1998:

appendix 1, character 19); Norell et al. (2000: appendix 1, character 18); Norell et al. (2001: appendix 1, character 59); J. M. Clark et al. (2002a: appendix 2.2, character 58); Xu (2002: suite II, character 99); Hwang et al. (2004: supplement, character 57); Xu and Norell (2004: supplement, character 57).

0136. Pneumaticitas processi (e.g., foramina pneumatica), status:
a. absent, processus with "solid" basis;
b. present, processus with "hollow" basis.
Note.—See (including references to "periotic pneumatophores"): Bakker et al. (1988); Holtz (1994a: appendix 1, character 116); Currie (1995: appendix, character 15); Sues (1997: appendix 1, character 14); Xu et al. (1999a: character 19); Xu et al. (1999b: character 93); Azuma and Currie (2000: appendix 1, character 40), in which pneumatization of "paroccipital process" attributed to ossa exoccipitale et opisthoticum; Holtz (2000 [1998]: appendix I, character 86); Norell et al. (2000: appendix 1, character 19), "posterior tympanic recess *invad*[*ing*] body of paroccipital process"; Xu et al. (2000: supplement, character 73); Maryanska et al. (2002: appendix 1, character 46); Currie et al. (2003: appendix, character 2); Rauhut (2003: character 53).

Os Squamosum

0137. Recessus pneumaticus squamosi (Witmer 1997), status:
a. absent; **b.** present.
Note.—See: Holtz (2000 [1998]: appendix I, character 55), regarding "squamosal recess"; Maryanska et al. (2002: appendix 1, character 32); Brochu (2003).

0138. Cotyla quadratica squamosi, facies (margo) ventralis (lateral perspective), situs dorsoventralis relative to rostrum maxillae:
a. essentially level; **b.** projects well ventrad.
Note.—See: Holtz (2000 [1998]: appendix I, character 69).

0139. Cotyla quadratica squamosi, lamina caudolateralis cotylae (**new term**), status:
a. absent; **b.** present.
Note.—See: Sereno and Novas (1992: appendix, character 13); Sereno et al. (1993: legend for fig. 3a); Novas (1994 [1993]: appendix, character 12); Holtz (2000 [1998]: appendix I, character 56), in reference to "squamosal flange covering quadrate head in lateral view"; Xu et al. (2002a: supplement, character 172), also with respect to "posterolateral shelf on squamosal overhanging quadrate head."

0140. Fossa musculorum temporalium, fenestra craniolateralis (lateralis) temporalis (**new term**), delimitation dorsally by os squamosum, ventrally by os quadratojugale, and margo caudalis by fenestra laterotemporalis, forma (**ordered**):
a. fenestra unconstricted dorsally;
b. fenestra profoundly constricted dorsally, "keyhole-shaped" aspect;
c. fenestra constricted subdorsally, presumably by os squamosum.
Note.—See: Holtz (1994b: appendix 7.1, character 4); Currie and Carpenter (2000: appendix 1, character 4); Holtz (2000 [1998]: appendix I, character 57).

0141. Fossa musculorum temporalium, fenestra infratemporalis (**new term**), status et forma (**ordered**):
a. present, large, a true fenestra;
b. rudimentary or vestigial, a foramen or porus;
c. absent.
Note.—See: Sereno and Novas (1992: appendix, characters 6 and 14); Sereno and Novas (1992: appendix, character 7), regarding "taper" and "excavation" of facies lateralis of pars ventralis squamosi (**new term**), possibly related to constriction of fenestra temporalis; Sereno et al. (1993: legend for fig. 3a); Holtz (1994a: appendix 1, character 15), with respect to the "infratemporal fenestra"; Novas (1994 [1993]: appendix, character 11), in reference to caudal of two fenestrae temporales of Diapsida, pars cranialis being fenestra craniolateralis temporalis, citing "post-temporal perforation"; Holtz (2000 [1998]: appendix I, character 62); Maryanska et al. (2002: appendix 1, character 30), relative to form and position of "infratemporal fenestra"; G. Mayr and Ericson (2004: appendix I, character 16).

0142. Processus postorbitalis squamosi, involvement in delimitation of fenestra infratemporalis, pars dorsalis, status:
a. present; **b.** absent;
x. noncomparable by absence of fenestra (Neornithes).
Note.—See: Maryanska et al. (2002: appendix 1, character 31).

0143. Processus suprameaticus, status:
a. absent as distinct processus, in most or all cases the homologous bone evidently continuous as margo rostralis of meatus acusticus externus;
b. present as variably prominent processus, distinctly smaller than processus postorbitalis.
Note.—See: Chu (1998: appendix 1, character 18); Livezey (1998b: appendix A, character 81).

0144. Processus zygomaticus, angulus relative to processus oticus quadrati:
a. parallel; **b.** perpendicular.
Note.—See: Cracraft (1988: series V, character 3); Houde (1988: table 27, character 13); Cracraft and Mindell (1989: table 1, character 14); Cracraft and Clarke (2001: appendix 2, character 10); Norell et al. (2001: appendix 1, character 50); J. M. Clark et al.

(2002a: appendix 2.2, character 49); Xu (2002: suite II, character 92); Xu et al. (2002a: supplement, character 37); Hwang et al. (2004: supplement, character 48); Xu and Norell (2004: supplement, character 48).

0145. Margo ventralis squamosi—comprising lamina supra-zygomatica (**new term**) et processus zygomaticus—elongation, dorsoventral depth, and concealment (lateral perspective) of processus oticus quadrati, status:

a. absent, margo ventralis of os squamosum truncate and narrow, not obscuring os quadratum;

b. present, margo ventralis of os squamosum elongate and broad, obscuring os quadratum.

Note.—Assessed with os quadratum in articulation with pila otica (Kesteven 1942). See: Harrison and Walker (1976a: pl. i, fig. 2); Cracraft (1985: character 48); Elzanowski and Galton (1991: figs. 4D and 7B); Hughes (2000: appendix 2, characters 7–8), regarding variation in shape and concealment within Cuculiformes; Chiappe (2001a: appendix 1, character 12); Norell and Clarke (2001: appendix I, character 29), treated similarly by J. A. Clarke (2002: appendix I, character 29), J. A. Clarke and Norell (2002: appendix 2, character 29), and J. A. Clarke (2004: appendix 1, character 29); Norell et al. (2001: appendix 1, character 51); J. M. Clark et al. (2002a: appendix 2.2, character 51), terming this feature "posterolateral shelf on squamosal"; Xu (2002: suite II, character 227); Zhou and Zhang (2002: appendix III, character 29); Hwang et al. (2004: supplement, character 50); Makovicky and Norell (2004: character 213); Xu and Norell (2004: supplement, characters 50 and 213); Bourdon et al. (2005: appendix 1, characters 14–16); Ji et al. (2005: supplement, part I, character 29).

0146. Processus zygomaticus, status et forma (**ordered**):

a. present, long and stout, in some taxa associated with ventral lamina;

b. present, short, typically longer than processus suprameaticus, blunt or acuminate;

c. present, short and pointed, nearly identical in size and shape to processus suprameaticus;

d. obsolete or absent, although often associated with tendo ossificans;

x. noncomparable (Pelecaniformes, Ardeidae, *Nyctibius*, *Aegotheles*, Caprimulgidae).

Note.—See: Cracraft (1986: appendix, character 47); Siegel-Causey (1988: character 6); Cracraft and Mindell (1989: table 1, character 14); Chatterjee (1991: character 14); Livezey (1998b: appendix A, character 82), reassessment by Zusi and Livezey (2000); Hughes (2000: appendix 2, characters 6 and 8), the latter comparing foramen suprameaticus with length of processus postorbitalis; Norell and Clarke (2001: appendix I, character 29), treated similarly by J. A. Clarke (2002: appendix I, character 29), J. A. Clarke and Norell (2002: appendix 2, character 29); Chiappe (2002: appendix 20.2, character 12); G. Mayr and Clarke (2003: appendix A, character 33); Dyke and van Tuinen (2004: appendix 1, character 21).

0147. Processus zygomaticus, crista ventralis (**new term**), pronounced dorsolateral orientation and tuberculate shape—"pinnaform" aspect relative to cranium—status:

a. absent; **b.** present;

x. noncomparable (Dromornithidae).

Cotylae quadratica squamosi et otici

0148. Cotylae within planum of lamina basiparasphenoidalis, positions as measured by lesser angulus rostralis defined by axis passing through two cotylae relative to axis medialis (**ordered**):

a. axis nearly parallel, angulus less than 20°;

b. axis obliquely oriented, angulus 20–75°;

c. axis approaching perpendicularity, angulus 75–90°.

Note.—Basal polarity inferred *a priori* to be state "b." See: Xu et al. (2002a: supplement, character 40), with respect to inclination of element and resultant relative positions of extremities.

0149. Cotylae within planum normal to that of lamina basiparasphenoidalis, positions as measured by lateral (lesser) angulus defined by axis passing through centers of two cotylae relative to planum laminae basiparasphenoidalis:

a. axis obliquely oriented—i.e., having significant dorsal component in rostrocaudal perspective—angulus > 20°;

b. axis nearly parallel—i.e., transverse in rostrocaudal perspective—angulus ≤ 20°.

0150. Cotylae, numerus modalis et forma (**ordered**):

a. single cotyla apparent, oblong conformation suggesting that facet represents confluence of two cotylae;

b. two cotylae apparent, adjacent or juxtaposed, distance between centers of cotylae less than one-fourth of the maximal distance between the outer margins of the cotylae;

c. two cotylae apparent, moderately separated, distance between centers of cotylae between one-fourth and one-half of the maximal distance between the outer margins of the cotylae;

d. two cotylae apparent, well separated, distance between centers of cotylae greater than one-half of the maximal distance between the outer margins of the cotylae.

0151. Facies externa ossis, caudolateral to cotyla quadratica squamosi, status et forma:

a. absent;

b. present, limitus dorsalis not marked by sulcus muscularis;

c. present, comparatively limited, limitus dorsalis marked by open sulcus muscularis;

d. present, comparatively extensive, limitus dorsalis marked by canaliculus sulcus muscularis.

Note.—In some taxa, area corresponds to os squamosum caudolateral to cotyla quadratica squamosi.

Ossa Cranii, II

Note.—Ossa opisthoticum, proöticum, et metoticum of Neornithes unite early in ontogeny by synostosis, rendering individuation practically impossible in virtually all modern taxa (de Beer and Barrington 1934; Jollie 1957; Sandoval 1964; Toerien 1971; Hogg 1978; Zusi 1993). However, it is clear that these elements participate in a number of basicranial structures, including the recessus tympanicus, cavum tympanicum, processus paroccipitalis, and foramen magnum. Practically impossible to assess are synchondroses exoccipito-proötica et proötico-supraoccipitalis, among the first to close during ontogeny.

Os metoticum is a neomorph distinguishable in embryos of birds and perhaps other Archosauria (de Beer and Barrington 1934: 84; Baumel and Witmer 1993: 84). Status of foramina or canalicula neurovascularia in os metoticum—considered by Saiff (1988: table 1) to pertain to "vascular notches or canal in metotic process"—Chatterjee (1991: character 1), Siegel-Causey (1997: table I, character 1), Chatterjee (1999: entry 9), and Norell et al. (2000: appendix 1, character 13)—was deemed unreliable.

Os Proöticum

0152. Os proöticum, ala rostroventralis (**new term**), status:

a. present; **b.** absent.

Note.—See: Elzanowski and Wellnhofer (1996).

0153. Os proöticum, fossa ganglii trigemini, foramen n. trigeminus et canalis n. maxillomandibularis ossis proötici, situs relative to ossa laterosphenoidale, parasphenoidale, et proöticum:

a. canalis enclosed within os proöticum;

b. canalis enclosed principally or wholly by ossa laterosphenoidale et parasphenoidale.

Note.—See: Elzanowski and Wellnhofer (1996: 84–86); Coria and Currie (2002: appendix 1, character 2).

Pila et cotyla quadratica otici

0154. Cotyla quadratica otici, foramen pneumaticum magnum, status:

a. absent; **b.** present.

0155. Cotyla quadratica otici, jugamentum ossificans from margo caudolateralis cotylae quadratica squamosi along crista tympanica quadrati to ala parasphenoidalis, status:

a. absent;

b. present, ranging from incomplete jugamentum or series of ossa sesamoidea to a complete arcus osseus.

Note.—BMNH specimen of *Phodilus* was evidently damaged (perforated) on one side, and possessed vestigium tendinosum on the other.

0156. Pila otica (pars proötica), status et forma (**ordered**):

a. absent, cotyla quadratica otici sessile;

b. rudimentary, separation of cotyla quadratica otici from facies evident, at least the lateral portion of facies articularis diverges from the planum of the subtending facies of the meatus acusticus externus, but columnar support comparatively small;

c. pedicillate, separation of cotyla quadratica otici from wall marked, at least the lateral portion of facies articularis diverges from the planum of the subtending wall of the meatus acusticus externus, and columnar support comparatively substantial.

Note.—See: Elzanowski (1995); J. A. Clarke (2004: fig. 21). Possible variation in contributions of incorporated otic elements must await examination of juvenile specimens. Juvenile, disarticulated skull of *Rhea* indicates that capitulum oticum of processus oticus quadrati articulates with both os opisthoticum and os proöticum, and the marginally distinct capitulum squamosum primarily articulates with the same bones but with a lateral bracing from os squamosum.

Canales semicirculares otici

0157. Canalis semicircularis posterior within semicircular area enclosed by canalis semicircularis anterior, position, and (associated) forma fossae auriculae cerebelli (**ordered**):

a. caudal, fossa typically circular;

b. central, fossa typically narrow-elliptical;

c. rostral, fossa typically slitlike.

Note.—Caudoventral segment of canalis semicircularis anterior comparatively rounded in states "b" and "c."

0158. Canalis semicircularis anterior, dorsal segment exposed in ventral surface of fossa cranii rostralis, status:

a. absent; **b.** present.

Note.—This canalis is typically restricted to crista tentorialis, fossa tecti mesencephali, and crista marginalis tecti caudalis; variation in the latter region proved intractable for coding because of confounded variation in the prominence and relative positions of all landmarks.

0159. Canalis semicircularis anterior, caudodorsal extent relative to foramen magnum:
a. dorsolateral, canales well separated bilaterally;
b. essentially dorsal, canales closely approaching each other on midline and typically projecting comparatively prominently into calvaria.
Note.—State of *Pitta* hyper-apomorphic.

0160. Canalis semicircularis lateralis, exposure in solum ventralis fossae cranii rostralis (**new term**), status:
a. absent;
b. present, moderately prominent.

Os Parietale

Note.—Several characters relevant to Ornithischia were excluded, notably lobus supra-occipitalis (**new term**) and lamina parietales (**new term**) of ossa parietales (Coria and Currie 2002: appendix 1, characters 10 and 14).

0161. Os parietale, crista (linea) nuchalis transversa, lateral position to extend dorsad to ossa parietales, status et forma:
a. absent or negligible;
b. significant, overlap dorsal to os parietale significant.
Note.—See: J. M. Clark et al. (1994); Holtz (2000 [1998]), regarding purported involvement of ossa supraoccipitales; Coria and Currie (2002: appendix 1, character 11), regarding height among Tyrannosauridae; Xu (2002: suite I, character 28).

0162. Os parietale, fenestrae supratemporales, forma *sensu* bilateral confluence et relationship to crista (linea) nuchalis sagittalis (**unordered**):
a. separated by lamina horizontalis of ossa parietales;
b. confluent caudally but separated rostrally by caudally tapering, triangular eminentiae parietales;
c. confluent broadly over ossa parietales, latter forming crista (linea) nuchalis sagittalis.
Note.—See: Molnar et al. (1990); Holtz (2000 [1998]: appendix I, character 43); Rauhut (2003: character 43); Makovicky and Norell (2004: character 216) and Xu and Norell (2004: supplement, character 216), regarding conformation of os squamosal with respect to fenestra/fossa supratemporalis.

0163. Os parietale, facies externa, processus rostralis extending between margines mediales of ossa frontales, status:
a. absent, sutura frontoparietale linearly transverse;
b. present, sutura frontoparietale includes invagination between ossa frontales caused by rostral extension of ossa parietales;
x. noncomparable by indiscernable suturae (*Carnotaurus*).
Note.—See: Gauthier (1986: 14, unindexed synapomorphy of Aves); Currie (1987); Holtz (1994a: appendix 1, character 38); Azuma and Currie (2000: appendix 1, character 54); Holtz (2000 [1998]: appendix I, character 42).

0164. Os parietale, facies externa, regiones caudomediales, eminentia medialis (**new term**), status:
a. absent;
b. present, a mediodorsal, subcristulate eminence having width no greater than rostrocaudal length.
Note.—See: Bonaparte (1991); Holtz (1994a: appendix 1, character 14); Rauhut (2003: character 42).

Os Prefrontale

0165. Os prefrontale, facies dorsalis, status et forma (**ordered**):
a. present, preorbital (laterodorsal) exposure substantial to extent at least that of os lacrimale, with processus ventralis;
b. present, greatly reduced or vestigial in preorbital expanse and processus ventralis;
c. absent or indiscernable.
Note.—A point of nomenclatural confusion for some time (H. J. Müller 1963), os prefrontale is distinct from os lacrimale, only the latter being retained by Neornithes (Baumel and Witmer 1993: annotation 110). See: Currie (1985); Gauthier (1986: text character 68); Houde (1988: table 27, character 19); Benton (1990b: 24), in which "prefrontal with a long caudal ramus that overlaps the frontal" was listed as synapomorphic for Ornithischia; Chatterjee (1991: character 5); J. M. Clark et al. (1994); Holtz (1994a: appendix 1, character 37); Holtz (1994b: appendix 7.1, character 5); Novas (1994 [1993]: appendix, character 10); Russell and Dong (1994a [1993a]: table 2, character 5); Russell and Dong (1994b [1993b]: list B, character 1); Benton (1997); Sues (1997: appendix 1, character 11); Forster et al. (1998: supplement, character 8); J. D. Harris (1998: appendix 2, character 5); Makovicky and Sues (1998: appendix 1, character 11); Chatterjee (1999: appendix II, character 1, modified); Sereno (1999: character 139); Xu et al. (1999a: character 9, modified); Xu et al. (1999b: character 8); Currie and Carpenter (2000: appendix 1, character 9); Holtz (2000 [1998]: appendix I, character 37); Norell et al. (2000: appendix 1, character 10); Xu et al. (2000: supplement, character 6); Currie and Chen (2001: 1709), in reference to *Sinosauro-*

pteryx; Norell et al. (2001: appendix 1, character 42); J. M. Clark et al. (2002a: appendix 2.2, character 42); Maryanska et al. (2002: appendix 1, character 21), who distinguished "present" from "absent or fused with the lacrimal"; Suzuki et al. (2002: character 2); Xu (2002: suite II, character 88); Xu et al. (2002a: supplement, character 33); Rauhut (2003: character 34); Hwang et al. (2004: supplement, character 41); Xu and Norell (2004: supplement, character 41).

Os Frontale

0166. Os frontale, facies cerebralis, crista vallecularis, vertex with crista frontalis interna, situs relative to terminus rostralis fossae cranii rostralis:

a. essentially coincident; **b.** well caudal;

x. noncomparable by absent vertex (ratites, Dromornithiformes).

Note.—Although some taxa not available with exposed cranii internae, vertex confirmable through foramen magnum in most taxa. Superficially similar condition found in Psittaciformes, but latter associated instead with enlarged fossa bulbi olfactorii.

0167. Os frontale, facies dorsalis, margo rostralis (dorsal view), lateromedial width relative to that of margo caudalis and conformational corollaries, forma:

a. relatively broad, subrectangular;

b. relatively narrow, triangular.

Note.—See: Currie (1987); J. M. Clark et al. (1994); Holtz (1994a: appendix 1, character 65); Russell and Dong (1994a [1993a]: table 2, character 7); Forster et al. (1998: supplement, character 7); Xu et al. (1999b: character 7); Holtz (2000 [1998]: appendix I, character 39); Xu et al. (2000: supplement, character 5); Norell et al. (2001: appendix 1, character 43); J. M. Clark et al. (2002a: appendix 2.2, character 43, states reversed); Xu (2002: suite II, character 89); Xu et al. (2002a: supplement, character 34, states reversed); Rauhut (2003: character 36); Hwang et al. (2004: supplement, character 42); Xu and Norell (2004: supplement, character 42); Bourdon et al. (2005: appendix 1, character 11).

0168. Os frontale, facies dorsalis, pars (ramus) postorbitalis (if os frontale involved), forma relative to rima orbitalis:

a. projects laterally from os frontale, forming incisura supraorbitalis (**new term**) in rima orbitalis;

b. does not project laterally from os frontale, rima orbitalis proximal to os lacrimale is essentially smooth.

Note.—See: Russell and Dong (1994a [1993a]: table 2, character 7); Currie (1995: appendix, character 1); Sereno (1999: character 140); Holtz (2000 [1998]: appendix I, character 40); Suzuki et al. (2002: character 3); Xu et al. (2002a: supplement, character 176, states reversed).

0169. Os frontale, facies dorsalis, bilaterally compressed, marginally rounded carina ossea (**new term**), status:

a. absent; **b.** present.

Note.—Several taxa not included in analysis possess similar carinae; and the anhimid *Anhima* possesses a spinous, possibly homologous variant. See: Livezey (1986: appendix 1, characters 16–17); Livezey (1997a: characters 11–12; *corrigenda*, Livezey 1998a). Maryanska et al. (2002: appendix 1, character 25) referred to "elongate rostromedial process on the frontal" in basal Theropoda.

0170. Os frontale, facies dorsalis ossis—(*i*) enormous, rostrally expansive, galea (cassis) ossea composed of bilateral lamina of processes caudales ossae nasales and (caudobasally) ossae frontales; and (*ii*) thick, cuneate carina dorsomedialis of ossa mesethmoidales variably perforated by foramina pneumatica—status et composita ossea (**unordered**):

a. absent;

b. present, composed of dorsally rounded, expanded ossa frontales et os mesethmoidale, with variable, lesser contributions by ossa nasales;

c. present, composed of variably shaped, rostrodorsal elaborations of os mesethmoidale and ossa frontales et nasales, perhaps further modified by expansion of os maxillare and possibly os mesethmoidale.

Note.—Several less-similar, carinalike expansions of the ossa nasales et frontales also occur in some waterfowl (especially males). Excellent example of cassis in *Casuarius* is specimen BMNH 1956.1.1. See: Beddard (1901c); Hofer (1955), including both ratites and Gruidae; Livezey (1998b: appendix A, character 68), described bilateral eminentia frontales in Gruidae.

0171. Os frontale, fossa supratemporalis, margo rostralis, forma:

a. linear or slightly curvilinear;

b. strongly sinusoidal and extending to processus postorbitalis, facies lateralis.

Note.—See: Currie (1995); Norell et al. (2001: appendix 1, character 44); J. M. Clark et al. (2002a: appendix 2.2, character 44); Vickers-Rich et al. (2002), concerning *Avimimus*; Xu (2002: suite II, character 226); Hwang et al. (2004: supplement, character 43); Xu and Norell (2004: supplement, character 43).

0172. Os frontale, facies orbitalis, impressio glandula nasalis, status:

a. absent; **b.** present.

Note.—Position of the impressio varies among taxa with derived state. Impressiones typically accompanied by foramina neurovascularia that support the glandula. See also: Technau (1936); Siegel-Causey (1988: characters 12–15); Hesse (1990); Siegel-Causey (1990); Livezey (1998b: appendix A, character 72).

0173. Os frontale, facies orbitalis, margo supraorbitalis, regio medialis, ventral expansion (convexity) acting as rima dorsalis oculae, status:
a. absent; **b.** present.
Note.—See: Rauhut (2003: character 37).

0174. Os frontale, facies orbitalis, margo supraorbitalis, variably prominent, rounded, highly pneumatic, hornlike processus supraocularis (**new term**), status:
a. absent; **b.** present.
Note.—Synonymous with "fronto-orbital process" of Shufeldt (1900a–b). This structure can be confused with processus supraorbitalis of os lacrimale by G. Mayr et al. (2003: appendix 1, character 5).

0175. Os frontale, facies orbitalis, margo supraorbitalis, prominent, lateroventrally oriented angulus postocularis (**new term**), delimiting a crescentiform lacuna rostral to processus postorbitalis, status:
a. absent; **b.** present;
x. noncomparable by absence of processus (Apterygidae, Anhingidae, Phalacrocoracidae).
Note.—Synonymous with "processus postorbitalis rostralis" of Barnikol (1952) and "processus postorbitalis" of Dullemeijer (1951a–b) and Bas (1954).

0176. Ossa frontale et lacrimale, impressio glandula nasalis rostral margo caudalis ossis lacrimale, processus supraorbitalis, status:
a. absent; **b.** present.
Note.—Familial variation in apomorphy, in that derived state not in cathartid genera *Vultur* or *Gymnogyps*. Impressio is delimited caudally by processus lacrimalis ossis frontale.

0177. Ossa frontale et parietale, relative lengths:
a. os frontale smaller or subequal to os parietale;
b. os frontale approximately twice as long as os parietale.
Note.—See: J. M. Clark et al. (1994); Russell and Dong (1994a [1993a]: table 2, character 7), which included mention of "postorbital ramus"; Forster et al. (1998: supplement, character 9); Xu et al. (1999b: character 9); Holtz (2000 [1998]: appendix I, character 40), with respect to two aspects of frontal morphology; Xu et al. (2000: supplement, character 7); Maryanska et al. (2002: appendix 1, character 26); Vickers-Rich et al. (2002), concerning *Avimimus*.

Os Septomaxillare

0178. Os septomaxillare, status (**ordered**):
a. present; **b.** absent.
Note.—See: Romer (1956); Benton and Clark (1988: appendix 1, character 8).

Os Postfrontale

0179. Os postfrontale, status (**ordered**):
a. prominent; **b.** reduced; **c.** absent.
Note.—See: Benton and Clark (1988: appendix 1, character 13); Benton (1990b); Sereno and Novas (1992: appendix, character 11).

Os Postparietale

0180. Os postparietale, status (**ordered**):
a. present, paired;
b. present and synostotic, perhaps asymmetrical;
c. absent.
Note.—See: Benton and Clark (1988: appendix 1, character 9); Benton (1990b); Sereno (1991a: appendix).

Os Supraorbitale

0181. Os supraorbitale, status:
a. present; **b.** absent.
Note.—See: Romer (1956).

Os Interparietale

0182. Os interparietale, status:
a. present; **b.** absent.
Note.—See: Romer (1956).

Os Intertemporale

0183. Os intertemporale, status:
a. present; **b.** absent.
Note.—See: Romer (1956).

Os Supratemporale

0184. Os supratemporale, status:
a. present; **b.** absent.
Note.—See: Romer (1956).

Os Tabulare

0185. Os tabulare, status:
a. present; **b.** absent.
Note.—See: Romer (1956).

Os Epijugale

0186. Os epijugale, status:
a. present; **b.** absent.
Note.—See: Romer (1956). Other cranial elements possessed of variable (polymorphic) distributions among nonarchosaurian reptiles include ossa postnasale et presphenoidale.

Os Mesethmoidale

0187. Os mesethmoidale, status definitivum osseum:
a. absent; **b.** present.
Note.—See: Chatterjee (1999: appendix II, character 22); and possibly Chatterjee (1999: appendix II, character 23), ossification of septum interorbitalis.

0188. Os mesethmoidale, lamina dorsalis, dorsomedial exposure between ossa premaxillares, processes frontales, ossa nasales, processes premaxillares, and ossa frontales, status definitivum:
a. absent; **b.** present.
Note.—Suturae frontomesethmoidalis, mesethmopremaxillaris, et mesethmonasalis variably obscured, especially caudally and in Apterygidae; in virtually all Neornithes, increasingly so with age. J. A. Clarke and Chiappe (2001: character 67) equated rostral extension of os mesethmoidale to pars caudalis of conchae nasales osseae as part of septum interorbitale.

Os Ectethmoidale

0189. Os ectethmoidale, status et forma (**ordered**):
a. absent; **b.** moderately developed;
c. well developed, typically rectangular and composing majority of paries antorbitalis ossificans;
x. noncomparable, involved with unique conchae nasales (*Apteryx*).
Note.—Most Galliformes as well as *Eurypyga* have very small ventral elements attributable to septum ectethmoidalis. Characters of os ectethmoidale are especially problematic in part because of unusually great ontogenetic variation in ossification of this region. We follow Baumel and Witmer (1993: 72), in which foramina orbitonasales laterale et mediale, and os ectethmoidale correspond to the "ventral part" evident rostral to the oculus, whereas an associated "dorsal part" corresponds to capsula nasi osseum or other ossified membrana between margo dorsalis of os ectethmoidale and facies ventralis of os frontale.

See: W. K. Parker (1888a), regarding development in *Apteryx*; Pycraft (1902), regarding Falconiformes; de Kock (1955); D. Starck (1955), for uniquely shared apomorphies of Apterygidae and Dinornithiformes; Ligon (1967: table 1); Cracraft (1968a); Payne and Risley (1976: characters 10–12), regarding Ardeidae; Cracraft (1988: series VII, character 1), Siegel-Causey (1988: characters 17–19), Cracraft and Mindell (1989: table 1, character 27), Ericson (1996: character 1), K. Lee et al. (1997: appendix 1, character 58), regarding ratites; Livezey (1995c: appendix II, character 1); Chu (1998: appendix 1, characters 27–28); Livezey (1998b: appendix A, character 65), regarding presence; Livezey (1998b: appendix A, character 66), regarding conformation; Rotthowe and Starck (1998: appendix, character 14); Hughes (2000: appendix 2, characters 15–19); Chiappe et al. (2001), regarding *Gobipteryx*; Cracraft and Clarke (2001: appendix 2, character 32); Dyke and Gulas (2002: appendix 1, character 51); Dyke et al. (2003: appendix 1, character 8); G. Mayr (2003a: appendix I, character 7); G. Mayr and Clarke (2003: appendix A, character 14); G. Mayr et al. (2003: appendix 1, character 8); Dyke and van Tuinen (2004: appendix 1, character 7); G. Mayr (2004a: appendix 1, character 7); G. Mayr (2004b: appendix 1, character 7); G. Mayr (2004d: appendix I, character 3); G. Mayr and Ericson (2004: appendix I, character 6, part); G. Mayr (2005a: appendix 1, character 3).

Os Epipterygoideum

0190. Os epipterygoideum, status:
a. present; **b.** absent.
Note.—Prominent in some carnosaurs, this element is slow to ossify, positioned dorsolateral to junctura palatino-quadratus, and may contribute to the fovea basal to processus basipterygoideus; also referred to as os alisphenoidale by some (Romer 1956). See: J. M. Clark et al. (2002b), regarding oviraptorid.

Os Lacrimale

0191. Os lacrimale, status generalis (**ordered**):
a. present; **b.** vestigial;
c. absent or indiscernable.
Note.—Homology and nomenclatural propriety of os lacrimale *vs.* os prefrontale in Aves has been the focus of perennial discussion (A. Newton 1896: 876; H. J. Müller 1963) and recent comparative work involving nonavian theropods (Baumel and Raikow 1993; Baumel and Witmer 1993). Some taxa considered to lack the element by Cracraft (1968b) were found in the present study to retain a vestigium. Os lacrimale of the "Pici" were considered by S. F. Simpson and Cracraft (1981: character 10) to be ab-

sent or synostotic with os ectethmoidale. Some Charadriiformes and Passeriformes also show extreme reduction.

See: Livezey (1986: appendix 1, character 10); Livezey (1989: table 1, character 10); J. M. Clark et al. (1994); Ericson (1997: table 1, character 5; table 2, character 3); Livezey (1997a: appendix 1, character 13; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, character 57); Rotthowe and Starck (1998: appendix, character 38, under "prefrontal bone"); G. Mayr et al. (2003: appendix 1, character 6), incorrectly as "os prefrontale."

0192. Os lacrimale, forma lateralis (**unordered**):

a. subrectangular or subtriangular;

b. essentially linear or top-perpendicular ("inverted L-shaped"), lacking bipartite processus supraorbitalis or rostral extension by ramus preorbitalis of os lacrimale (**new term**)—sometimes referred to as "anterodorsal process," rostral counterpart of ramus supraorbitalis (**new term**) of processus—and exposed broadly on externum cranii dorsalis;

c. symmetrically cruciate ("T-shaped"), rami dorsales essentially equally long or ramus preorbitalis of processus supraorbitalis much longer than ramus supraorbitalis;

x. noncomparable by absence of os lacrimale or part(s) thereof (*Podargus*, *Aegotheles*, *Hemiprocne*, *Glaucis*, *Momotus*, most Coraciiformes, *Pitta*, some oscine Passeriformes).

Note.—See: Berger (1960b: table 4, character 8), contrasting Cuculidae with Musophagidae; Payne and Risley (1976: character 7), regarding Ardeidae; J. M. Clark et al. (1994); Currie (1995: appendix, character 7); Makovicky and Sues (1998: appendix 1, character 13); Xu et al. (1999b: character 86); Holtz (2000 [1998]: appendix I, character 32); Norell et al. (2000: appendix 1, characters 9 [general shape] and 11 [comparative length of ramus preorbitalis]); Xu et al. (2000: supplement, character 66); Norell et al. (2001: appendix 1, character 41); J. M. Clark et al. (2002a: appendix 2.2, character 41); Xu (2002: suite II, character 87); Xu et al. (2002a: supplement, character 32); Xu et al. (2002b); Rauhut (2003: characters 28 and 33), regarding inverted "L-shaped" and "T-shaped" elements; Hwang et al. (2004: supplement, character 40); Xu and Norell (2004: supplement, character 40).

0193. Os lacrimale, tumulus pneumaticus (**new term**), status:

a. absent; **b.** present, conspicuous;

x. noncomparable by absence of os lacrimale or part(s) thereof (*Podargus*, *Aegotheles*, *Hemiprocne*, *Glaucis*, *Momotus*, most Coraciiformes, *Pitta*, some oscine Passeriformes).

Note.—See: Witmer (1990: 372, character 10).

0194. Os lacrimale, processus orbitalis—curvatura, incisura, aut foramen ducti nasolacrimalis—forma:

a. rudimentary or obsolete, as weakly defined curvatura medialis processi orbitalis ducti;

b. distinct, as incisura semicircularis ducti nasolacrimalis (typically with apices dorsal and ventral to hiatus subforaminis) aut foramen ducti nasolacrimalis (latter evidently derived from incisura by ossification of arcus lateralis ostiae ducti);

x. noncomparable by absence of os lacrimale or part(s) thereof (*Podargus*, *Aegotheles*, *Hemiprocne*, *Glaucis*, *Momotus*, most Coraciiformes, *Pitta*, some oscine Passeriformes).

Note.—Foramen or incisura marks passage of ductus nasolacrimalis (common ostium for ductus glandulae nictitantis et lacrimalis to cavitas nasalis), typically lateral to processus orbitalis ossis lacrimale. Ductus nasolacrimalis evidently homologous and virtually uniformly present among Archosauria and perhaps Tetrapoda (de Beer 1926, 1937; Romer 1956). Apparently plesiomorphic absence of accommodation of ductus by processus ossis lacrimale evidently permits passage of former by medial angulation or curvatura processi.

See: Payne and Risley (1976: character 9), regarding Ardeidae; Strauch (1978: figs. 5 and 7c); Molnar et al. (1990); Holtz (1994a: appendix 1, character 27); Forster et al. (1998: supplement, character 19); J. D. Harris (1998: appendix 2, character 10); Livezey (1998b: appendix A, character 61); Sereno et al. (1998: footnote 22, character 42), with respect to dorsoventral position; Chiappe et al. (1999), regarding *Confuciusornis*; Xu et al. (1999b: character 17); Azuma and Currie (2000: appendix 1, character 67, part); Norell et al. (2001: appendix 1, character 40); J. M. Clark et al. (2002a: appendix 2.2, character 40); Xu (2002: suite II, character 86); Xu et al. (2002a: supplement, character 31), regarding enlarged lateral foramen (foramina) in the "angle of the lacrimal"; Xu et al. (2000: supplement, character 13) with respect to "accessory lacrimal fenestration"; Currie et al. (2003: appendix, character 25); Rauhut (2003: characters 30–31) regarding incisura et foramen (ductus), respectively; Hwang et al. (2004: supplement, character 39); G. Mayr (2004a: appendix 1, character 6); G. Mayr and Ericson (2004: appendix I, character 4); Xu and Norell (2004: supplement, character 39).

0195. Os lacrimale, processus orbitalis, pes ossis lacrimale (**new term**) effecting articularis jugalis (directly or via abbreviate ligamentum), status et forma (**unordered**):

a. absent;

b. present, typically subspheroidal expansion;

c. present, expansion including distinctly caudal tuberculum;

x. noncomparable by absence of os lacrimale or part(s) thereof (*Podargus*, *Aegotheles*, *Hemiprocne*, *Glaucis*, *Momotus*, most Coraciiformes, *Pitta*, some oscines).

0196. Os lacrimale, processus orbitalis, lamina medialis (**new term**), perforatio laminae obliquus **(new term)**, status:

a. absent; **b.** present;

x. noncomparable by absence of os lacrimale or part(s) thereof (*Podargus*, *Aegotheles*, *Hemiprocne*, *Glaucis*, *Momotus*, most Coraciiformes, *Pitta*, some oscines).

0197. Os lacrimale, processus orbitalis, recessus et/aut foramina/pori pneumaticus, status:

a. absent; **b.** present;

x. noncomparable by absence of os lacrimale or part(s) thereof (*Podargus*, *Aegotheles*, *Hemiprocne*, *Glaucis*, *Momotus*, most Coraciiformes, *Pitta*, some oscine Passeriformes).

Note.—Often especially conspicuous in bulbus terminalis processi (**new term**) aut sulcus lateralis incisurae ducti (**new term**). See: Sereno et al. (1994: footnote 12) and Sereno et al. (1996: footnote 45, characters 2 and 34), with respect to “lacrimal pneumatic excavation”; Livezey (1998b: appendix A, character 59); Currie and Carpenter (2000: appendix 1, character 13), with respect to “lacrimal pneumatic recess”; Xu et al. (2002b); Currie et al. (2003: appendix, character 25).

0198. Os lacrimale, processus orbitalis, lamina medialis processi (**new term**) occluding at least one-half of lamina lacrimo-ectethmoidalis (**new term**) within fossa antorbitalis, status et forma (**unordered**):

a. absent;

b. present, with extensive sutura aut synostosis lacrimo-ectethmoidalis;

c. present, with small os ectethmoidale occluding incisura medialis processi orbitalis ossis lacrimale;

d. present, with os ectethmoidale bilaminar (“overlapping”) with facies caudomedialis processi orbitalis ossis lacrimale;

x. noncomparable by absence of os lacrimale or part(s) thereof (*Podargus*, *Aegotheles*, *Hemiprocne*, *Glaucis*, *Momotus*, most Coraciiformes, *Pitta*, some oscine Passeriformes).

0199. Os lacrimale, facies articularis frontonasalis, margo ventromedialis ossis nasale, extentio rostralis, status:

a. present, dorsoventrally thick;

b. absent, dorsoventrally thin, ventrolateral in position;

x. noncomparable by absence of os lacrimale or part(s) thereof (*Podargus*, *Aegotheles*, *Hemiprocne*, *Glaucis*, *Momotus*, most Coraciiformes, *Pitta*, some oscine Passeriformes).

Note.—See: Sereno et al. (1996: footnote 45, character 33); Holtz (2000 [1998]: appendix I, character 35).

0200. Os lacrimale, processus orbitalis, extentio rostralis, status et forma (**ordered**):

a. significantly less extensive ventrally than orbita, typically failing to extend to margo ventralis orbitae;

b. not extending ventrolaterally beyond junctura lacrimo-ectethmoidalis (if present) or homologous point, not approaching arcus jugalis;

c. extending ventrolaterally beyond junctura lacrimo-ectethmoidalis (if present) or homologous point, typically *approaching* arcus jugalis;

d. as deep as orbita, typically *articulating* with arcus jugalis at margo ventralis orbitae;

x. noncomparable by absence of os lacrimale or processus orbitalis (Megapodiidae, *Podargus*, *Aegotheles*, *Hemiprocne*, *Glaucis*, *Momotus*, most Coraciiformes, *Pitta*, some oscine Passeriformes).

Note.—Cf. assessment of “extent” relative to orbita et arcus jugalis.

See: Livezey (1986: appendix 1, character 10); Siegel-Causey (1988: character 20); Andors (1992: table 2, character 6); Livezey (1995b: appendix 1, character 4); Ericson (1997: table 1, character 5; table 2, character 3); Livezey (1997a: appendix 1, character 14; *corrigenda*, Livezey 1998a); Chu (1998: appendix 1, character 29); Livezey (1998b: appendix A, character 58); Hughes (2000: appendix 2, character 3), in which structure attributed to os frontale; G. Mayr and Clarke (2003: appendix A, character 12); G. Mayr et al. (2003: appendix 1, character 7); Rauhut (2003: character 29); Dyke and van Tuinen (2004: appendix 1, character 5); G. Mayr (2004a: appendix 1, character 5); G. Mayr (2004d: appendix I, character 2); G. Mayr and Ericson (2004: appendix I, character 4); G. Mayr (2005a: appendix 1, character 2).

0201. Os lacrimale, processus orbitalis, angulus medialis et terminus acuminatus (**new term**), status:

a. absent; **b.** present, pronounced;

x. noncomparable (Megapodiidae, *Podargus*, *Aegotheles*, *Hemiprocne*, *Glaucis*, *Momotus*, most Coraciiformes, *Pitta*, some oscine Passeriformes).

0202. Os lacrimale, processus orbitalis, terminus ventralis, sulcus articularis jugalis, status:

a. absent; **b.** present;

x. noncomparable (Megapodiidae, *Podargus*, *Aegotheles*, *Hemiprocne*, *Glaucis*, *Momotus*, most Coraciiformes, *Pitta*, some oscine Passeriformes).

Note.—Intended to encode structural modification of os lacrimale associated with junctura jugolacrimalis (if present), i.e., accommodation of probable contact. See: Payne and Risley (1976: character 8), regarding Ardeidae; Sereno et al. (1996: footnote 45, character 3); Holtz (2000 [1998]: appendix I, character 34).

0203. Os lacrimale, processus supraorbitalis et facies articularis lacrimo-frontalis, status:

a. absent, element not exposed on cranium, facies dorsalis;

b. present, element broadly exposed on cranium, facies dorsalis;

x. noncomparable (*Podargus*, *Aegotheles*, *Hemiprocne*, *Glaucis*, *Momotus*, most Coraciiformes, *Pitta*, some oscine Passeriformes).

Note.—See: Gauthier (1986); Benton (1990b: 21), who listed exposure of os lacrimale on skull roof as synapomorphic of all Theropoda; Novas (1994 [1993]: appendix, character 40); Holtz (2000 [1998]: appendix I, character 30); G. Mayr and Ericson (2004: appendix I, character 3).

0204. Os lacrimale, processus supraorbitalis et corpus lacrimalis (**new term**), facies dorsalis, elongation (dorsal perspective), status:

a. absent; **b.** present;

x. noncomparable (*Podargus*, *Aegotheles*, *Hemiprocne*, *Glaucis*, *Momotus*, most Coraciiformes, *Pitta*, some oscine Passeriformes).

Note.—New term corresponds to portion including facies articularis frontonasalis. See: Livezey (1986: appendix 1, character 11); Livezey (1989: table 1, character 11); Livezey (1991: appendix 1, character 153); Andors (1992: table 2, character 7); Livezey (1995b: appendix 1, character 1); Livezey (1996a: appendix 1, character 7); Livezey (1996b: appendix 1, character 5); K. Lee et al. (1997: appendix 1, character 52); Chu (1998: appendix 1, characters 30–31); Livezey (1998b: appendix A, characters 62–63); G. Mayr and Clarke (2003: appendix A, character 13); Dyke and van Tuinen (2004: appendix 1, character 6).

0205. Os lacrimale, processus supraorbitalis, caudolateral elongation of at least one-half of margo dorsalis orbitae, status:

a. absent; **b.** present;

x. noncomparable (*Podargus*, *Aegotheles*, *Hemiprocne*, *Glaucis*, *Momotus*, most Coraciiformes, *Pitta*, some oscine Passeriformes).

Note.—In *Accipiter* and *Psophia*, presence of ossa supraorbitalia complicates coding. See: Chu (1998: appendix 1, character 31); Livezey (1998b: appendix A, characters 62–63); G. Mayr et al. (2003: appendix 1, character 5).

0206. Os lacrimale, processus supraorbitalis, forma (**unordered**):

a. variably elongate, typically narrow and attenuated caudad, sutura lacrimo-frontalis extends to terminus caudalis of processus;

b. elongate-rectangular, laterocaudal or caudolateral in orientation, separate from margo lateralis of os frontale;

c. subtriangular to subconical (i.e., broad basally and abruptly narrowed to terminal angulus, dorsum subplanar to convex), laterocaudal orientation, variably emancipated from os frontale caudad;

x. noncomparable (*Podargus*, *Aegotheles*, *Hemiprocne*, *Glaucis*, *Momotus*, most Coraciiformes, *Pitta*, some oscine Passeriformes).

Note.—See: Holdaway (1991: appendix 5.1, character 12); Chu (1998: appendix 1, character 22); Hughes (2000: appendix 2, characters 11–14), limited to variation among Cuculiformes; G. Mayr et al. (2003: appendix 1, character 5).

0207. Os lacrimale, processus supraorbitalis, prominentia (cornua) lacrimales (**new term**) et/aut crescentia nasolacrimales (**new term**), status:

a. absent;

b. present, as bilaterally paired triangular cornulae or bilateral, caudal continuations of cristae nasales;

x. noncomparable (*Podargus*, *Aegotheles*, *Hemiprocne*, *Glaucis*, *Momotus*, most Coraciiformes, *Pitta*, some oscine Passeriformes).

Note.—See: J. M. Clark et al. (1994); Russell and Dong (1994a [1993a]: table 2, character 6), with respect to “postorbital horns” of os lacrimale; J. D. Harris (1998: appendix 2, character 11); Azuma and Currie (2000: appendix 1, character 66); Currie and Carpenter (2000: appendix 1, character 14), in reference to “lacrimal horn,” and categorized as absent, a low crista, jugum, or prominent conus; Holtz (2000 [1998]: appendix I, characters 27 [paired crescentia] and 31); Norell et al. (2001: appendix 1, character 39); J. M. Clark et al. (2002a: appendix 2.2, character 39); Xu (2002: suite II, character 85); Xu et al. (2002a: supplement, character 30); Currie et al. (2003: appendix, character 24); Rauhut (2003: character 32); Hwang et al. (2004: supplement, character 38); Xu and Norell (2004: supplement, character 38).

Suturae Cranii

0208. Sutura supraoccipito-parietalis, typus:

a. suturae squamosa, margines ossium significantly overlapping;

b. sutura serrata or plana, a simple abutment.

Note.—Involvement of this sutura in the crista nuchalis transversa in some taxa merits comparison with that character. See: Currie and Zhao (1994b [1993b]); Forster et al. (1998: supplement, character 10); Chatterjee (1999: appendix II, character 28); Xu et al. (1999a: character 8); Xu et al. (1999b: character 10); Xu et al. (2000: supplement, character 8).

0209. Sutura interparietalis, status definitivum:

a. present, elements medially distinguishable;

b. absent, medial synostosis of elements renders junctura interparietalis indiscernable.

Note.—See: Norell et al. (2001: appendix 1, character 49); J. M. Clark et al. (2002a: appendix 2.2, character 48); Xu (2002: suite II, character 91); Xu et al. (2002a: supplement, character 36); Hwang et al. (2004: supplement, character 47); Xu and Norell (2004: supplement, character 47).

0210. Ossa parietales, foramen interparietalis (**new term**), status:
a. present; **b.** absent.
Note.—See: Romer (1956: 59); Benton and Clark (1988: appendix 1, character 3); Benton (2004: 19).

0211. Sutura interparietalis, rostrocaudal foreshortening associated with pronounced narrowing of ossa parietales, status:
a. absent; **b.** present, distinct.

0212. Sutura prefronto-frontalis (**new term**), forma:
a. sutura squamosa (os prefrontale dorsad to os frontale), os prefrontale diminutive;
b. sutura plana, os prefrontale relatively lateral;
x. noncomparable by absence of os prefrontale (Neornithes).
Note.—See: Barsbold and Osmolska (1999); Xu (2002: suite I, character 26).

0213. Sutura frontoparietalis, status:
a. discernable in adults;
b. absent, rendered indiscernable by synostosis.
Note.—Polymorphism here is typically of ontogenetic nature, in which the feature is present in early semaphorants but indistinguishable in adults, and the developmental interval to closure is variable and comparatively protracted. See: J. M. Clark et al. (1994); Elzanowski (1995: character NG2); Norell and Clarke (2001: appendix I, character 51), treated similarly by J. A. Clarke (2002: appendix I, character 51), J. A. Clarke and Norell (2002: appendix 2, character 51); Zhou and Zhang (2002: appendix III, character 51); Currie et al. (2003: appendix, character 15); G. Mayr and J. A. Clarke (2003: appendix A, character 32), including erroneous characterization of Apterygidae as plesiomorphic; J. A. Clarke (2004: appendix 1, character 51); Dyke and van Tuinen (2004: appendix 1, character 20); Ji et al. (2005: supplement, part I, character 51).

0214. Juncturae supraoccipito-squamosa et exoccipito-squamosa, typus:
a. articulatio aut sutura synovialis;
b. sutura.
Note.—See: Cracraft (1986: appendix, character 62); Cracraft (1988: series I, character 10).

0215. Suturae frontosquamosa et laterospheno-squamosa, margo laterocaudalis orbitae, elongate, pointed, extensio dorsolateralis squamosi, terminus dorsal to os parietale, status praedefinitivum:
a. absent; **b.** present.
Note.—Columbiformes, Gruiformes, and Charadriiformes, and some Procellariiformes may show intermediacy; Apodidae also challenging.

0216. Sutura laterospheno-parietalis, status (**ordered**):
a. present, comparatively broad;
b. present, but limited to a rostrally oriented point;
c. absent, ossa laterosphenoidale et parietale separated by broad sutura frontosquamosa.
Note.—Secondary exemplar taxa used for coding characters of juveniles.

0217. Junctura laterospheno-parietalis (**new term**), typus and status definitivum:
a. sutura, discernable;
b. synchondrosis, not remaining discernable.
Note.—See: Barsbold (1983); Holtz (1994a: appendix 1, character 18); Forster et al. (1998: supplement, character 21); Xu et al. (1999b: character 19); Xu et al. (2000: supplement, character 14), with respect to "fusion between parietals and laterosphenoid in adults."

Synchondroses Cranii

Note.—A diversity of synchondroses cranii are recognized formally (Baumel and Raikow 1993). Synchondrosis interoticae aut synostosis ossium proötica, epiotica, et opisthotica—so as to compose a single component of the auris interna of Neornithes—occurs during very early ontogeny (Jollie 1957; Sandoval 1964; H. J. Müller 1963). An additional element (os metoticum) evidently is a neomorph of embryogenesis of Aves and perhaps Archosauria, is lateral to the cavum tympanicum ultimately formed by the former elements, joins the lamina parasphenoidalis, arcus occipitalis (ossa basioccipitale, supraoccipitale, et basioccipitale), et cavum tympanicum (de Beer and Barrington 1934), and contributes much to the definitive processus paroccipitalis (Toerien 1971). A dearth of ontogenetic series of most taxa of Aves precludes a reliable assessment of these structures and their development; however, the presence of useful information in sequences of synchondrosis, conformation, and definitive structure and function is likely.

Several bilateral pairs of primordia cranii are joined by understudied synchondroses during early ontogeny, including two partes comprising the definitive os laterosphenoidale (synchondrosis interlaterosphenoidalis), os orbitosphenoidale (facies caudalis orbitae), and several other pairs of elements in the "sphenoid" complex. Further ontogenetic variation attends the synchondrosis interlaterosphenoidalis (Jollie 1957; Goodrich 1958; H. J. Müller 1963; Hogg 1978).

Cavum tympanicum

0218. Crista interfenestralis (**emended term**)—lamina ossea between fenestrae ovalis et cochleae (pseudorotunda), juxtaposed with confluence of ossa proöticum et/aut opisthoticum—and recessus tympanicus accessorius (**new term**) delimited thereby, ventral to crista—status:

a. absent, canalis (meatus) ophthalmicus externus encloses depressio;

b. present, variably prominent.

Note.—Evidently, recessus tympanicus "accessorius" (synonymous with "anterior" or "rostralis") conducts arteria carotis interna and is one of three typical of stem Theropoda, the other two being recessus dorsalis (alternatively, "superior") and recessus ventralis (Witmer 1990); this recessus is evidently absent in Aves.

See (including redundant treatments of "accessory recess"): Watt (1917); Saiff (1974, 1976, 1978, 1981, 1982, 1983, 1988); Elzanowski (1991: table 3); Elzanowski and Galton (1991: character 12); Makovicky and Sues (1998: appendix 1, character 17), both of the former in terms of number of recessi pneumatici paratympanici; Holtz (2000 [1998]: appendix I, character 90); Norell et al. (2001: appendix 1, characters 14 and 24); J. M. Clark et al. (2002a: appendix 2.2, characters 7 and 17); Xu (2002: suite II, characters 61 and 69); Xu et al. (2002a: supplement, character 6), for "middle ear opening"; Hwang et al. (2004: characters 7 and 17); Xu and Norell (2004: supplement, characters 7 and 17).

0219. Canalis ophthalmicus externus, lamina lateralis, forma et status ossificans (**ordered**):

a. complete, forming entire tuba;

b. incomplete, forming irregularly open tuba (tuba imperfecta);

c. absent, forming variably indicated, completely exposed sulcus.

Note.—See: Cracraft (1988: series VII, character 4), regarding foramina in (basi)parasphenoidal plate for "carotid/stapedial arteries, lateral head vein, and the hymomandibular branch of nerve VII, with a large foramen for nerves IX and X along its posterior margin" (p. 347); Saiff (1988: table 1), for preliminary family-level compilation, in which this was termed "stapedial canal," compiled largely from previous ordinal studies (Saiff 1974, 1976, 1978, 1981, 1982, 1983, 1988); Rotthowe and Starck (1998: appendix, character 6).

0220. Canalis ophthalmicus externus, ramus accessorius (**new term**), status:

a. absent;

b. present, originating in ostium canalis carotici with arteria carotici.

Note.—Canalis ophthalmicus externus, ramus accessorius (**new term**), lies rostral to recessus columellae and unites with more-diminutive canalis ophthalmicus externus to pass rostromediad to os quadratum.

0221. Recessus columellae, status et forma (**ordered**):

a. obsolete or absent, margo recessi poorly defined, fenestra vestibuli appearing coplanar with surrounding bone, fenestra cochleae only weakly bounded caudally or caudoventrally, recessus tympanicus caudalis (if present) conspicuous;

b. shallow, recessus distinct, but fenestra vestibuli and fenestra cochleae only slightly deep to margo recessi, recessus tympanicus caudalis (if present) with internum exposed;

c. deep, recessus well defined, fenestra vestibuli and fenestra cochleae distinctly deep to margo recessi, recessus tympanicus caudalis (if present) largely obscured.

Note.—Recessus columellae accommodates the single ossicula auris avium (columella). Fenestrae vestibuli (enclosing clipeolus columellae) et cochleae (os opisthoticum, supporting membrana tympanica secundaria), as well as the recessus tympanicus caudalis open into this spatium (Baumel and Witmer 1993: annotation 22). See: Saiff (1974, 1976, 1978, 1981, 1982, 1983, 1988); Kühne and Lewis (1985). Reported absence of recessus among Mesozoic birds based on Witmer (1990); Baumel and Witmer (1993: annotation 21).

0222. Fenestra vestibuli, excavatio paravestibularis (**new term**), status:

a. present; **b.** absent.

Note.—Also referred to by some as a "ventral" or "lateral" recess. Here excavatio is taken to be larger than recessus. See: Bakker et al. (1988); Holtz (1994a: appendix 1, character 69), in reference to excavation near "fenestra ovalis"; Norell et al. (2000: appendix 1, character 20), regarding status of "subotic recess"; Norell et al. (2001: appendix 1, character 17); J. M. Clark et al. (2002a: appendix 2.2, character 8); Vickers-Rich et al. (2002), concerning *Avimimus*; Xu (2002: suite II, character 62); Xu et al. (2002a: supplement, character 7), in reference to "subotic recess (pneumatic fossa ventral to fenestra ovalis)"; Hwang et al. (2004: supplement, character 8); Xu and Norell (2004: supplement, character 8).

Recessus pneumatici paratympanici

0223. Recessus pneumatici paratympanici, recessus tympanicus dorsalis (perspective perpendicular to cotylae), situs relative to cotylae quadratica squamosi et quadratica otici (**ordered**):

a. caudal to cotylae;

b. intermediate, between cotylae;

c. rostral to cotylae.

Note.—Known also as a "lateral" or "ventral" recess in some taxa where the homologue has undergone a shift craniad. Comparability of recessus tympanicus dorsalis in ratites problematic. Character summarized for neoavian families by Saiff (1988: table 1) as position of "upper tympanic recess" relative to "quadrate facets," compiled largely from previous ordinal studies (Saiff 1974, 1976, 1978, 1981, 1982, 1983, 1988). See: Siegel-Causey (1988: characters 29–30), and following character, related by criterion of position; G. Mayr (2003a: appendix I, character 15); G. Mayr (2004b: appendix 1, character 16); Bourdon et al. (2005: appendix 1, character 31).

0224. Recessus pneumatici paratympanici, recessus tympanicus dorsalis, sectio caudal to cotyla quadratica otici, including pila otica, foramina or pori pneumatici, status et numerus modalis (**unordered**):

a. none; **b.** single foramen;

c. multiple foramina or exposed os spongiosum;

d. pori pneumatici, aspectus of fine os spongiosum.

Note.—In ratites, portion involved includes only the ventral half of the cotyla quadratica otici.

See: Lowe (1925b, 1926a); Cracraft (1982: series 1, character 4); Cracraft (1985: character 2); Witmer (1990: 371–372, characters 1, 3, and 12); Rotthowe and Starck (1998); Cracraft and Clarke (2001: appendix 2, character 15, part); Maryanska et al. (2002: appendix 1, character 55), in reference to presence-absence of "three tympanic recesses" (presumably rostralis, dorsalis, et caudalis of Neornithes). See diverse treatments by: Saiff (1978); Cracraft (1985: character 2); Cracraft (1988: series V, character 6); Cracraft (1988: series IX, character 5), in reference to probably synonymous foramen pneumaticum dorsale of recessus tympanicus dorsalis, and the unsequenced mention of a "large fenestra/foramen . . . immediately posterior to the facet for the medial head of the quadrate . . . posteromedially [located] to the upper tympanic recess and on a buttress for the quadrate . . . ," proposed as synapomorphic for Gruiformes (Cracraft 1988: 351); Cracraft and Mindell (1989: table 1, character 17). The last, perhaps best-named "fenestra proötica postquadratocotylaris," was included by Rotthowe and Starck (1998: character 31) as "large window in prooticum" and illustrated in considerable detail; a simplified version of this character, included by Cracraft and Clarke (2001: appendix 2, character 14), was interpreted as synapomorphic for palaeognathous birds by Witmer (1990: 372, character 18); G. Mayr and Clarke (2003: appendix A, character 31); Dyke and van Tuinen (2004: appendix 1, character 19); G. Mayr and Ericson (2004: appendix I, character 18), attributing pila otica and fenestrae to ossa opisthoticum et proöticum.

0225. Recessus pneumatici paratympanici, recessus tympanicus dorsalis, cotyla quadratica, pila subcotylaris (**new term**), status:

a. absent; **b.** present.

Note.—Serves to confine processus oticus quadrati within cotyla quadratica otici, exposed in ventral perspective.

0226. Recessus pneumatici paratympanici, recessus tympanicus dorsalis, depressio foraminis pneumaticum dorsale on ossa proöticum et/aut opisthoticum, status et forma (**unordered**):

a. absent;

b. present, dorsally exposed fossa;

c. present, deep caudolaterally exposed concavitas.

Note.—See: Norell et al. (2001: appendix 1, character 23); J. M. Clark et al. (2002a: appendix 2.2, character 16); Xu (2002: suite II, character 68); Xu et al. (2002a: supplement, character 13), regarding "depression for pneumatic recess on proötic" in selected nonavian Theropoda; Ji et al. (2003b); Hwang et al. (2004: supplement, character 16); Xu and Norell (2004: supplement, character 16); Bourdon et al. (2005: appendix 1, character 32).

0227. Recessus pneumatici paratympanici, recessus tympanicus dorsalis, enlargement of recessus and development of margo of recessus lateralis as prominent crista crescentiformis (**new term**), status:

a. absent; **b.** present.

Note.—See: Currie and Zhao (1994a–b [1993a–b]); Norell et al. (2001: appendix 1, character 12); J. M. Clark et al. (2002a: appendix 2.2, character 6); Xu (2002: suite II, character 60), regarding crista et recessus pneumaticus between ossa proöticum et basisphenoidale; Hwang et al. (2004: supplement, character 6); Xu and Norell (2004: supplement, character 6), in reference to "otosphenoidal crest . . . on basisphenoid and prootic." Also, Witmer (1990: character 14) and Cracraft and Clarke (2001: appendix 2, character 15, part) characterized the status of a "foramen pneumaticum ipsilaterale" that effects communication between recesses tympanicus dorsalis et caudalis (recessus pneumatici paratympanici), noting much homoplasy among Neornithes.

0228. Recessus pneumatici paratympanici, recessus tympanicus rostralis, status (**unordered**):

a. absent; **b.** present; **c.** vestigial.

Note.—See: Makovicky and Sues (1998); Maryanska et al. (2002: appendix 1, character 55), in reference to presence of "three tympanic recesses"; Rauhut (2003: character 59); Bourdon et al. (2005: appendix 1, character 28), including different distribution of feature among Pelecaniformes. Similar but independently derived recessus occurs among Crocodylomorpha (Gower and Weber 1998).

0229. Recessus pneumatici paratympanici, recessus tympanicus rostralis, facies ventralis, ostium, forma:

a. occluded ventrally, forming entire circular rima ossea;

b. rima ossea imperfect rostroventrad, including a variably deep incisura.

Note.—See: Cracraft (1985: characters 14–15); Siegel-Causey (1997: table I, characters 12 and 16), regarding differing treatments of "lateral wall" or "bony ring" of "presphenoid sinus," for which a limited survey segregated taxa Phalacrocoracidae, Sulidae, and Pelecanidae from others.

0230. Recessus pneumatici paratympanici, recessus tympanicus rostralis, synostosis of ala parasphenoidalis and processus paroccipitalis, resulting from (*i*) caudal displacement of ostium recessi pneumatici rostralis and (*ii*) incisura between ostium and processus paroccipitalis, status et forma (**ordered**):

a. absent; **b.** present, rima cum incisura;

c. present, rima entire.

0231. Recessus pneumatici paratympanici, recessus tympanicus rostralis, paries caudolateralis, forma (**ordered**):

a. markedly thickened, cancellous;

b. moderately thickened, cancellous;

c. thin lamina, acancellous;

x. noncomparable by undeveloped paries lateralis (*Diomedea*, *Anhinga*, *Phalacrocorax*).

0232. Recessus pneumatici paratympanici, recessus tympanicus caudalis, aspectus superficialis:

a. variably concealed within recessus columellae;

b. superficial.

Note.—See: Cracraft (1981a: 686); Cracraft (1986: appendix, character 55); Cracraft (1988: series IX, character 1), with respect to enlargement of upper tympanic recess; Chiappe et al. (1996: appendix 1, character 81).

0233. Recessus pneumatici paratympanici, recessus tympanicus caudalis, apertura pneumaticum, orientation:

a. toward ossa otica, penetrating processus paroccipitalis, margo rostralis;

b. toward cavum tympanicum, confined to recessus columellae.

Note.—See: Currie (1985); Witmer (1990: 372, character 13); Chiappe et al. (1996: appendix 1, character 81); Chiappe et al. (1998: character 10); Ji et al. (1998: supplement, character 10), with respect to "caudal tympanic recess opens on the rostral margin of the paraoccipital process or into the columellar recess"; Livezey (1998b: appendix A, character 84); Makovicky and Sues (1998: appendix 1, character 14), with respect to states contrasted as "parasphenoid flat and nonpneumatic" *vs.* "inflated and pneumatized by anterior tympanic recess" citing J. M. Clark et al. (1994); Chatterjee (1999: appendix II, character 13), who cited Witmer (1990) in context of "squamosal roof to the superior tympanic recess"; Holtz (2000 [1998]: appendix I, character 92), in reference to "posttympanic recess," and citing Makovicky and Norell (1998) with respect to "squamosal recess" of Witmer (1997); Chiappe (2001a: appendix 1, character 22); Cracraft and Clarke (2001: appendix 2, character 15, part); Chiappe (2002: appendix 20.2, character 22); Maryanska et al. (2002: appendix 1, character 54); Xu (2002: suite II, character 70); Xu et al. (2002a: supplement, character 15, modified and polarity reversed), in reference to "caudal (posterior) tympanic recess" relative to "paroccipital process."

0234. Recessus pneumatici paratympanici, recessus tympanicus caudalis, status et situs relative to processus paroccipitalis et os opisthoticum:

a. recessus tympanicus caudalis not evident;

b. on facies rostralis of processus paroccipitalis;

c. extending into os opisthoticum caudodorsal to fenestra ovalis.

Note.—The recessus referred to as "caudalis" here, moves to dorsal or superior position in some taxa, but caudalis remains most appropriate for inclusion of Aves. See: Norell et al. (2001: appendix 1, character 25); J. M. Clark et al. (2002a: appendix 2.2, character 18); Xu (2002: suite II, character 70); Xu et al. (2002a: supplement, character 15), in reference to "caudal (posterior) tympanic recess" and position relative to "paroccipital process"; Maryanska et al. (2002: appendix 1, character 55), in reference to presence-absence of "three tympanic recesses." Problematic determinations may accompany many Neornithes in light of the ontogenetically early synostosis of the ossa otica (ossa proöticum, epioticum, opisthoticum, et metoticum); Hwang et al. (2004: supplement, character 18); Xu and Norell (2004: supplement, character 18).

0235. Recessus pneumatici paratympanici, status et forma (**ordered**):

a. absent; **b.** present, shallow;

c. present, deep.

Note.—See: J. D. Harris (1998); Currie et al. (2003: appendix, character 5); Rauhut (2003: character 57).

0236. Recessus pneumatici paratympanici, ossa inclusiva:

a. ossa basisphenoidale et basioccipitale;

b. entirely os basisphenoidale.

Note.—See: Makovicky and Norell (1998); Holtz (2000 [1998]: appendix I, character 93), in reference to cranial tympanic recess and os basisphenoidale; Chiappe (2001a: appendix 1, character 23); Norell et al. (2001: appendix 1, character 18); Chiappe (2002: appendix 20.2, character 23); J. M. Clark et al.

(2002a: appendix 2.2, character 9); Vickers-Rich et al. (2002), concerning *Avimimus*; Xu (2002: suite II, character 63); Xu et al. (2002a: supplement, character 8); Hwang et al. (2004: supplement, character 9); Xu and Norell (2004: supplement, character 9).

0237. Recessus pneumatici paratympanici, recessus tympanicus rostralis, forma:

a. comprises single, confluent recessus delimited by enlarged crista basisphenoidalis (otosphenoidalis) aut depressio lateralis;

b. comprises separate partes proötica et basisphenoidalis;

x. noncomparable or undetermined (Avialae, including Neornithes).

Note.—See: Norell et al. (2000: appendix 1, character 22).

Columella (Stapes)

Note.—Reviews given by G. W. Smith (1905), H. J. Müller (1963), Feduccia (1975a–c), Smit and Frank (1979), and Kühne and Lewis (1985). Information on the columella of Dinornithiformes was provided by Worthy and Holdaway (2002: 109–110). Cartilago extracolumellaris articulates with extremitas distalis columellae and is attached to membrana tympanica (Evans and Martin 1993: annotations 53–54), and together are drawn by a single muscle—m. columellae—which passes through foramen m. columellae, adjacent to hiatus subtympanicus.

Feduccia (1975a–c) concluded that the vast majority of nonpasseriform taxa and virtually all passeriform birds retained a plesiomorphic condition of the columella, one strongly reminiscent of that of Reptilia and varying little in most or all of the primary features of the columella (e.g., *stipes* for shaft, *clipeolus* for disc or "small shield"), and resemble known columellae of Dinosauria (Colbert and Ostrom 1958). Basic sources of conformational data were Krause (1901) and J. M. Starck (1995: figs. 45–50). Feduccia (pers. comm.) provided unpublished data on a number of critical taxa.

0238. Columella, stipes columellae (**new term**)—corpus, basis, et fenestrae—forma (**unordered**):

a. unicolumnar, variably hollow, unfenestrated;

b. unicolumnar, variably hollow, perforated by one or two fenestrae;

c. unicolumnar, variably hollow, multiply micro/macro-fenestrate;

d. bicolumnar or multistipulate.

Note.—See: Krause (1901); Feduccia (1974, 1975a–c, 1976b, 1977a–b); Feduccia and Ferree (1978); J. M. Starck (1995: fig. 45); G. Mayr (2003a: fig. 2; appendix I, character 6); G. Mayr (2003b: appendix I, character 6), regarding Trogonidae; G. Mayr (2004b: appendix 1, character 23), in reference to "tubular" columella.

0239. Columella, stipes columellae (**new term**), extremitas lateralis stipitis, processus supracolumellaris (processus rostralis) et processus infracolumellaris (processus caudalis), prominence (relative to stipes) et orientation (relative to stipes), forma:

a. comparatively short, distal, and oriented laterodistad;

b. comparatively elongate, intermediate, and oriented perpendicularly, contributing to an "anvil-like" aspect.

Note.—Terms follow Krause (1901), H. J. Müller (1963), and J. M. Starck (1995); processes synonymous with "distal condyle" and "distal process" of Feduccia (1975c: fig. 2), and the synonyms of Kühne and Lewis (1985) after Stellbogen (1930), are shown in square brackets. See: Feduccia (1974, 1975a–c, 1976b, 1977a–b); Van Tyne and Berger (1976: fig. 10); Smit and Frank (1979: fig. 6); Feduccia and Olson (1982); J. M. Starck (1995: fig. 45); G. Mayr (2002a: legend for fig. 9, node 5, character 2); Worthy and Holdaway (2002: fig. 423); G. Mayr (2003a: appendix I, character 20). May pertain to the feature described by Rotthowe and Starck (1998: appendix, character 39) as "ossification of proc. infracolumellaris columellae (= lateral basitemporal process)" and credited to Bock and McEvey (1969a).

0240. Columella, clipeolus columellae (**new term**), forma generalis (**unordered**):

a. laminar, margo basalis (sub)circular, diameter variable, typically including one to several fenestra caudalis et fossa interna;

b. hemiglobular or "umbrelliform," facies ventralis distinctly convex, with dorsal or internal aspect of clipeolus fenestrate;

c. (semi)globular, margo basalis (sub)triangular or (sub)circular, typically including one fenestra caudalis et fossa interna.

Note.—Terms follow: Krause (1901), H. J. Müller (1963), and J. M. Starck (1995), from which the term "clipeolus" is intended as a diminutive of "clipeus" meaning "(round) shield"; the latter corresponds to the "foot plate" of Feduccia (1974, 1975a–c, 1976b, 1977a–b), Van Tyne and Berger (1976: fig. 10), Feduccia and Ferree (1978), Feduccia and Olson (1982), and Raikow (1987: table 1; character 27). See: Smit and Frank (1979: fig. 6); J. M. Starck (1995: figs. 45–50); J. A. Clarke et al. (2002), regarding oviraptorosaur *Citipati*; G. Mayr (2003a: appendix I, character 20); G. Mayr (2003b: fig. 2; appendix I, character 6); G. Mayr and Clarke (2003: appendix A, character 39); G. Mayr et al. (2003: appendix 1, character 18); Dyke and van Tuinen (2004: appendix 1, character 25); G. Mayr (2004d: appendix I, character 6); G. Mayr (2005a: appendix 1, character 6).

Orbita

Note.—Phylogenetically informative features of the orbita of Theropoda, including Aves, include aspects of the bounding elements (ossa prefrontale, lacrimale, frontale, postorbitale, laterosphenoidale, mesethmoidale, ectethmoidale, orbitosphenoidale, et squamosum), secondary ossifications (e.g., septum interorbitalis, or deficiencies thereof, fonticulae interorbitales), and the spatium defined thereby (Chure 1998).

0241. Orbita, length relative to fenestra antorbitalis internus:

a. shorter than internal antorbital fenestra length;

b. subequal or moderately longer than internal antorbital fenestra length;

c. expanded, markedly greater than internal antorbital fenestra length.

Note.—Length quantified by maximal or dorsoventrally intermediate, craniocaudal length of margines ossea relative to that of fenestra antorbitalis. See: Holtz (1994a: appendix 1, character 73); Pérez-Moreno et al. (1994: legend for fig. 3, character 7); Chure (1998); Holtz (2000 [1998]: appendix I, character 44); Maryanska et al. (2002: appendix 1, character 24); Xu et al. (2002b); J. A. Clarke (2004: fig. 19).

0242. Margines orbitae (lateral perspective), forma (**unordered**):

a. orbiculate;

b. ovate or claviform (“key-shaped”), dorsum rounded, ventrum narrow.

Note.—See: Gauthier (1986); Holtz (1994a: appendix 1, character 28); Russell and Dong (1994b [1993b]: troödontid character 5), with respect to “anteromedially inclined orbit”; J. D. Harris (1998: appendix 2, character 18); Currie and Carpenter (2000: appendix 1, character 22), in which orbita characterized by “expanded and circular”; Holtz (2000 [1998]: appendix I, character 45); Norell et al. (2001: appendix 1, character 8); J. M. Clark et al. (2002a: appendix 2.2, character 2); Xu (2002: suite II, character 57); Xu et al. (2002a: supplement, character 2), in which the alternative to “round” was “dorsoventrally elongate.” Holtz (1994a: appendix 1, character 73) included circular shape with assessment of size; Hwang et al. (2004: supplement, character 2); Xu and Norell (2004: supplement, character 2). Review of orbita in theropods by Chure (1998).

0243. Paries caudalis orbitae, septum postocularis (**new term**), status:

a. absent; **b.** present.

Note.—See: Benton (1990b: 24). Septum postocularis (**new term**) is synonymous with the “palpebral”—a term reserved for integumental “eyelids”—which in Mesozoic Aves refers to osseus laminae caudal to the bulbus oculi within the orbita and comprising contributions from both ossa postorbitale et jugale (Maryanska 1977).

0244. Paries caudalis orbitae, generalized deficiency of ossification of entire paries leaving only lateromedial trabecular representation of crista tentorialis and linea cerebralis optici (**new term**) separating dorsal and ventral, elongate fenestrae, status:

a. absent, including presence of more-restricted deficiencies in paries;

b. present.

Note.—Principally or wholly os laterosphenoidale.

0245. Paries medialis orbitae, septum interorbitale, status:

a. absent; **b.** present.

Note.—Septum interorbitale often assumed to be primarily or wholly a derivation of os mesethmoidale. Includes relative development of lamina interna, crista frontalis interna (Livezey 1998b: character 73).

See: Zusi (1978); Bang and Wenzel (1985); Cracraft (1985: characters 19–20); Cracraft (1986: appendix, character 50); Gauthier (1986: 13, unindexed synapomorphy of Ornithurae); Houde (1988: table 27, character 14); Chatterjee (1991: character 25); Holdaway (1991: appendix 5.1, character 22); Andors (1992: table 2, character 1); Siegel-Causey (1997: table I, character 17); Chu (1998: appendix 1, character 23); Chure (1998), for review of orbita in nonavian theropods; Chatterjee (1999: appendix II, character 23); J. A. Clarke and Chiappe (2001: character 67); Norell and Clarke (2001: appendix I, character 25), who erroneously attributed septum entirely to os mesethmoidale, treated similarly by J. A. Clarke (2002: appendix I, characters 25 [status]–26 [position]), J. A. Clarke and Norell (2002: appendix 2, characters 25–26), and J. A. Clarke (2004: appendix 1, characters 25–26); Coria and Currie (2002: appendix 1, character 4); Zhou and Zhang (2002: appendix III, character 25). G. Mayr (2002a: appendix 1, character 5) and G. Mayr et al. (2003: appendix 1, character 14), characterized related “cone-like bony protrusion at caudal margin of foramen nervi optici,” herein determined to be unacceptably variable and widespread; G. Mayr and Ericson (2004: appendix I, character 1); Ji et al. (2005: supplement, part I, characters 25–26), mistakenly attributed to os mesethmoidale; G. Mayr (2005a: appendix 1, character 1); G. Mayr (2005b: appendix 1, character 5).

0246. Paries medialis orbitae, large cavum ethmomandibularis (**new term**) lateral to septum interorbitale and caudodorsal in orientation, status:

a. absent; **b.** present.

Note.—Closed internally by membrana, partially occupied by origo m. ethmomandibularis. See: D. W. Thompson (1899).

0247. Fonticulus interorbitalis (septae), status et forma (**unordered**):

a. absent;

b. present, separated from foramen opticum;

c. present, lacking osseus partition from (continuous with) foramen opticum.

Note.—Intraspecifically, ontogenetically variable. Some nonexemplar Coraciiformes, Piciformes, and Passeriformes vary from exemplar taxa (Donatelli 1996a, 1997; Pascotto and Donatelli 2003). See: Bellairs (1958); Payne and Risley (1976: characters 5–6), regarding Ardeidae; Cracraft (1985: character 19); Siegel-Causey (1988: character 16); Holdaway (1991: appendix 5.1, character 22); Chu (1998: appendix 1, character 32); Chure (1998); Livezey (1998b: appendix A, character 67).

0248. Fonticulus orbitocranialis (if present), confluence with foramen nervorum olfactorii et foramen opticum, status:

a. absent; **b.** present.

Note.—See: Shufeldt (1902a: pls. ii and vi); Harrison and Walker (1976b: pl. i, fig. c); Chu (1998: appendix 1, characters 33–35), in which an attempt was made to determine participation of individual nervi with fonticulus (e.g., n. olfactorii et opticum); Bourdon et al. (2005: appendix 1, character 35), emphasizing bipartite form of foramina; Bourdon et al. (2005: appendix 1, character 36), regarding confluence of foramina nervorum oculomotorii, trochlearis, et opthalmici.

0249. Ventrum (solum) orbitae, fenestra suborbitalis (**new term**), status et rostrocaudal length relative to that of orbita et ossa inclusiva (**unordered**):

a. present, approximately equal;

b. present, moderately reduced by os ectethmoidale, approximating three-fourths of orbita;

c. present, moderately reduced by processus lateralis palatini, approximating three-fourths of orbita.

Note.—This ill-defined character ("suborbital fenestra") evidently refers to solum orbitae as delimited by ossa enclosing the ventrum oculi (ossa varying among taxa), or the spatium or fenestra representing the lack thereof. Ossa facialis aut cranii rarely occlude this "fenestra" among Theropoda, the ventrum orbitae closed in life by musculi mandibulae and associated ligamenta. The present character refers to relative lengths (parallel to axis majoris cranii) of orbita and fenestra ventral to orbita, and provisionally included given the usage in the paleontological literature. See: Norell et al. (2001: appendix 1, character 11); J. M. Clark et al. (2002a: appendix 2.2, character 66); Xu (2002: suite II, character 104); Xu et al. (2002a: supplement, character 49); Hwang et al. (2004: supplement, character 65); Xu and Norell (2004: supplement, character 65).

0250. Orbita, septum interorbitalis, paries dorsalis, canalis (sulcus) n. olfactorius, ostium rostralis, forma:

a. variably occult fissura;

b. prominent, voluminous, involucral tuba.

Note.—Form and position vary moderately among taxa possessed of prominent canalis.

Foramina orbitonasales mediale et laterale

Note.—These ostia manifest extreme variation in expanse, position, and shape, a condition consistent with their anatomical derivation—i.e., the failure of a suite of skeletal elements (ossa ectethmoidale, mesethmoidale, lacrimale, et frontale) to meet or occlude the fossa et/aut fenestra orbitonasale and included foramina propria (e.g., foramina n. olfactorius, fenestra aut sulcus ducti nasolacrimalis, ostia glandulae, et ducti nasalis). Accordingly, much of the reliably scored variation is compiled under the os(sa) involved. *Absence* of ossification *per se* is prone to variation among conspecifics and related to age, nutrition, or preparation of specimens, and homologies are virtually impossible to determine with respect to specific soft structures without dissections. Nevertheless, *Gestalten* suggestive of informative variation is obvious (e.g., in parrots and columbiforms). To the contrary, the virtual absence of ossification within the fossa antorbitalis in palaeognathous taxa, and marked contrasts in ossification between closely related families (e.g., Phalacrocoracidae and Anhingidae), underscore the need for caution in the characterization of variations in this region.

0251. Foramen orbitonasale laterale, extensive ossification such that foramen (i.e., ostium dorsolateralis) is (*i*) markedly restricted by ossa lacrimale, ectethmoidale, et frontale, (*ii*) subovate or subcircular in form, and (*iii*) larger than foramina neurovascularia (e.g., foramen n. olfactorius) also perforating lamina (paries) ossificans antorbitalis (**new term**), status et forma *sensu* principal orientation (**unordered**):

a. absent; **b.** present, rostrocaudal;

c. present, partly lateromedial—by rostral extension of processus orbitalis ossis lacrimale with respect to planum ossis ectethmoidale;

x. noncomparable by absence of ossa lacrimale aut ectethmoidale or articulatio lacrimo-ectethmoidalis (*Apteryx*, *Anatoidea*, *Pelecanoides*, *Spheniscus*, *Gavia*, *Podiceps*, *Fregata*, *Sula*, *Pelecanus*, *Cochlearius*, *Scopus*, *Ciconia*, *Phoenicopterus*, *Balaeniceps*, *Thinocorus*, *Podargus*, *Aegotheles*, Apodidae, *Glaucis*, *Momotus*, most Piciformes and Passeriformes).

Note.—See: Technau (1936); Chu (1998: appendix 1, character 36).

0252. Margo supraorbitalis, dorsolateral expansion from axis majoris craniofacialis into rima supraorbitalis (**new term**), status:

a. absent, margo orbitalis smooth;

b. present, rima moderately distinct.

Note.—Primarily or completely encompassed by os frontale. See: Holtz (1994a: appendix 1, character 76); Livezey (1997a: appendix 1, character 9; *corrigenda*, Livezey 1998a); Chure (1998); Livezey (1998b: appendix A, character 69); Holtz (2000 [1998]: appendix I, character 46); Hughes (2000: appendix 2, character 4). In Charadriiformes, treated by Strauch (1985: character 5) for Alcidae, and Chu (1998: appendix 1, character 5) for Laridae, variably confounded by variation in the sulcus glandulae nasalis.

0253. Margines supraorbitales, regio interorbitalis dorsalis (dorsal perspective), forma:

a. concave, regio interorbitalis dorsalis distinctly narrow, producing an "hourglass" profile;

b. sublinear to slightly concave, regio interorbitalis dorsalis not differing markedly from, or conformal with general caudorostral taper between, adjacent regiones.

Note.—Primarily or completely encompassed by ossa frontales; pronounced effects caused by ossa lacrimales to be discounted.

See: Livezey (1998b: appendix A, character 71).

0254. Margo infraorbitalis, arcus suborbitalis, evidently representing ligamentum suborbitale ossificans, status:

a. absent; **b.** present.

Note.—See: Livezey (1986: appendix 1, character 10); Livezey (1995a: appendix 1, character 1); Livezey (1996a: appendix 1, character 1). Confamilials of exemplars of Anatidae (*Dendrocygna*), Scolopacidae (*Scolopax*, *Gallinago*, and *Limnocryptes*), and *Trichoglossus* (some Psittaciformes) also show apomorphy of this character.

Rostrum Maxillae (Maxilla)

0255. Hiatus craniofacialis septi osseum, status definitivum:

a. present, septum nasi variably manifested;

b. absent, forming a continuous medial lamina ossea craniofacialis (**new term**), and rostrum parasphenoidale that passes rostrad to processes maxillaris nasale aut nasalis maxillare.

Note.—Apomorphy is most obvious in taxa possessed of extensive, lateroventrally conspicuous rostrum parasphenoidales or expanded margo ventralis septi; associated with rostro-cranial kinesis. Some confamilials of taxa Scolopacidae (e.g., *Scolopax*, *Gallinago*, *Limnodromas*) and Trochilidae (e.g., *Ensifera*), lacking hiatus craniofacialis, possess a continuous medial lamina ossea craniofacialis (**new term**), but rostrum parasphenoidale fails to pass rostrad to processes maxillaris nasale aut nasalis maxillare.

See: Butendieck (1980); Butendieck and Wissdorf (1981); Butendieck et al. (1981); Bühler et al. (1988); Baumel and Witmer (1993: annotation 10); Norell and Clarke (2001: appendix I, character 26), and treated similarly by J. A. Clarke (2002: appendix I, character 26) and J. A. Clarke and Norell (2002: appendix 2, character 26), treated in part in terms of septum interorbitalis; Zhou and Zhang (2002: appendix III, character 26), in which continuity of septa interorbitalia was attributed solely to derivatives of os mesethmoidale; G. Mayr and Clarke (2003: appendix A, character 10), in terms of rostral continuity of septa.

Rostrum maxillae

Note.—Previous treatments have been limited largely to lower-scale contexts (e.g., Livezey 1986; James et al. 2003), a scale that permits more subtle differences to be coded without intermediacy or exception and avoids problems of comparability among higher-order taxa.

0256. Facies dorsalis rostri, diastema subnarialis at sutura premaxillaro-maxillaris, margo tomialis (alveolus), status:

a. absent; **b.** present;

x. noncomparable by absence of alveoli et dentes (Neornithes).

Note.—Sutural modifications related to this hiatus commonly manifested by difference in dorsoventral positions of margines tomiales of ossa premaxillare et maxillare, and typically effects diastemae in alveoli maxillae et/aut dentales; one or more diastema maxillae et dentale with corresponding, variably recurved dentes falchioniformes (**new term**; "fangs") typify the Crocodylia (Romer 1956), often with maxillary "fangs" passing entirely laterad to mandibula with mandibular counterparts accommodated by foveae dentorum dorsales (latter evidently derived from primordia for alveoli dentales). See: Welles (1984); Gauthier (1986); Rowe (1989); Rauhut (2003: character 9), regarding "subnarial gap"; Novas et al. (2004: appendix, character 44).

0257. Rostrum maxillae, crista tomialis, lateroventral convexity continuous from gape to base of hamulus terminalis, status:

a. absent; **b.** present.

0258. Rostrum maxillae, facies ventralis rostri, sulcus paratomialis (**new term**), status et extentio (**ordered**):

a. absent;

b. present, rudimentary or absent rostrad;

c. present to apex.

Note.—Sulcus paratomialis is distinct from gape to apex of the rostrum, delimited throughout by medial linea, and terminating caudally through fluted antrum. Excludes the abbreviated sulci of some Procellariformes and Ciconiiformes. See: Cracraft (1985: character 4); Ericson (1997: table 1, character 14); G. Mayr (2003a: appendix 1, character 4).

0259. Rostrum maxillae, facies dorsalis rostri, foramen (suturalis maxillaro-premaxillaris) subnasalis (**new term**), status et forma (**unordered**):

a. present, a suborbiculate foramen;

b. present, a narrow fissura;

c. absent, suturae maxillaro-premaxillares complete.

Note.—Variously referred to as "fenestra antorbitalis tertius" or "accessory antorbital fenestra," this lacuna suturalis is present in a number of nonavian, principally basal Theropoda (Witmer 1997), in which the sutura maxillaro-premaxillaris and an expanse of os premaxillare are caudal to the margo rostralis of the apertura nasalis (Sereno and Novas 1992: figs. 1 and 9–10). See: Sereno and Novas (1992: appendix, character 15), in reference to a "subnarial foramen"; Sereno et al. (1993: legend for fig. 3a); J. M. Clark et al. (1994); Holtz (1994a: appendix 1, character 6); Novas (1994 [1993]: appendix, character 24), who included Tetanurae among taxa possessing foramen; Forster et al. (1998: supplement, character 22); Xu et al. (1999b: character 20); Holtz (2000 [1998]: appendix I, character 11), coding *Protarchaeopteryx*, *Caudipteryx*, and *Confuciusornis* as "0."

0260. Rostrum maxillae, facies dorsalis rostri, medial length relative to that of cranium (**ordered**):

a. 0.40–2.00; **b.** 2.01–3.00;

c. 3.01–3.50; **d.** greater than 3.51.

Note.—Relative midline length is assessed by chord from zona flexoria craniofacialis to apex divided by length of remainder of skull. Note that intervals associated with states "a"–"c" were 1.5, 1.0, and 0.5, respectively. Failure of exemplars to be representative of families especially vexing here. Comparatively common state "a" proved indivisible using the method of Thiele (1993). See: Payne and Risley (1976: character 1), regarding Ardeidae; Cracraft (1982: series 1, character 3, part); Raikow (1994: table 2, character 30); Livezey (1998b: appendix A, character 45), for dorsoventral depth; Livezey (1998b: appendix A, character 46), for lateromedial width; Livezey (1998b: appendix A, character 47); Xu (2002: suite I, character 72), using relative mandibular length.

0261. Rostrum maxillae, facies dorsalis rostri, fenestra (suturalis maxillaro-premaxillaris) subnasalis (**new term**), status:

a. present; **b.** absent.

Note.—Evidently caused by failure of ossa to meet, thereby forming an intervening foramen aut fissura maxillaro-premaxillaris, possibly indicative of kinesis between the two elements of the rostrum maxillare at the junctura maxillaro-premaxillaris. This perforation is a comparatively small, orbiculate foramen interposed within the sutura maxillaro-premaxillaris, ventral to the fenestra subnasalis (above), and variably dorsal to and more prominent than the supratomial series of foramina neurovascularia (Welles 1984; Gauthier 1986; Rowe 1989). This laterorostral feature is distinct from the *accessorische Gamenlucken* of Hofer (1949), termed fenestra ventrolateralis (**new term**) herein, which is a feature of the caudolateral apex of the palatum osseum and typically not visible in lateral perspective.

See: Gauthier (1986); Sereno and Novas (1992: appendix, character 2), termed "premaxilla-maxilla fenestra"; Holtz (1994a: appendix 1, character 25), in reference to "premaxillary-maxillary fenestra" and credited to Osborn (1912); also by Holtz (1994a: appendix 1, character 108), in reference to "pronounced, round accessory antorbital fenestra"; Sereno et al. (1994: footnote 12); Sereno et al. (1996: footnote 45, character 1); K. Carpenter (1997); Sues (1997: appendix 1, character 4); Makovicky and Sues (1998: appendix 1, character 8), terming this feature the "accessory maxillary fenestra"; Chatterjee (1999: appendix II, character 9), refers to a "maxillary fenestra" that is present in nonavian theropods, *Archaeopteryx*, and *Avimimus*, but lost in others; Xu et al. (1999a: character 6); Ji et al. (2001), regarding unnamed dromaeosaurid NGMC 91-A and absence of "accessory antorbital foramen"; Norell et al. (2001: appendix 1, character 4); J. M. Clark et al. (2002a: appendix 2.2, character 28); Maryanska et al. (2002: appendix 1, character 15), regarding "accessory maxillary fenestrae"; Vickers-Rich et al. (2002), concerning *Avimimus*; Xu (2002: suite I, character 75; suite II, character 23); Xu et al. (2002a: supplement, character 20); Xu et al. (2002b); Hwang et al. (2004: supplement, character 27); Xu and Norell (2004: supplement, character 27).

0262. Rostrum maxillae, basis rostri (ossa maxillare et palatinum), distension well ventrad (lateral perspective) to crista tomialis et complement of palatum osseum, status:

a. absent; **b.** present.

Note.—Ventralmost jugae of distension typically composed of partes caudales of processes maxillares palatini. See: Bourdon et al. (2005: appendix 1, character 38).

0263. Rostrum maxillae, facies dorsalis rostri, fenestra suturalis maxillaro-premaxillaris (**new term**), situs rostrocaudalis relative to fossa antorbitalis:

a. at margo rostralis of latter;

b. caudal to margo rostralis of latter;
x. noncomparable (Neornithes).

Note.—See: Norell et al. (2001: appendix 1, character 6); J. M. Clark et al. (2002a: appendix 2.2, character 29); Xu (2002: suite II, character 242); Hwang et al. (2004: supplement, character 28); Xu and Norell (2004: supplement, character 28).

0264. Rostrum maxillae, facies dorsalis rostri, fenestra suturalis maxillaro-premaxillaris (**new term**), size:
a. small; **b.** large.

Note.—See: Norell et al. (2000: appendix 1, character 6).

0265. Rostrum maxillae, facies dorsalis rostri, hamulus rostri maxillae osseum (**new term**), status:
a. absent; **b.** present.

Note.—Hamulus present where line from apex maxillae, dorsally tangential to crista tomialis, defines an angulus exceeding 45° (diagonality) with line passing through sutura jugomaxillaris at the anterior terminus of arcus jugalis and dorsalmost point of crista tomialis.

See: Cracraft (1985: character 5); Cracraft (1988: series IX, character 4); Siegel-Causey (1988: character 137); G. A. Clark (1993b: annotation 12); J. M. Clark et al. (1994); Livezey (1998b: appendix A, character 22); G. Mayr (2003a: appendix I, character 1); G. Mayr and Clarke (2003: appendix A, character 2); Dyke and van Tuinen (2004: appendix 1, character 1); G. Mayr (2004b: appendix 1, character 1); Bourdon et al. (2005: appendix 1, character 1).

0266. Rostrum maxillae, facies dorsales rostri, eminentia internariales (**new term**), status (**unordered**):
a. absent;
b. present, a single, median cornu or crista;
c. present, paired linear crista along ossa nasales, extending onto margo rostralis of frons;
d. present, rugose tuberositae, including foveae et cristulae.

Note.—See: Currie and Carpenter (2000: appendix 1, character 6), pertaining to "sculpturing" of ossa maxillare et nasale; Holtz (2000 [1998]: appendix I, character 26); G. Mayr (2002a: fig. 2C), regarding *Scopus*.

0267. Rostrum maxillae, facies dorsales rostri, cristae nasolacrimales (**new term**), status:
a. absent; **b.** present, crescentiform.

Note.—See: Rowe (1989); Holtz (2000 [1998]: appendix I, character 27).

0268. Rostrum maxillae, latus rostri, virtual linearity (lateral perspective) throughout basal three-fourths of rostrum, status:
a. absent; **b.** present.

Note.—See: Payne and Risley (1976: character 1), regarding Ardeidae.

0269. Rostrum maxillae, latus rostri, forma recurvatura, status:
a. absent; **b.** present.

Note.—Paralled by rostrum mandibulae. See: Livezey (1997a: appendix 1, character 29; *corrigenda*, Livezey 1998a); see related character by Livezey (1997a: appendix 1, character 30; *corrigenda*, Livezey 1998a); Livezey (1997b: appendix 1, characters 2–3).

0270. Rostrum maxillae, latus rostri, forma decurvatura (lateral profile), status:
a. absent; **b.** present.

Note.—Apomorphy corresponds to uniform decurvature (lateral profile) in which a tangent line to the midpoint of the culmen defines a 45° angulus with planum of lamina basiparasphenoidalis.

See: Raikow (1994: table 2, character 28); Livezey (1996a: appendix 1, character 4), with respect to rostrum; Livezey (1997b: appendix 1, character 1); Veron (1999: appendix: character 16); Murray and Vickers-Rich (2004: table 9, character 1).

0271. Rostrum maxillae, facies laterodorsalis rostri, regio nasalis, pneumaticitas, magnitude:
a. limited; **b.** extensive.

Note.—See: Norell et al. (2001: appendix 1, character 3); J. M. Clark et al. (2002a: appendix 2.2, character 32); Vickers-Rich et al. (2002), concerning *Avimimus*; Xu (2002: suite I, character 25; suite II, character 78); Hwang et al. (2004: supplement, character 31); Xu and Norell (2004: supplement, character 31).

0272. Rostrum maxillae, facies dorsalis rostri, sulci nasi (**new term**), status:
a. absent;
b. present, complete to terminus rostri.

Note.—New term in reference to narrow groove from rostral margin of apertura nasi ossea significantly toward or to terminus of maxilla, the "nasal groove" of Cottam (1957); manifested by overlying rhamphotheca as well (Bang 1971). Comparatively broad and shallow among Ciconiiformes, especially some Ardeidae. Examinations of definitive sulci indicative of possible ontogenetic origin from mediolateral closure of plesiomorphically elongate apertura.

See: Payne and Risley (1976: characters 1–2), regarding Ardeidae; Cracraft (1985: character 4); Cracraft (1988: series IX, character 3); G. Mayr (2003a: appendix 1, character 4); G. Mayr and Clarke (2003: appendix A, character 4); G. Mayr (2004a: appendix 1, character 1); G. Mayr (2004b: appendix 1, character 5); Bourdon et al. (2005: appendix 1, character 4).

0273. Rostrum maxillae, facies dorsalis rostri, sulci basi-laterales aperturae nasi ossea, foramina neurovascularia et pneumatica, status:

a. absent; **b.** present, dense and prominent.

Note.—See: Gadow (1877); Jenkin (1957).

0274. Rostrum maxillae, facies dorsalis rostri (lateral perspective), forma:

a. smoothly rounded, convexity with modest increase in curvature immediately caudal to terminus rostralis;

b. abruptly subcornuate, convexity with dramatic increase in curvature immediately caudal to terminus rostralis.

Note.—See: J. M. Clark et al. (1994); Currie et al. (1994 [1993]), regarding caenagnathid theropod; Holtz (2000 [1998]: appendix I, character 13; fig. 6).

0275. Rostrum maxillae, facies dorsalis rostri, dorsoventral flattening and bilateral, subcircular rounding of anterior segment (which markedly exceeds breadth of basal segment of rostrum), accompanied by loss of ventral dimension of crista tomialis and coplanar arrangement of all anterior components of ossa premaxillares, as well as parallel conformation of rostrum mandibulae, status:

a. absent; **b.** present.

Note.—See: Payne and Risley (1976: character 1), regarding Ardeidae; Currie et al. (1994 [1993]), regarding caenognathid theropod.

0276. Rostrum maxillae, facies dorsalis rostri, straight and pointed conformation virtually lacking decurvature, crista tomialis (lateral perspective) rostral to apertura nasi osseum straight, status:

a. absent;

b. present, including lateromedially narrow, falchionate forms and comparatively broad, cuneate forms.

Note.—See: Payne and Risley (1976: character 1), regarding Ardeidae; Cracraft (1982: series 1, character 3, part).

0277. Rostrum maxillae, facies dorsalis rostri, forma characterized by elongation, broadening, and apical rounding with parallel sides, status:

a. absent; **b.** present.

Note.—See: S. L. Olson and Feduccia (1980a: 15); Livezey (1986: appendix 1, character 12); Livezey (1989: table 1, character 12); Livezey (1991: appendix 1, character 157); Livezey (1996a: appendix 1, characters 4, 10, 12, and 13); Ericson (1997: table 1, characters 15 and 20; table 2, characters 10 and 17); Livezey (1997a: appendix 1, characters 31 and 33; *corrigenda*, Livezey 1998a). Unique forms of *Eurynorhynchus* (Charadriiformes) and *Ajaia* (Ciconiiformes) not homologous with state "b," separable by violation of bilateral parallelism.

0278. Rostrum maxillae, apex (terminus) rostri, convexitas terminalis, foramina neurovascularia, status:

a. absent; **b.** present, variably prominent.

Note.—Vernacular synonym in Anseriformes is "dertrum" or "nail."

See: Livezey (1995b: appendix 1, character 3); Livezey (1997a: appendix 1, characters 32 and 34; *corrigenda*, Livezey 1998a). *Eurynorhynchus* (Charadriiformes) qualitatively distinct from state "b." Typically distinguished by contrasting pigmentation of overlying integument.

0279. Rostrum maxillae, apex (terminus) rostri, bulbositas apicalis (**new term**), status:

a. absent; **b.** present.

Note.—Bulbositates apicales typically occur in parallel on rostrum mandibulae. Demarcated caudally by pronounced jugum, externum differentiated from rest of bill by pori pneumatici et foramina neurovascularia, and accounting for roughly two-fifths of length of bill.

0280. Rostrum maxillae, conformational *Gestalt* rostri comprising: (*i*) distinctly triangular dorsoventral and lateromedial form, (*ii*) dorsoventral compression, (*iii*) variably prominent medial carina, (*iv*) short but strong terminal hamulus, (*v*) mediocaudal portion composed of triangular-shaped os maxillare, and (*vi*) arcus jugalis with variable, largely lateral orientation, status:

a. absent; **b.** present.

Note.—Descriptive of flattened, triangular bills of caprimulgiform birds, usually associated functionally with aerial capture of insect prey. See: G. Mayr (2002a: appendix 1, character 6), with respect to Caprimulgiformes; G. Mayr et al. (2003: appendix 1, character 2); G. Mayr (2005b: appendix A, character 6).

0281. Rostrum maxillae, conformational *Gestalt* rostri principally characterized by extreme lateromedial and dorsoventral narrowness relative to rostrocaudal length (i.e., variably long and slender, manifesting diversely curved or lanceolate form), status:

a. absent;

b. present, retained through adulthood.

Note.—Developing young showing apomorphic state manifest similarity to those of young of Hemiprocnidae and Apodidae showing apomorphy in adult.

0282. Rostrum maxillae, facies dorsalis rostri, basis rostri (approximating basal one-fifth of maxillary length), pronounced bilateral compression, status:

a. absent; **b.** present.

0283. Facies dorsalis rostri, extreme bilateral compression rostral to apertura nasi ossea (approximating rostral two-thirds of maxillary length), status:

a. absent; **b.** present.

0284. Rostrum maxillae, dorsum rostri (lateral perspective), prominent ventral bowing of ossa maxillares (primarily) et palatini near sutura palatinomaxillaris, exposing significant expanses of palatum rostral to the junctura (lateral perspective) of the arcus jugalis with rostrum maxillae and ventral to crista tomialis (if present), status:

a. absent; **b.** present.

Note.—Does not refer to simple ventral prominence of processus palatini, but a bowing and prominence of the entire complex.

0285. Facies ventralis rostri, medial carina (lateral perspective) extending from sutura maxillaropalatinus to apex maxillae, and extending ventrad to crista tomialis (coincident with synostosis interpremaxillaris), status:

a. absent; **b.** present.

Note.—Distinct from elongate, rounded jugum of *Phoenicopterus*, which does not extend to apex.

0286. Rostrum maxillae, facies ventralis rostri, extremely deep concavity encompassing virtually the entire structure, with associated extreme broadening and pronounced, monotonic convexity throughout length of facies dorsolateralis, status:

a. absent; **b.** present.

0287. Rostrum maxillae, facies ventralis rostri, elongate, rounded, jugum medialis terminating caudad to apex maxillae, status:

a. absent; **b.** present.

Note.—Not to be confused with comparatively abbreviated, ventrally prominent carina that extends to apex maxillae in *Falco* and *Polyborus*. See: Gadow (1877); Jenkin (1957).

0288. Rostrum maxillae, facies ventralis rostri, recessus caudalis rostri (**new term**), status:

a. absent; **b.** present.

Note.—In reference to uniquely deep concavitas between pars rostralis palatini and arcus jugas, in the deep, boxlike rostrum of *Balaeniceps*.

0289. Rostrum maxillae, facies ventralis rostri, fenestra ventromedialis (**new term**), status et forma (**unordered**):

a. present, variably prominent, confluent with fenestra choanalis, producing aspect of "schizognathy";

b. present, prominent, partitioned from fenestra choanalis by medial sutura vomeromaxillaris;

c. present, variably prominent, partitioned from fenestra choanalis by medial synostosis of ossa maxillares, processes palatini, producing aspect of "desmognathy";

d. present, but vestigial, reduced to fissura or series of foramina, unless otherwise indicated, by encroachment of os(sa) spongiosum;

e. absent, typically through occlusion by os spongiosum;

x. noncomparable (Psittaciformes).

Note.—New term refers to a variably conformed apertura medialis between the ossa maxillares in the palatum osseum. Termed by Hofer (1949, 1955) as *Oberschnabellucke*, related to "schizognathy" and "desmognathy" of Huxley (1867) and Hofer (1955), and considered in additional detail by Elzanowski (1995). See: D. W. Thompson (1899); Swart (1946); Simonetta (1957); Ligon (1967: table 1); Andors (1992: table 2, character 10).

0290. Rostrum maxillae, facies ventralis rostri, fenestra ventrolateralis (**new term**), status:

a. absent, not entirely circumlimited, lacking caudal osseus lamina;

b. present, closed caudally by osseus pons maxillaro-jugalis (**new term**).

Note.—First new term refers to variably exposed fenestra within os maxillare at basis rostralis of arcus jugalis, formed by enclosure of spatium by "strut" between processes palatinus et jugalis of os maxillare—pons maxillaro-jugalis (**new term**)—united by sutura jugomaxillaris. Termed by Hofer (1949) as *accessorische Gamenlucken* or accessory fenestra, also studied by Elzanowski (1995). Structure may be present and dorsally occluded to form fovea; problematic for most Passeriformes; Laridae and Otididae variable, Pedionomidae deeply recessed, Psophiidae and Heliornithidae ventrally obstructed. Pons maxillaro-jugalis is synonymous with strut "B" of Zusi and Jehl (1970).

See also: Livezey (1998b: appendix A, characters 29 and 41); the "strut" (here pons maxillaro-jugalis) apparently identical to "maxillopalatine strut" of many Charadriiformes defined by Strauch (1978: characters 14–17) and Strauch (1985: character 1), and reanalyzed by Björklund (1994: appendix) and Chu (1995).

Arcus jugalis

0291. Synostosis maxillo-arcualis (lateral perspective of tomium), angulus rostroventralis (**ordered**):

a. 180° or more, i.e., arcus jugalis descends ventrad relative to palatum osseum;

b. 170°–180°, i.e., arcus jugalis essentially coplanar with palatum osseum;

c. 160°–170°, i.e., arcus jugalis defining moderate angulus with palatum osseum;

d. 150°–160°, i.e., arcus jugalis defining pronounced angulus with palatum osseum;

e. 150° or less, i.e., approximating diagonality between arcus jugalis and palatum osseum.

Note.—Curvature of arcus jugalis manifested in *Spheniscus*, *Cathartes*, *Aegotheles*, and *Caprimulgus* necessitated defining angulus using only rostral portion of arcus. Reflects in part degree of "airencephaly." See: Livezey (1998b: appendix A, character 42).

0292. Junctura maxillo-arcualis (**new term**) relative to terminus caudalis of tomium maxillae (lateral perspective), situs dorsoventralis (**unordered**):

a. approximately coplanar with tomium;

b. distinctly dorsal to tomium, intersecting approximately one-fourth of dorsoventral height of maxilla dorsal to tomium at margo caudalis;

c. moderately dorsal to tomium, intersecting approximately one-third of dorsoventral height of maxilla dorsal to tomium at margo caudalis;

d. markedly dorsal to tomium, intersecting approximately one-half of dorsoventral height of maxilla dorsal to tomium at margo caudalis.

Note.—See: Hughes (2000: appendix 2, character 20).

0293. Aspectus comprising truncation, lateromedial compression, and markedly increased relative robustness, status:

a. absent; **b.** present.

Note.—Autapomophic form of arcus in *Balaeniceps*, notably similar in some *Pseudodontornis* (Harrison and Walker 1976a: figs. 15–16), and perhaps vaguely approached by some Psittaciformes.

0294. Abrupt longitudinal torsion and distinct sulcus on facies ventralis of arcus, including a triangular facies articularis, approximately coincident with sutura jugomaxillaris, status:

a. absent; **b.** present.

Note.—Conformation to accommodate ramus mandibulae, margo dorsalis. See: Gadow (1877); Jenkin (1957).

0295. Gross shape and robustness of arcus, status:

a. robust; **b.** thin and straight.

Note.—See: Ostrom (1976a, c); J. M. Clark et al. (1994); Forster et al. (1998: supplement, character 11); Xu et al. (1999b: character 11); Holtz (2000 [1998]: appendix I, character 36), attributing "suborbital bar" to os lacrimale; Xu et al. (2000: supplement, character 9).

0296. Relative caudal extents of os jugale, processus caudodorsalis (**new term**) et processus caudoventralis (**new term**) of os quadratojugale, situs within arcus (**unordered**):

a. processes dorsalis et ventralis approximately equal in caudal extent;

b. processus dorsalis extending significantly caudad to processus ventralis;

c. processus ventralis extending significantly caudad to processus dorsalis.

Note.—See: Currie and Carpenter (2000: appendix 1, character 18); Holtz (2000 [1998]: appendix I, character 60).

0297. Reduction of arcus to extremely thin, filamentous form, status:

a. absent, although including considerable variation in diameter and flexibility;

b. present.

Note.—Apomorphic state typically fails to hold shape in dried skeleton.

0298. Pronounced lateral bowing (convexity) of arcus, status:

a. absent, arcus essentially straight;

b. present, moderate, manifested as continuous curvature, or subangularity in rostral segment.

0299. Pronounced ventral bowing (convexity) of arcus, status:

a. absent;

b. present, position of termination of curvature rostrally producing almost sigmoid conformation in lateral view.

Note.—See: Zusi (1975); Stephan (1979), a comprehensive atlas of Spheniscidae.

0300. Sectio caudalis (presumptively os quadratojugale), distinct lateral bowing of arcus immediately cranial to condylus quadraticus to accommodate os quadratum, condylus lateralis, status:

a. absent; **b.** present.

Note.—See: Livezey (1997a: appendix 1, character 48; *corrigenda*, Livezey 1998a).

0301. Pronounced, subangular decurvature of arcus in which dorsalmost point of arcus is ventral to os lacrimale, processus orbitalis, status:

a. absent; **b.** present.

0302. Margo dorsalis of arcus, lateromedially compressed flange at approximate midpoint of arcus, status:

a. absent; **b.** present.

Note.—May represent tuberculum ligamentum anulus sclerae.

0303. Rostroventrally oriented flange of arcus immediately caudal to junctura maxillaris, status:

a. absent; **b.** present.

0304. Foramen pneumaticum arcualis (**new term**) and significant investment by cellulae pneumaticae, status:

a. absent; **b.** present.

Note.—Limited, variable pneumaticitas rostralis of ossa jugales in large Psittaciformes and Bucerotidae.

Palatum osseum

Note.—The classical palatal "types" of modern birds proposed by Huxley (1867), revised in important details by Pycraft (1900, 1901), have a long tradition of citation as "characters" for systematic classification and limited, variably controversial inclusion in phylogenetic (cladistic) analyses. The latter included some seemingly contradictory treatments—e.g., Cracraft (1988: 345) eschewed the "palaeognathous palate" as a typological abstraction not amenable to direct analysis, while including the "aegithognathous palate" as a synapomorphy of Passeriformes (Cracraft 1988: series XX, character 1). Similarly, Raikow (1982: character 1) included the "aegithognathous palate" as a synapomorphy of Passeriformes, while noting historical and personal difficulties of diagnosis, e.g., variation in the "maxillopalatine processes," a focal, innovative element in the original treatise by Huxley (1867). Prum (1988: character 28) cited two of the classical types with respect to the piciforms, whereas Prum (1988: characters 13, 15, 16, 21, 22, and 24) also cited other aspects of the vomer, ossa palatini, et ossa maxillares. The other "types" proposed by Huxley (1867)—"schizognathous" and "desmognathous"—met with even less success, at least as indicated by subsequently published works (Zusi and Livezey 2006). The "secondary palate" (palatum osseum) was considered paleontologically by: Houde (1988: table 27, character 6); Holtz (2000 [1998]: appendix I, character 72); Xu et al. (2002a: supplement, character 18), with respect to two states differing by inclusion of (*a*) os premaxillare only or (*b*) ossa premaxillare, maxillare, et vomeris.

Broad segments of the palatum osseum are in most respects consonant with those defined by Weber (1996) and Zusi and Livezey (2006):

Sectio rostralis.—Ossa premaxillare, maxillare, dentes (rostrum maxillae proprius).

Sectio intermedius.—Ossa palatinum, vomeris, et jugale (secondary palate).

Sectio caudalis.—Ossa pterygoideum, ectopterygoideum, mesopterygoideum, et quadratum (junctura between palatum osseum *sensu stricto* and mandibula).

In light of treating these explicitly topological categories—(*i*) based on complexes of a number of separate, critical skeletal elements; (*ii*) diagnostic criteria afflicted with multiple difficulties; and (*iii*) numerous taxa showing intermediate or exceptional combinations of characters—these traditional categories were dispensed with for purposes of analysis. Instead, as for other anatomical systems surveyed, characterizations included states of separate bones, muscles, or unique structural interfaces among these in the descriptions and reconstructions in our collaborative works.

0305. Palatum osseum ("secondary palate"), ossa inclusivae:

a. ossa premaxillares only;

b. ossa premaxillares, maxillares, et vomera.

Note.—See: Witmer and Martin (1987: character 9), regarding "processus palatinus forming false palate"; Norell et al. (2001: appendix 1, character 31); J. M. Clark et al. (2002a: appendix 2.2, character 26); Xu (2002: suite II, character 73); Hwang et al. (2004: supplement, character 25); Xu and Norell (2004: supplement, character 25).

0306. Palatum osseum, recessus pterygoidei (**new term**), status:

a. absent; **b.** present.

Note.—We provisionally list this apomorphy under a name listed in the *Nomina* (Baumel et al. 1993) but not annotated or attributed to any taxon; further specification was effected by the inclusion of the primary formative elements (ossa pterygoidea), although it remains possible that the ossa palatini contribute minimally ventrolaterally (see McDowell 1948: fig. 5B). See: Houde (1988: 19), in reference to "pterygoid fossa" in *Lithornis*.

0307. Canalis neurovascularis maxillae, foramina neurovascularia, status and forma:

a. foramina neurovascularia superficial and perforate facies superficialis of os dentale;

b. foramina neurovascularia enclosed within deep sulcus labialis (**new term**) of os dentale.

Note.—See: Norell et al. (2000: appendix 1, character 7), termed "dentary labial foramina"; Xu et al. (2002a: supplement, character 53).

Dentes

0308. Dentes premaxillares, status:

a. present;

b. absent, rostrum maxillae typically edentulous.

Note.—See: Howgate (1984); Cracraft (1986: appendix, character 2); Gauthier (1986: text character 38); Cracraft (1988: series IV, character 1), pertaining to loss of dentes in all elements; Houde (1988: table 27, character 3); Cracraft and Mindell (1989: table 1, character 1); Chatterjee (1991: characters 9, 11, 22, and 29); Sereno and Rao (1992); Baumel and Witmer (1993: 80); Chiappe and Calvo (1994: appendix I, character 4); J. M. Clark et al. (1994); Holtz (1994a: appendix 1, character 119); Russell and Dong (1994a [1993a]: table 2, character 2); Chatterjee (1995: character 1); Chiappe (1995b: character 4); Elzanowski (1995: characters E5 and N'8); Sanz et al. (1995, 1997: character 4); Chiappe (1996b: character 4); Chiappe et al. (1996: appendix 1, character 4); Hou et al. (1996: characters 2–3); Sues (1997: appendix 1, character 2); D. A. Winkler et al. (1997: appendix 1, character 1); Forster et al. (1998: supplement, character 1); Makovicky and Sues (1998: appendix 1, character 1); Xu et al. (1999a: character 4);

Xu et al. (1999b: character 1); Azuma and Currie (2000: appendix 1, character 104); Holtz (2000 [1998]: appendix I, character 2); Zhou et al. (2000); Chiappe (2001a: appendix 1, character 5, part); J. A. Clarke and Chiappe (2001: character 55); Currie and Chen (2001); Norell and Clarke (2001: appendix I, character 2), similarly by J. A. Clarke (2002: appendix I, character 2), J. A. Clarke and Norell (2002: appendix 2, character 2), and J. A. Clarke (2004: appendix 1, character 2); Norell et al. (2001: appendix 1, character 82); Chiappe (2002: appendix 20.2, character 5, part); Chiappe and Walker (2002: appendix 11.1, character 1); J. M. Clark et al. (2002a: appendix 2.2, character 82); Maryanska et al. (2002: appendix 1, character 95); Sereno et al. (2002), regarding *Sinornis*; Xu (2002: suite II, character 116); Xu et al. (2002a: supplement, character 61); Xu et al. (2002b); Zhou and Zhang (2002: appendix III, character 2); Hwang et al. (2004: supplement, character 81); Xu and Norell (2004: supplement, character 81). Cracraft (1986: appendix, character 2) and J. M. Clark et al. (2001a) referred simply to presence or absence of teeth (regardless of form or supporting element); Gauthier (1986: text character 38) extended issue to caudal extent. Pérez-Moreno et al. (1994: legend for fig. 3, character 1) and Holtz (2000 [1998]: appendix I, character 126) encoded a two-state character pertaining to the *total numbers* of teeth present in the *entire skull*; similarly Holtz (2000 [1998]: appendix I, character 127) characterized numbers of dentes dentales relative to dentes maxillares. Pérez-Moreno et al. (1994: legend for fig. 3, character 1) also included a character for the presence-absence of teeth (regardless of foundational maxillary or mandibular element); Norell et al. (2000: appendix 1, character 1), similarly contrasted "few" (< 100) with "numerous" (> 100) dentes; Norell et al. (2001: appendix 1, character 88), J. M. Clark et al. (2002a: appendix 2.2, character 87), Xu (2002: suite II, character 119), Hwang et al. (2004: supplement, character 85), Xu and Norell (2004: supplement, character 85), characterized both dentes dentales et maxillares in a single character; Ji et al. (2003b), regarding *Shenzhoursaurus*; Ji et al. (2005: supplement, part I, character 2).

0309. Dentes premaxillares, numerus per latus (**ordered**):
a. zero (edentuly); **b.** one to three;
c. four; **d.** four to seven;
x. noncomparable by edentuly (Neornithes).

Note.—See: J. D. Harris (1998: appendix 2, character 47); Sereno et al. (1998: footnote 22, character 19); Holtz (2000 [1998]: appendix I, character 3); Vickers-Rich et al. (2002), for *Avimimus*; Rauhut (2003: characters 5 [number] and 81 [presence]); Xu et al. (2002b).

0310. Dentes premaxillares, axis majoris porticalis (of arcade), situs:
a. rostrocaudal; **b.** mediolateral;
x. noncomparable by edentuly (Neornithes).

Note.—See: Holtz (1994b: appendix 7.1, character 2).

0311. Dentes maxillares, status:
a. present; **b.** absent;
x. noncomparable by edentuly (Neornithes).

Note.—See: Cracraft (1986: appendix, character 2) and Cracraft and Clarke (2001: appendix 2, character 1), referred simply to presence or absence of teeth (regardless of form or supporting element or in "maxilla and dentary," respectively); Gauthier (1986: text character 38), extended issue to caudal extent; Cracraft (1988: series IV, character 1), pertaining to loss of all dentes, regardless of element; Cracraft and Mindell (1989: table 1, character 1); Chatterjee (1991: characters 9, 11, 22, and 29); Baumel and Witmer (1993: 80); J. M. Clark et al. (1994); Holtz (1994a: appendix 1, character 56); Pérez-Moreno et al. (1994: legend for fig. 3, character 3), who included a general comparison of size of "maxillary" and "dentary" teeth; Chatterjee (1995: character 1); Chiappe (1995b: character 4); Elzanowski (1995: characters E5 and N'8); Sanz et al. (1995, 1997: character 4); Chiappe (1996b: character 4); Hou et al. (1996: characters 2–3); Sues (1997: appendix 1, character 5); Xu et al. (1999a: character 22); Azuma and Currie (2000: appendix 1, character 104, part); Holtz (2000 [1998]: appendix I, character 12); Zhou et al. (2000); Chiappe (2001a: appendix 1, character 5, part); J. A. Clarke and Chiappe (2001: character 55); Currie and Chen (2001: 1711), in reference to *Sinosauropteryx*; Norell and Clarke (2001: appendix I, character 3), treated similarly by J. A. Clarke (2002: appendix I, character 3), J. A. Clarke and Norell (2002: appendix 2, character 3), and J. A. Clarke (2004: appendix 1, character 3); Norell et al. (2001: appendix 1, character 84); Chiappe (2002: appendix 20.2, character 5, part); J. M. Clark et al. (2002a: appendix 2.2, character 84); Maryanska et al. (2002: appendix 1, character 96), in reference to Oviraptorosauria; Vickers-Rich et al. (2002), concerning *Avimimus*; Xu (2002: suite II, character 117); Xu et al. (2002a: supplement, character 62); Xu et al. (2002b); Zhou and Zhang (2002: appendix III, character 3); G. Mayr and Clarke (2003: appendix A, character 1); Rauhut (2003: character 82), who considered simple status of dentes maxillares et dentales as a single character by correlation; Hwang et al. (2004: supplement, character 83); Xu and Norell (2004: supplement, character 83); Ji et al. (2005: supplement, part I, character 3).

0312. Dentes dentales (mandibulae), status:
a. present; **b.** absent;
x. noncomparable by edentuly (Neornithes).

Note.—See: Cracraft (1986: appendix, character 2); Gauthier (1986: text character 38), extended issue to caudal extent; Currie (1987), regarding avianlike characteristics of dentes of troödontids; Cracraft (1988: series IV, character 1), pertaining to loss of all dentes, regardless of element; Cracraft and Mindell (1989: table 1, character 1); Chatterjee (1991: characters 9, 11, 22, and 29); Sereno and Rao (1992); Baumel and Witmer (1993: 80); J. M. Clark et al. (1994); Holtz (1994a: appendix 1, character 120); Pérez-Moreno et al. (1994: legend for fig. 3, character 3), who included a general comparison of size of "maxillary" and "dentary" teeth; Russell and Dong (1994a [1993a]: table 2, characters 18–19, part), construed in terms of relative numbers in os dentale *vs.* os maxillare or possibly rostrum maxillae; Chatterjee (1995: character 1); Chiappe (1995b: character 4); Currie (1995: appendix, character 2), regarding subtle differences in curvature of the carinae rostrales of dentes dentales; Elzanowski (1995: characters E5 and N'8); Sanz et al. (1995, 1997: character 4); Chiappe (1996b: character 4); Chiappe et al. (1996: appendix 1, character 92, part); Hou et al. (1996: characters 2–3); Sues (1997: appendix 1, character 18); Makovicky and Sues (1998: appendix 1, character 2); Sereno et al. (1998: footnote 22, character 26); J. A. Wilson and Sereno (1998: appendix, character 67), including tallies among Sauropoda; Xu et al. (1999a: character 23); Azuma and Currie (2000: appendix 1, character 104, part); Holtz (2000 [1998]: appendix I, characters 104 and 127); J. A. Clarke and Chiappe (2001: character 55); Cracraft and Clarke (2001: appendix 2, character 1), in reference to presence of teeth regardless of supporting element; Currie and Chen (2001: 1711), in reference to *Sinosauropteryx*; Ji et al. (2001), regarding unnamed dromaeosaurid NGMC 91-A; Norell and Clarke (2001: appendix I, character 4), treated similarly by J. A. Clarke (2002: appendix I, character 4), J. A. Clarke and Norell (2002: appendix 2, character 4), and J. A. Clarke (2004: appendix 1, character 4); Maryanska et al. (2002: appendix 1, character 97), in reference to Oviraptorosauria; Sereno et al. (2002), regarding *Sinornis*; Xu et al. (2002a: supplement, character 64), who related dentes of mandibula and rostrum maxillae in terms of both number and size; Zhou and Zhang (2002: appendix III, character 4); Ji et al. (2003b), regarding plesiomorphic ornithomimosaur *Shenzhoursaurus*; Rauhut (2003: character 82), who considered presence of dentes maxillares et dentales as a single character; Makovicky and Norell (2004: character 217); Xu and Norell (2004: supplement, character 217); Ji et al. (2005: supplement, part I, character 4).

0313. Dentes of rostri maxillae et mandibulae, implantation, typus:
a. separate alveoli osseae;
b. sulcus communis;
x. noncomparable by edentuly (Neornithes).

Note.—See: Chiappe et al. (1996: appendix 1, character 92, part); L. D. Martin and Stewart (1999); Sereno (1999: character 142); Holtz (2000 [1998]: appendix I, character 134), with respect to "sockets" and "paradental groove"; Chiappe (2001a: appendix 1, character 27); Chiappe (2002: appendix 20.2, character 27); Suzuki et al. (2002: character 5).

0314. Dentes premaxillares, maxillares, et dentales ("dentes rostrales"), circumsulcus ("constriction" or "waist") demarcating corona ("crown") from radix ("root"), status:
a. absent on all dentes;
b. present, at least on dentes rostrales;
x. noncomparable by edentuly (Neornithes).

Note.—See: L. D. Martin et al. (1980); Gauthier (1986: 12, unindexed synapomorphy of Avialae); J. M. Clark et al. (1994); Holtz (1994a: appendix 1, character 126); Pérez-Moreno et al. (1994: legend for fig. 3, character 4); Russell and Dong (1994a [1993a]: table 2, character 20, part); Russell and Dong (1994b [1993b]: troödontid character 9); Chiappe (1995a: fig. 1); Hou et al. (1996: character 4); Novas (1996: appendix, character 63); Novas (1997: appendix, character 64); Novas and Puerta (1997), identically treated by Novas (1997); Forster et al. (1998: supplement, character 4); Makovicky and Sues (1998: appendix 1, character 3); Xu et al. (1999a: character 29, modified); Xu et al. (1999b: character 4, modified); Holtz (2000 [1998]: appendix I, character 130); Xu et al. (2000: supplement, character 3, ordered); Ji et al. (2001), regarding unnamed dromaeosaurid NGMC 91-A; Norell et al. (2001: appendix 1, character 92); J. M. Clark et al. (2002a: appendix 2.2, characters 90–91); Xu (2002: suite II, character 122); Xu et al. (2002a: supplement, character 67); Rauhut (2003: character 87); Hwang et al. (2004: supplement, character 88); Xu and Norell (2004: supplement, character 88).

0315. Dentes premaxillares, dens secundus, size relative to dentes tertius et quartus:
a. smaller than or approximately equal;
b. significantly larger;
x. noncomparable by edentuly (Neornithes).

Note.—Where dentes present, this character treats heterogeneity of overall size (height) along axis craniocaudalis. See Currie (1995: appendix, character 4); Sereno et al. (1998: footnote 22, character 38); Xu et al. (1999b: character 84); Xu et al. (2000: supplement, character 64), with respect to "secondary premaxillary tooth, size relative to third and fourth premaxillary teeth"; Norell et al. (2001: appendix 1, character 83); J. M. Clark et al. (2002a: appendix 2.2, character 83); Xu (2002: suite I, character 11; suite II, character 230); Xu et al. (2002a: supplement, character 175); Xu et al. (2002b);

Hwang et al. (2004: supplement, character 82); Xu and Norell (2004: supplement, character 82).

0316. Dentes premaxillares et maxillares, relative size and rostrocaudal spacing *in seriatum*:

a. uniform, dentition homodontous;

b. progressive decline in size (and increase in density and apparent appression) from rostral to (at least) middle elements, in some diminishing in size and attaining even higher numbers of dentes per unit of enclosing element farther caudad;

x. noncomparable by edentuly (Neornithes).

Note.—Where dentes present, this character treats heterogeneity of overall size (height) along craniocaudal axis. See: Sereno et al. (1993: legend for fig. 3a); Russell and Dong (1994b [1993b]: troödontid character 8); Sereno et al. (1998: footnote 22, character 38); Zhao and Xu (1998); Sereno (1999: character 144); Xu et al. (1999a: character 25); J. M. Clark et al. (2002a: appendix 2.2, character 92), including craniocaudal heterogeneity in spatia interdentales, numbers of dentes; Suzuki et al. (2002: character 6); Xu (2002: suite II, character 123); Xu et al. (2002a: supplement, character 68); Hwang et al. (2004: supplement, character 89); Xu and Norell (2004: supplement, character 89).

0317. Dentes dentales, bilateral pair of distinctly enlarged, "fanglike" dentes—often associated with occlusal diastema between ossa premaxillare et maxillare or diastema within dentes maxillares, status:

a. absent; **b.** present;

x. noncomparable by edentuly (Neornithes).

Note.—See: Gauthier (1986: text character 36); J. D. Harris (1998: appendix 2, character 48); Rauhut (2003: character 83).

0318. Dentes premaxillares et maxillares, caudalmost locus of dens relative to orbita (**ordered**):

a. locus at level of midpoint of orbita;

b. locus at level of margo rostralis of orbita;

c. locus rostral to os lacrimale, processus orbitalis;

x. noncomparable by edentuly (Neornithes).

Note.—See: Gauthier (1986); Holtz (1994a: appendix 1, character 110); Sereno et al. (1994: footnote 12); Sereno et al. (1996: footnote 45, character 6); J. D. Harris (1998: appendix 2, character 3); Makovicky and Sues (1998: appendix 1, character 6); Sereno et al. (1998: footnote 22, character 8); Currie and Carpenter (2000: appendix 1, character 5); Holtz (2000 [1998]: appendix I, character 133); Maryanska et al. (2002: appendix 1, character 96); Rauhut (2003: character 70).

0319. Dentes generales, forma *sensu* (*i*) recurved *vs*. foliform, (*ii*) bilateral compression, and (*iii*) size of denticulae aut serratia:

a. recurved, acuminate, with small serratia;

b. foliform ("leaf-shaped") with enlarged serratia;

x. noncomparable by edentuly (Neornithes).

Note.—Treats relative size and shape of teeth (where present) in various parts of the dentition after Rauhut (2003: character 86). See: Ostrom (1976a); Farlow et al. (1991); Abler (1992); Sereno et al. (1993: legend for fig. 3a); J. M. Clark et al. (1994); Russell and Dong (1994b [1993b]: troödontid character 9); Currie (1995: appendix, character 2), regarding curvature of the carinae rostrales of dentes dentales; Forster et al. (1998: supplement, character 3); Sereno et al. (1998: footnote 22, character 35); Zhao and Xu (1998); Xu et al. (1999a: character 27); Xu et al. (1999b: character 3); Xu et al. (2000: supplement, character 2); Rauhut (2003: character 86).

0320. Dentes premaxillares, forma coronae (plana transversalia dentalium):

a. subovate to subcircular;

b. asymmetrical or "D-shaped," i.e., having flattened facies lingualis but convex facies externus;

x. noncomparable by edentuly (Neornithes).

Note.—See: Holtz (1994a: appendix 1, character 126); J. A. Wilson and Sereno (1998: appendix, character 32), regarding Sauropoda; Norell et al. (2001: appendix 1, character 93); J. M. Clark et al. (2002a: appendix 2.2, character 94); Xu (2002: suite II, character 125); Xu et al. (2002a: supplement, character 70); Brochu (2003); Hwang et al. (2004: supplement, character 91); Xu and Norell (2004: supplement, character 91); Ji et al. (2005: supplement, part I, character 205).

0321. Dentes premaxillares, congruentia, status (plana transversalia dentalium):

a. symmetrical, typically conical;

b. asymmetrical, typically strongly convex on facies labialis, relatively flattened on facies lingualis;

c. incisiform, diminutive;

x. noncomparable by edentuly (Neornithes).

Note.—See: Bakker et al. (1988); Holtz (1994a: appendix 1, character 126); J. D. Harris (1998: appendix 2, character 46); Sereno et al. (1998: footnote 22, character 17); Currie and Carpenter (2000: appendix 1, character 41); Holtz (2000 [1998]: appendix I, character 132).

0322. Dentes dentales definitivum (if present), corona, serratia et/aut denticulae, status:

a. present; **b.** absent throughout;

x. noncomparable by edentuly (Neornithes, including *Lithornis*).

Note.—See: Gauthier (1986: 12, unindexed synapomorphy of Avialae); Abler (1992); J. M. Clark et al. (1994); Chiappe et al. (1996: appendix 1, character 71); Novas (1996: appendix, character 62); Novas (1997: appendix, character 63); Novas and Puerta (1997), see identical characters in Novas (1997); Chiappe et al. (1998: character 12); Ji et al. (1998: supplement, character 12); Makovicky and Sues (1998: appendix 1, character 5); Sereno et al. (1998:

footnote 22, character 36); J. A. Wilson and Sereno (1998: appendix, character 78), regarding presence in Sauropoda; Holtz (2000 [1998]: appendix I, character 128); Norell et al. (2000: appendix 1, character 2), using simple presence-absence scheme (element unspecified); Chiappe (2001a: appendix 1, character 28); Currie and Chen (2001: 1711), in reference to *Sinosauropteryx*; Norell and Clarke (2001: appendix I, character 5), treated similarly by J. A. Clarke (2002: appendix I, character 5), J. A. Clarke and Norell (2002: appendix 2, character 5), and J. A. Clarke (2004: appendix 1, character 5); Ji et al. (2001), regarding unnamed dromaeosaurid NGMC 91-A; Norell et al. (2001: appendix 1, character 87); Chiappe (2002: appendix 20.2, character 28); J. M. Clark et al. (2002a: appendix 2.2, character 86); Xu (2002: suite II, character 118, part); Xu et al. (2002a: supplement, character 63); Zhou and Zhang (2002: appendix III, character 5); Rauhut (2003: character 85); Hwang et al. (2004: supplement, character 84); Xu and Norell (2004: supplement, character 84).

0323. Dentes premaxillares definitivum (carinae craniales et caudales), serratia et/aut denticulae, status:

a. present on carinae craniales et/aut caudales;
b. absent on both carinae craniales et caudales;
x. noncomparable by edentuly (Neornithes).

Note.—See: L. D. Martin et al. (1980); J. M. Clark et al. (1994); Russell and Dong (1994a [1993a]: table 2, character 20, part); Russell and Dong (1994b [1993b]: troödontid character 9); Forster et al. (1998: supplement, character 2); J. D. Harris (1998: appendix 2, character 45), in reference to contiguous distribution of denticulation; Makovicky and Sues (1998: appendix 1, character 4); Xu et al. (1999a: character 26, but states differently defined); Xu et al. (1999b: character 2, modified); Xu et al. (2000: supplement, character 1, ordered); Ji et al. (2001), regarding unnamed dromaeosaurid NGMC 91-A; Xu et al. (2002a: supplement, character 69); Rauhut (2003: character 84).

0324. Dentes maxillares definitivum (if present), corona, serratia et/aut denticulae, status:

a. present; **b.** absent throughout;
x. noncomparable by edentuly (Aves, including Neornithes).

Note.—See: Norell et al. (2000: appendix 1, character 3), in reference to serratia (element unspecified), denticulae treated in another character; Norell et al. (2001: appendix 1, character 85); J. M. Clark et al. (2002a: appendix 2.2, character 85); Xu (2002: suite II, character 118, part); Rauhut (2003: character 85), treating status with serratia of dentes maxillares; Hwang et al. (2004: supplement, character 84); Xu and Norell (2004: supplement, character 84).

0325. Dentes, facies laterales, forma superficialis:

a. glabrous; **b.** rugose;
x. noncomparable by edentuly (Neornithes).

Note.—See: Currie and Carpenter (2000: appendix 1, character 42); Holtz (2000 [1998]: appendix I, character 131), in reference to "wrinkling" of lateral surfaces of teeth.

0326. Dentes maxillares et mandibulares, denticulae (serratia), forma *sensu* overall size:

a. large; **b.** small;
x. noncomparable by edentuly (Neornithes).

Note.—See: Farlow et al. (1991); Norell et al. (2001: appendix 1, character 89); J. M. Clark et al. (2002a: appendix 2.2, character 88); Xu (2002: suite II, character 120); Xu et al. (2002a: supplement, character 65); Hwang et al. (2004: supplement, character 86); Xu and Norell (2004: supplement, character 86).

0327. Dentes maxillares et mandibulares, denticulae (serratia) rostrales (where present), size relative to denticulae (serratia) caudales:

a. approximately equal;
b. rostral significantly smaller than caudal;
x. noncomparable by edentuly (Neornithes).

Note.—Where dentes present, this character treats presence and distribution and differential size of "denticles" thereof. See: Currie (1995: appendix, character 5); Xu et al. (1999b: character 85); Azuma and Currie (2000: appendix 1, character 103); Holtz (2000 [1998]: appendix I, character 129); Xu et al. (2000: supplement, character 65).

0328. Dentes maxillares et mandibulares, denticulae (serratia), forma:

a. simple, convex;
b. hamulate, oriented toward the apex of the dental corona;
x. noncomparable by edentuly (Neornithes).

Note.—See: Norell et al. (2001: appendix 1, characters 90–91); J. M. Clark et al. (2002a: appendix 2.2, character 89); Xu (2002: suite II, character 121); Xu et al. (2002a: supplement, character 66); Hwang et al. (2004: supplement, character 87); Xu and Norell (2004: supplement, character 87).

0329. Dentes palati ossium—i.e., dentes ossium pterygoidea, palatina, et/aut vomera (**new term**)—status:

a. absent; **b.** present.

Note.—See: Benton and Clark (1988); Sereno (1991a: appendix, character 1); Rauhut (2003: character 69).

0330. Ossa premaxillares et dentales, pseudodentes (**new term**), status:

a. absent; **b.** present.

Note.—Structures are dentiform conical protrusions along margines tomiales of ossa premaxillares et dentales. In present analytical context, given exclusion of Odontoptyergiformes, this character will appear invariant. See: Howard (1957); Howard and White (1962); Zusi and Warheit (1992); Bourdon (2006: supplement, character 52).

Cavum Nasi (Cavitas Nasalis)

Apertura nasi (nasalis) ossea

Note.—Unless indicated otherwise, margines aperturae delimited herein by included margines of ossa premaxillare, nasale, et maxillare, and exclusive of potentially confounding by conchae or capsulae.

0331. Apertura nasi ossea, status:
a. present; **b.** vestigial or absent.
Note.—See: MacDonald (1960), regarding rictal "secondary nares," likely (if valid) venting from margo rostrale of basalmost of two lamina rhinothecae "one or two smaller labials" of Lönnberg (1904: 493–495) or "supra-labialia" of Boetticher (1928: fig. 12); Cracraft (1985: character 3); Cracraft (1988: series IX, character 2); Siegel-Causey (1997: table I, character 4); G. Mayr (2003a); G. Mayr and Clarke (2003: appendix A, character 7); G. Mayr (2004b: appendix 1, character 3).

0332. Apertura nasi (nasalis) ossea, numerus definitivum (if present):
a. two, bilateral;
b. one, medial, by multi-elemental apomorphy;
x. noncomparable by ontogenetically, structurally distinct osseous occlusion of nares (Phalacrocoracidae, Sulidae).

0333. Apertura nasi ossea, forma as bilateral pair of distinctly rimmed, orbiculate perforationes, status:
a. absent; **b.** present.
Note.—See: Bang and Wenzel (1985).

0334. Apertura nasi ossea, size relative to fossa antorbitalis:
a. former considerably smaller than latter;
b. former larger than latter.
Note.—Typically quantified by comparison between rostrocaudal dimensions of apertura nasi and fossa antorbitalis (Sereno 2001). Witmer (2001) noted potentially misleading sizes of apertura ossea and overlying integumentum among archosaurs.

See: Chiappe and Calvo (1994: appendix I, character 5); Chiappe (1995b: character 5); Sanz et al. (1995, 1997: character 5); Chiappe (1996b: character 5); Chiappe et al. (1996: appendix 1, character 5); Livezey (1998b: appendix A, character 2); Zhou et al. (2000); Norell and Clarke (2001: appendix I, character 12), treated similarly by J. A. Clarke (2002: appendix I, character 12), J. A. Clarke and Norell (2002: appendix 2, character 12), and J. A. Clarke (2004: appendix 1, character 12); Sereno (2001: table 2, character 40), as synapomorphic of Aves; Zhou and Zhang (2002: appendix III, character 12); Ji et al. (2005: supplement, part I, character 12).

0335. Apertura nasi ossea (or homologous locus), micro-apertura nasi ossea (**new term**) immediately caudal, status:
a. absent; **b.** present.
Note.—See: Cracraft (1985: character 3); Bourdon et al. (2005: appendix 1, character 2); Bourdon (2006: supplement, character 94). Disputed by: G. Mayr (2003b: character 3); Bourdon et al. (2005: appendix 1, character 2).

0336. Apertura nasi ossea, functional restriction to terminus distalis rostri maxillae, status:
a. absent; **b.** present.

0337. Apertura nasi ossea, bilateral, rostrocaudal subdivision (partial or complete) into large, subtriangular rostral subapertura and narrow, subelliptical subapertura by lateromedially oriented lamina, status:
a. absent; **b.** present.

0338. Apertura nasalis, margo caudalis, rostrocaudal situs relative to margo rostralis of fossa antorbitalis within rostrum maxillae:
a. former distinctly rostral to latter;
b. former approaching or coincident with latter.
Note.—See: Chatterjee (1991: character 7); J. M. Clark et al. (1994); Chiappe et al. (1998: character 4); Ji et al. (1998: supplement, character 4); Livezey (1998b: appendix A, character 7), situs of apertura in rostrum maxillae; Chatterjee (1999: appendix II, character 26); Xu et al. (1999b: character 102); Xu et al. (2000: supplement, character 82); Chiappe (2001a: appendix 1, character 6); Norell et al. (2001: appendix 1, character 2); Witmer (2001), for functional analysis among archosaurs; Chiappe (2002: appendix 20.2, character 6); J. M. Clark et al. (2002a: appendix 2.2, character 24); Maryanska et al. (2002: appendix 1, character 19); Xu (2002: suite II, character 237); Xu et al. (2002a: supplement, character 182); Zhou and Zhang (2002: appendix III, character 12); Hwang et al. (2004: supplement, character 23); Xu and Norell (2004: supplement, character 23).

0339. Apertura nasalis, lateral extension of margo caudalis and (partial) rostral orientation of apertura, status:
a. absent, apertura oriented laterad;
b. present, apertura oriented anterolaterad.
Note.—See: Rauhut (2003: character 7).

0340. Apertura nasi ossea, terminus caudalis, forma (**unordered**):
a. angular or subangular, including forms having rounded vertex caudalis;
b. (sub)orbiculate; **c.** fissuriform;
x. noncomparable, obsolescence or loss of apertura (Pelecaniformes, *Geococcyx*).

Note.—Taxa showing intermediacy were included in state "a"; state "b" includes many "holorhinal" forms; and state "c" includes most "schizorhinal" forms. "Rhiny" (Garrod 1873a), formally diagnosed herein by reference to zonae flexoriae. See: Cracraft (1988); Andors (1992: table 2, character 2); Livezey (1998b: appendix A, character 1); Rotthowe and Starck (1998: appendix, character 26); G. Mayr and Clarke (2003: appendix A, character 6); G. Mayr and Ericson (2004: appendix I, character 2).

0341. Apertura nasi ossea, terminus caudalis, margo caudalis relative to zona flexoria craniofacialis, situs:
a. rostral or approximately equal;
b. significantly caudal.
Note.—Present character pertains to position of caudal extremity of apertura relative to zona flexoria.

0342. Apertura nasi ossea, terminus caudalis, marked depressio nasalis medialis (**new term**), status:
a. absent; **b.** present.
Note.—See: Sereno et al. (1994: footnote 12); Holtz (2000 [1998]: appendix I, character 9).

0343. Apertura nasi ossea, vertex caudalis, partial occlusion by thin capsula nasi ossea (**new term**), status et forma (**unordered**):
a. absent;
b. present, restricted, comparatively densely perforated with foramina neurovascularia;
c. present, variably extensive, not densely perforated with foramina neurovascularia, with laterally expanded rostral rima;
d. present, restricting apertura to single rostral ostium.
Note.—Some Trochilidae (cf. Phaethornithinae) have ossification at vertex differing from state shown by exemplar. Occurrence of minute tubulae rostrad from apertura nasi between rhamphotheca and rostrum maxillae in some pelecaniforms (e.g., *Fregota*) is suggestive of tubae nasales of Procellariiformes. See: Garrod (1873a); Forbes (1881b); Feduccia (1967); Van Tyne and Berger (1976); G. Mayr et al. (2003: appendix 1, character 3); G. Mayr (2004b: appendix 1, character 4), limited to tubular forms.

0344. Apertura nasi ossea, vertex caudalis, partial occlusion by ossification of capsula nasi (regio olfactoris) with synostosis inclusive of os mesethomoidale but exclusive of processus maxillaris ossis nasale, status:
a. absent; **b.** present.
Note.—See: Technau (1936).

0345. Apertura nasi ossea, lamina partitioning apertura into subaperturae or ostia ("amphirhiny"), status et forma (**ordered**):
a. absent;
b. present, subaperturae (ostia) dorsolaterally oriented, lacking rounded rims, separated by comparatively broad, thin lamina, and typically of irregular shape;
c. present, subaperturae (ostia) largely dorsally oriented, with distinctly rounded rims, separated only by narrow partitions, and elliptical.
Note.—Jyngidae and some Trochilidae and have ossified conchae nasales that effect an incomplete partition of apertura nasi ossea. See: Feduccia (1967) with respect to amphirhiny in Passeriformes.

0346. Apertura nasi ossea, extreme rostral position and extent so as to approach terminus rostralis rostri maxillae, status:
a. absent; **b.** present.
Note.—See: G. Mayr (2002a: appendix 1, character 6, part), with respect to Caprimulgiformes; G. Mayr (2005b: appendix A, character 6, part).

Pila supranasalis (ossa premaxillares et nasales)

0347. Pila supranasalis, dorsal convexity (lateral perspective) distinctly greater (especially rostral segment) than that of medial rostrum maxillae, status:
a. absent, pila essentially straight or comparably curved with rostrum maxillae;
b. present, pila distinctly "rounded."
Note.—See: Livezey (1986: appendix 1, character 19); Livezey (1989: table 1, character 19); Livezey (1996a: appendix 1, character 2).

0348. Pila supranasalis, transverse convexity (rostrocaudal perspective) of facies dorsalis pilae, status:
a. present, pila "rounded" or convex dorsally;
b. absent, pila "flat" or laminar dorsally;
x. noncomparable (Neornithes).
Note.—See: Norell et al. (2001: appendix 1, character 28); J. M. Clark et al. (2002a: appendix 2.2, character 22); Xu (2002: suite II, character 254); Xu et al. (2002a: supplement, character 199); Hwang et al. (2004: supplement, character 21); Xu and Norell (2004: supplement, character 21).

Septum nasi (nasale) osseum

Note.—Incorporating one or more of ossa mesethmoidales, vomera, maxillares, ectethmoidales, et/aut conchae nasales ossificantes.

0349. Septum nasi (nasale) osseum, status (**ordered**):
a. absent;
b. present, variably developed, may contact but asynostotic with processus palatus maxillaris;
c. present, typically extensive, synostotic with processus palatus maxillaris.

Note.—Some authors assumed (incorrectly) that the septum nasi osseum is derived from os mesethmoidale, whereas it actually represents, at least in large part, the ossification of a cartilaginous partition. Derived state includes taxa in which conchae nasales osseae variably conceal or enclose the septum in lateral view; problematic to confirm in some taxa (e.g., Tytonidae and Strigidae) if the osseus partition represents septum, conchae, or both. Intraspecific variation is presumably associated with the ontogenetic origin of the septum as membrana ossificans.

See: Bang and Wenzel (1985); Cracraft (1985: character 20); Cracraft (1986: appendix, character 50); Gauthier (1986: 13, unindexed synapomorphy of Ornithurae); Chatterjee (1991: character 25); Andors (1992: table 2, character 1); Ericson (1997: table 1, character 13); Chu (1998: appendix 1, character 24); Livezey (1998b: appendix A, character 3); G. Mayr (2003a: appendix I, character 5); G. Mayr (2003b: appendix I, character 2) regarding Trogonidae; G. Mayr and Clarke (2003: appendix A, character 8); G. Mayr et al. (2003: appendix 1, character 1); Dyke and van Tuinen (2004: appendix 1, character 3); G. Mayr (2004d: appendix I, character 1); G. Mayr (2005a: appendix 1, character 1).

0350. Septum nasi (nasale) osseum (part), terminus caudalis, alulae transversariae angulares (**new term**), status:
a. absent;
b. present, typically conformed as isoceles triangle with basis medialis longest and positioned immediately or closely dorsal to pars rostralis, rostrum parasphenoidale, approximating sutura palatinomaxillaris in rostrocaudal position.
Note.—Bilateral, osseus, bilaterally projecting flanges evidently associated with comparatively expansive capsulae nasales in Dinornithiformes. In exceptionally well-preserved specimens, a delicate osseus pons from the corresponding ossa ectethmoidales extend to unite with the alulae in question.

0351. Septum nasi (nasale) osseum (part), margo caudalis, lamina dorsalis mesethmoidalis, pars nasi (**new term**), status:
a. absent; **b.** present.

Conchae nasales

Note.—Reviews of pneumaticity of regio craniofacialis of Archosauria provided by Witmer (1990, 1995b, 1997). See: Technau (1936), Wenzel (1971), and Bang and Wenzel (1985), for related characters of septum et operculum nasi osseum; K. Lee et al. (1997: appendix 1, character 58); Livezey (1998b: appendix A, characters 4–6); Maryanska et al. (2002: appendix 1, character 18); G. Mayr (2003a: appendix I, character 3); G. Mayr (2003b: appendix 1, character 6); G. Mayr and Clarke (2003: appendix A, character 9).

0352. Conchae nasales osseae, status:
a. present; **b.** vestigial or absent.
Note.—See: Technau (1936); Bang and Wenzel (1985); G. Mayr (2003b: appendix 1, character 6).

0353. Conchae nasales osseae, pars caudalis, facies lateralis, deep, rounded, involucral depression in rostral portion of orbita, triangular in outline, with apex dorsocaudal and basis medial to os lacrimale, processus orbitalis, status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes).
Note.—See: Bang and Wenzel (1985); K. Lee et al. (1997: appendix 1, character 58), regarding ratites.

0354. Conchae nasales osseae, caudomedial terminus, conformation as laminar surface perpendicular to zona flexoria craniofacialis and in which nares internae are separated by thick osseus septum, status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes).
Note.—See: D. W. Thompson (1899); Bang and Wenzel (1985).

Recessus pneumatici paranasales

0355. Conchae nasales osseae, facies ventralis, at sutura palatinomaxillaris, bilaterally paired, prominent, recessus pneumatici paranasales separated medially by thick septum osseum, status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes).
Note.—See: Bang and Wenzel (1985); Holdaway (1991: appendix 5.1, character 14).

0356. Fenestra infratemporalis (**revised term**), status et size relative to orbita (**ordered**):
a. absent;
b. present, length subequal to or less than that of orbita;
c. present, length at least 1.5 times that of orbita.
Note.—Identity of feature uncertain; codings based primarily on Rauhut (2003), which differed significantly from other sources. See: Bonaparte (1991); Currie and Zhao (1994b [1993b]); Rauhut (2003: character 38), listing feature following os frontale and before ossa lacrimale et postorbitale.

Fossa antorbitalis

Note.—See Witmer (1997) for revised nomenclature and descriptive anatomy of this archosaurian feature; functional reconstructions for fossil and modern archosauriforms were presented by Witmer

(1990, 1995b); earlier functional treatments include Osmólska (1985). Most importantly, Witmer (1997) referred to contributions by multiple elements bordering the fossa, and included recesses, separately, resulting in the use of variably abbreviated references to element-specific recesses in the literature (e.g., Holtz 2000 [1998]). For example, Witmer (1997: fig. 29) included the following constituents for the fossa antorbitalis and associated features for *Allosaurus*: excavatio pneumatica rami ascendenti, recessus pneumaticus nasalis, recessus pneumaticus lacrimalis, recessus pneumaticus jugalis, canalis nasolacrimalis, fenestra antorbitalis interna, pila interfenestralis, and fenestra maxillaris (some other taxa possess additional features, notably fenestra promaxillaris, recessus promaxillaris, pila promaxillaris, and antrum maxillaris). The complexity of internal fenestrae within the fossa antorbitalis renders diagnosis problematic for many fossil taxa, e.g., Oviraptorosauria (J. M. Clark et al. 2002b); one treatment of compromise was that by J. D. Harris (1998: appendix 2, character 2) and adapted by Currie and Carpenter (2000: appendix 1, character 3), in which a single multistate character comprising presence of one, both, or "more" fenestrae promaxillaris et/aut maxillaris, etc., was employed.

0357. Fossa antorbitalis, status:
a. absent; **b.** present.
Note.—In Crocodylia, fossa can be concealed laterodorsally by osseous lamina, part of a dermal "bony roof" that forms an external "armor" for the skull in many taxa; perhaps optimally treated for Crocodylomorpha as present but variably occult. See: Benton (1990a), under "antorbital *fenestra*"; Witmer (1990, 1995b, 1997); Sereno et al. (1998: footnote 22, character 9); J. A. Wilson and Sereno (1998: appendix, character 20).

Regarding fenestra aut sinus fossae, see: Gauthier (1986: text character 37); Witmer (1987); Witmer and Martin (1987: character 10); K. Carpenter (1997); Baumel and Witmer (1993); J. M. Clark et al. (1994); Russell and Dong (1994b [1993b]: troödontid character 4); Holtz (1994a: appendix 1, character 108); Chiappe (1995b: character 6); Pérez-Moreno et al. (1994: legend for fig. 3, character 10); Elzanowski (1995: 39, character unindexed); Sanz et al. (1995, 1997: character 6); Chiappe et al. (1996: appendix 1, character 88), regarding "caudal maxillary sinus"; Sereno et al. (1996: footnote 45, character 56), regarding shape; Forster et al. (1998: supplement, character 5); Sereno et al. (1998: footnote 22, character 40), regarding relative size; Xu et al. (1999b: character 5); Lamanna et al. (2002: appendix 1, character 11); Ji et al. (2003b).

0358. Fossa antorbitalis, rima ossea, status:
a. well developed;
b. absent or poorly developed.
Note.—See: Sues (1997: appendix 1, character 3); Xu et al. (1999a: character 5); Azuma and Currie (2000: appendix 1, character 2); Xu et al. (2002a: supplement, character 22).

0359. Fossa antorbitalis, distinct bordering rima ossea rostroventralis (**new term**), status:
a. absent; **b.** present;
x. noncomparable (Neornithes).
Note.—See: J. M. Clark et al. (1994); Norell et al. (2001: appendix 1, character 5); J. M. Clark et al. (2002a: appendix 2.2, character 31); Xu (2002: suite II, character 77); Hwang et al. (2004: supplement, character 30); Xu and Norell (2004: supplement, character 30).

0360. Fossa antorbitalis, "sculpting" of margines osseae maxillare et/aut nasale, status:
a. moderate;
b. pronounced, extending to margines maxillaris et nasalis fossae;
x. noncomparable (Neornithes).
Note.—See: Currie and Carpenter (2000: appendix 1, character 6).

0361. Fossa antorbitalis (pars) maxillaris (Witmer 1997), forma *sensu* depth of fossa and distal prominence of margines:
a. fossa deep, margines prominent;
b. fossa shallow, margines low, in some taxa margo comparatively prominent or "sharp" only rostral to foramen promaxillaris.
Note.—See: Sereno and Novas (1994 [1993]); J. M. Clark et al. (1994); Sues (1997); Rauhut (2003: character 12).

0362. Fossa antorbitalis (pars) maxillaris (Witmer 1997), margo rostralis, forma:
a. rounded or acuminate; **b.** squared.
Note.—See: Sereno and Novas (1992: appendix, character 3); Rauhut (2003: character 13).

0363. Fossa antorbitalis pars maxillaris, depressio cranialis "pneumaticum" sine fenestrae, status:
a. absent; **b.** present.
Note.—See: Holtz (2000 [1998]: appendix I, character 22).

0364. Fossa antorbitalis (pars) maxillaris (Witmer 1997), forma *sensu* approximate proportion of total area (lateral perspective) of fossa antorbitalis occupied:
a. 25% or less; **b.** greater than 40%.
Note.—See: Holtz (2000 [1998]: appendix I, character 15), regarding "maxillary antorbital fossa"; Sereno et al. (1998: footnote 22, character 9), pertaining to size relative to orbita; Azuma and Currie (2000: appendix 1, character 1), effectively limited to state "a"; Rauhut (2003: character 14).

0365. Fossa antorbitalis (pars) maxillaris (Witmer 1997), margo ventralis, jugum fossae maxillaris (**new term**), status:

a. absent; **b.** present.

Note.—See: Xu (2002: suite I, character 1), with respect to "ridge ventral to the maxillary fossa"; Rauhut (2003: character 15).

0366. Fossa antorbitalis (pars) nasalis (Witmer 1997), status:

a. absent; **b.** present.

Note.—See: Sereno et al. (1994: footnote 12); Sereno et al. (1996: footnote 45, character 39); Sereno et al. (1998: footnote 22, character 41), regarding "subcircular depression in anterior corner"; Holtz (2000 [1998]: appendix I, character 29), regarding "nasal recesses" of Theropoda; Currie et al. (2003: appendix, characters 36–37); Rauhut (2003: character 19).

0367. Fossa antorbitalis (pars) lacrimalis (Witmer 1997), status et inclusion of fenestrae (**unordered**):

a. absent; **b.** present, a single fenestra;

c. present, comprising several fenestrae or perforata.

Note.—See: Currie (1985) pertaining to Troödontidae; Holtz (2000 [1998]: appendix I, character 33), regarding "lacrimal recess"; Maryanska et al. (2002: appendix 1, character 22), regarding presence of "lacrimal recessus"; Xu (2002: suite I, character 62), regarding "depressed lacrimal" of *Sinornithosaurus*.

0368. Fossa antorbitalis, margo fossae interna, situs et participation of os jugale, terminus rostralis, forma (**unordered**):

a. os jugale extends only to margo caudalis fossae;

b. os jugale not extending into internum fossae;

c. os jugale expressed at margo of internum fossae and with processus rostroprofundus (**new term**) extending rostrad and deep to fossa.

Note.—See: J. D. Harris (1998: appendix 2, character 14); Currie and Carpenter (2000: appendix 1, character 17), concerning "jugal . . . expressed on rim of antorbital fenestra"; Holtz (2000 [1998]: appendix I, character 58); Rauhut (2003: character 24).

0369. Fossa antorbitalis (pars) jugalis (Witmer 1997), status:

a. present, as large, crescentiform depressio;

b. absent or shallow depressio.

Note.—See: Holtz (2000 [1998]: appendix I, character 61), Xu et al. (2002a: supplement, character 26), for "jugal recesses"; Rauhut (2003: character 25).

0370. Fossa antorbitalis (pars) jugalis (Witmer 1997), recessus pneumaticus caudoventralis, status:

a. present; **b.** absent.

Note.—See: Norell et al. (2001: appendix 1, character 35); J. M. Clark et al. (2002a: appendix 2.2, character 35); Xu (2002: suite II, character 81), treating recessus pneumaticus " . . . in posteroventral corner of antorbital fossa"; Hwang et al. (2004: supplement, character 34); Xu and Norell (2004: supplement, character 34).

0371. Fossa antorbitalis (pars) palatinus (Witmer 1997), status:

a. absent; **b.** present.

Note.—See: J. D. Harris (1998: appendix 2, character 33), described as being positioned on the medial side of element, at "confluence of vomeropterygoid, maxillary, and jugal processes"; Azuma and Currie (2000: appendix 1, character 85); Currie and Carpenter (2000: appendix 1, character 35); Holtz (2000 [1998]: appendix I, character 78), regarding "palatine recesses."

0372. Fossa antorbitalis, fenestra premaxillaris (**new term**), status:

a. absent; **b.** present.

Note.—See: Bourdon et al. (2005: appendix 1, character 8).

0373. Fossa antorbitalis, fenestra maxillaris (Witmer 1997), status:

a. absent; **b.** present.

Note.—See: Ostrom (1969: fig. 6), in which "subsidiary antorbital fenestrae" were depicted in pars rostralis of os maxillare; Gauthier (1986); Chiappe and Calvo (1994: appendix I, character 6); Chiappe et al. (1996: appendix 1, character 6); J. D. Harris (1998: appendix 2, character 2, part); Currie and Carpenter (2000: appendix 1, character 3, part); Holtz (2000 [1998]: appendix I, character 17); Rauhut (2003: character 17).

0374. Fossa antorbitalis, fenestra maxillaris (Witmer 1997), forma:

a. orbiculate; **b.** elongate, ellipsoidal, low.

Note.—See: Ostrom (1969: fig. 6), in which "subsidiary antorbital fenestrae" were shown as present in the rostral portion of the element; Holtz (2000 [1998]: appendix I, character 18), coding state of "1" for *Caudipteryx*; Ji et al. (2003b).

0375. Fossa antorbitalis (lateral perspective), fenestra (fovea) promaxillaris (Witmer 1997), status:

a. absent;

b. present, as laterally exposed or obscured fenestra.

Note.—See: Holtz (1994a: appendix 1, character 84); Sereno et al. (1994: footnote 12); Sereno et al. (1996: footnote 45, character 22); J. D. Harris (1998: appendix 2, character 2, part); Currie and Carpenter (2000: appendix 1, character 3, part); Holtz (2000 [1998]: appendix I, character 16); Norell et al. (2001: appendix 1, character 7); J. M. Clark et al. (2002a: appendix 2.2, character 30); Lamanna et al. (2002: appendix 1, character 2); Xu (2002: suite II, character 76); Xu et al. (2002a: supplement, character 21), in binary coding of "tertiary antorbital fenestra," considered by these authors to be synonymous with "fenestra promaxillaris"; Rauhut (2003: character 16), a binary treatment; Hwang et al. (2004: supplement, character 29); Xu and Norell (2004: supplement, character 29).

0376. Fossa antorbitalis, fenestrae promaxillaris et maxillaris (Witmer 1997), relative caudoventral positions:

a. promaxillaris rostral to maxillaris;

b. promaxillaris dorsal to maxillaris.

Note.—See: Holtz (2000 [1998]: appendix I, character 19).

0377. Fossa antorbitalis, fenestrae promaxillaris et maxillaris (Witmer 1997), relative sizes:

a. promaxillaris smaller than maxillaris;

b. promaxillaris larger than maxillaris.

Note.—See: Holtz (2000 [1998]: appendix I, character 20).

0378. Fossa antorbitalis, inclusion of excavatio pneumatica of ramus ascendens postnarialis of os maxillare, corpus ossis maxillaris, status:

a. absent; **b.** present, pneumatic.

Note.—See: Sereno et al. (1996: footnote 45, character 22); Holtz (2000 [1998]: appendix I, character 21), in reference to "ascending ramus" of rostrum maxillae.

0379. Fossa antorbitalis, os marginis rostralis fossae, status:

a. includes element other than os premaxillare;

b. os premaxillare only.

Note.—See: Maryanska et al. (2002: appendix 1, character 14).

0380. Fossa antorbitalis, margo dorsalis, situs relative to os nasale, processus frontalis:

a. ventral to os nasale, extending only to sutura nasomaxillaris (latter forming margo), typically invading dorsad to premaxillaris maxillare;

b. extends dorsad onto facies lateroventralis of os nasale, at least one among the elements delimiting margo fossae.

Note.—See: Sereno et al. (1994: footnote 12); Sereno et al. (1996: footnote 45, character 39); Witmer (1997); J. D. Harris (1998: appendix 2, character 4); Azuma and Currie (2000: appendix 1, character 84); Currie and Carpenter (2000: appendix 1, character 7); Holtz (2000 [1998]: appendix I, characters 23–24), apparently redundant; Maryanska et al. (2002: appendix 1, character 6); Rauhut (2003: character 20).

0381. Fossa antorbitalis (pars) accessoria (**new term**), situs rostrocaudalis relative to rima ossea fossae, margo rostralis:

a. coincident; **b.** caudal.

Note.—See: Xu et al. (2002a: supplement, character 187), in reference to "accessory antorbital fossa" of uncertain homology.

Os Nasale

0382. Os nasale, rostrocaudal length relative to that of os frontale:

a. latter shorter than former;

b. latter at least as long as former.

Note.—See: Maryanska et al. (2002: appendix 1, character 16).

0383. Os nasale, processus frontalis, blunt eminentia aut cornu dorsalis (**new terms**), status:

a. absent; **b.** present.

Note.—Without reference to juvenile specimens, cornu nasalis (**new term**) can be mistaken for processus supraorbitalis of os lacrimale.

0384. Os nasale, forma *sensu* caudal width:

a. lateromedially expanded caudad;

b. uniformly narrow throughout.

Note.—See: Bakker et al. (1988); Holtz (1994a: appendix 1, character 83); Holtz (2000 [1998]: appendix I, character 25); Rauhut (2003: character 21).

0385. Os nasale, processus frontalis, terminus caudalis and dorsal sutura internasalis relative to those of os premaxillae, processus frontalis, forma (**unordered**):

a. former well caudal to latter, area internasales frontale (**new term**) occupied by os mesethmoidale, lamina dorsalis, margo dorsalis;

b. former approximately equal to or moderately exceeding latter in caudal extent, lacking significant dorsal sutura internasalis caudal to os premaxillae, and where processus frontalis bifurcated caudally, spatium between furcata occupied by both ossa mesethmoidale et frontales;

c. former extending well caudad to latter, forming rostrocaudally broad, typically clipeate ("shield-like") sutura internasalis dorsocaudal to os premaxillae, with variably bifurcate, invaginate, or shallowly acuminate apex medialis, latter (if concave) occupied by os frontale;

d. former well caudad to latter, forming rostrocaudally broad, typically clipeate sutura internasalis dorsocaudal to os premaxillae, with variably bifurcate, invaginate, or shallowly acuminate medial apex, latter (if concave) spanned by os mesethmoidale;

e. former well caudad to latter, forming rostrocaudally broad, typically clipeate sutura internasalis dorsocaudal to os premaxillae, with medial apex forming a distinctly acuminate dorsal aspect;

f. former moderately caudal or subequal to latter in caudal extent, typically forming sublinear margo transversus or medially rounded apex on frons.

Note.—Diagnoses require juvenile specimens. See: Cracraft (1986: appendix, character 48); Cracraft (1988: series II, character 16; series V, character 4); Cracraft and Mindell (1989: table 1, character 15); Baumel and Witmer (1993: annotation 14); Currie et al. (2003: appendix, character 40).

0386. Os nasale, processus frontalis, margines lateralis, unique conformation in which element tapers caudad and curves mediad to form short sutura internasalis at midline, meeting on midline along sutura nasofrontale, status:

a. absent; **b.** present.

Note.—Diagnoses require juvenile specimens.

0387. Os nasale, processus frontalis, facies dorsalis, forma superficialis:

a. glabrous; **b.** rugose.

Note.—See: Rauhut (2003: character 18).

0388. Os nasale, margines laterales, sectiones craniales, crista aut jugae longitudinales, status:

a. absent; **b.** present.

Note.—See: Rauhut (2003: character 22).

0389. Os nasale, processus frontalis, et os frontale, facies dorsalis, eminentia pneumatica antorbitalis (**new term**), status:

a. absent;

b. present, variably prominent, comparatively low eminentia.

Note.—Confamilial exemplars of Cracidae (e.g., *Oreophasis*) typically possess prominent, comparatively elevated eminentia maxillare. See: Möller (1969a–c); Livezey (1986: appendix 1, character 16); Livezey (1989: table 1, character 16); Livezey (1995b: appendix 1, character 2); Livezey (1996a: appendix 1, character 8); Livezey (1996b: appendix 1, character 6); Livezey (1997a: appendix 1, character 10; *corrigenda*, Livezey 1998a); Livezey (1997b: appendix 1, character 4). In many taxa, displays substantial variation among individuals, protracted ontogenetic periods, and sexual dimorphism (generally being larger in males). Autapomorphies included primarily because of conspicuousness.

0390. Os nasale, processus maxillaris, truncation such that more than half of margo caudalis of apertura nasi osseum is composed of os maxillare, processus nasalis, status:

a. absent, typically composing substantial majority of pila postnasalis;

b. present.

Note.—See: Livezey (1998b: appendix A, character 27), alternatively worded in terms of os maxillare, processus nasalis, which included both taxa coded here as apomorphic.

0391. Os nasale, processus maxillaris, apparent torsion of processus beyond perpendicularity, status:

a. absent; **b.** present.

Note.—Apparent torsion evidently results from accommodation of closely associated arteria ethmoidalis, ramus lateralis.

0392. Os nasale, processus maxillaris, sutura with os maxillare, processus nasalis (i.e., junctura nasomaxillaris), expansion to form margo caudalis of apertura nasi ossea or pila nasomaxillaris (**new term**), status et forma (**ordered**):

a. complete, robust columna or broad lamina;

b. complete, pila or jugamentum complete but gracile, tenuous, typically majority composed of processus nasalis ossis maxillare;

c. incomplete, pila vestigialis ventralis, i.e., consisting only of ventral splint, principally representing failure of ossification in os nasale, processus *maxillaris*;

d. incomplete, pila vestigialis dorsalis, i.e., consisting only of dorsal splint, principally representing failure of ossification in os maxillare, processus *nasalis*.

Note.—Variation suggestive of origin as ligamentum ossificans. See: Russell and Dong (1994a [1993a]: table 2, character 4).

0393. Os nasale, processus rostralis (premaxillaris), forma:

a. elongate;

b. truncated, obsolete, or absent.

Note.—Structure in question synonymous with "processus subnarialis." See: Maryanska et al. (2002: appendix 1, character 17), in what may constitute the character of os nasale isomeric with that of the ossa premaxillare et maxillare which follows.

Os Premaxillare

0394. Os premaxillare, corpus ossis premaxillare, processus maxillaris, forma *sensu* (*i*) possession of ramus ascendens postnarialis (**new term**) of os premaxillare, processus maxillaris (contrast with processus nasalis maxillaris), and its contribution to margines ventralis et caudalis of apertura nasalis; (*ii*) exclusion of os maxillare from margines ventralis et caudalis of apertura nasalis; (*iii*) contact and resultant extension of sutura nasopremaxillaris caudoventrad to apertura nasalis; and (secondarily) by some authors (*iv*) length relative to apertura nasi ossea, fossa antorbitalis (margo rostralis), and ossa lacrimales, processes supraorbitales (**ordered**):

a. os premaxillare, processus maxillaris **broad and elongate**, including ramus ascendens postnarialis (lacked by Neornithes) of length sufficient to exclude os maxillare from reaching margo caudoventralis of apertura nasalis and effect extension of sutura nasopremaxillaris caudoventrad to apertura nasalis;

b. os premaxillare, processus maxillaris **moderately reduced**, including diminutive ramus ascendens postnarialis sufficient to achieve involvement in articulatio triosseus with both ossa maxillare and nasale in margo caudoventralis of apertura nasalis and attain minimal contact between ossa premaxillare et nasale caudoventrad to apertura nasalis;

c. os premaxillare, processus maxillaris **substantially truncated**, in which vestigial processus postnarialis is lacking, permits os maxillare to form part of margo caudoventralis of apertura nasalis, and fails to effect extension of sutura nasopremaxillaris caudoventrad to apertura nasalis.

Note.—Benton (1990b: 24) considered exclusion of os maxillare from margo aperturae nasalis by junctura of os premaxillare with os nasale to be synapomorphic of Ornithischia. See: Cracraft (1986: appendix, character 51), citing “processus nasalis”; Gauthier (1986: 12–13), as synapomorphic of Avialae and Ornithurae, respectively; Cracraft (1988: series II, character 18, in reference to “nasal process”); L. D. Martin et al. (1980); Chatterjee (1991: characters 18 and 24, part), but excluded by Chatterjee (1999: entry 13); Sereno and Novas (1992: appendix, character 1), in reference to size of “posterolateral process of premaxilla”; Chiappe and Calvo (1994: appendix I, characters 2–3); J. M. Clark et al. (1994); Novas (1994 [1993]: appendix, character 51); Pérez-Moreno et al. (1994: legend for fig. 3, characters 8–9); Russell and Dong (1994a [1993a]: table 2, character 1); Russell and Dong (1994b [1993b]: troödontid character 3); Chiappe (1995b: characters 2–3); Elzanowski (1995: 38); Chiappe (1996b: characters 2–3); Chiappe et al. (1996: appendix 1, characters 2–3); Chiappe et al. (1998: character 2); Hou et al. (1996: character 5); Sanz et al. (1995, 1997: characters 2–3); Elzanowski and Wellnhofer (1996); Forster et al. (1998: supplement, character 6); Ji et al. (1998: supplement, character 2); Chu (1998: appendix 1, character 41), for relative lengths of rostrum maxillae and corpus ossis premaxillaris; Livezey (1998b: appendix A, character 26); Makovicky and Sues (1998: appendix 1, character 7); Xu et al. (1999b: characters 6 and 101); Barsbold and Osmólska (1999); Holtz (2000 [1998]: appendix I, characters 6 and 8); Norell et al. (2000: appendix 1, character 5); Xu et al. (2000: supplement, characters 4 and 81); Chiappe (2001a: appendix 1, characters 2–3); Ji et al. (2001), regarding unnamed dromaeosaurid NGMC 91-A; Norell and Clarke (2001: appendix I, characters 8–9), treated similarly by J. A. Clarke (2002: appendix I, characters 8–9) and J. A. Clarke and Norell (2002: appendix 2, characters 8–9); Norell et al. (2001: appendix 1, characters 26–27); Chiappe (2002: appendix 20.2, characters 2–3 [latter primarily]); J. M. Clark et al. (2002a: appendix 2.2, character 20); Maryanska et al. (2002: appendix 1, character 9); Xu (2002: suite I, character 61; suite II, characters 71 and 232); Xu et al. (2002a: supplement, character 16); Xu et al. (2002a: supplement, character 177), in reference to extent of “posterior premaxillary process” and “nares”; Zhou and Zhang (2002: appendix III, characters 8–9); Rauhut (2003: character 6); Hwang et al. (2004: supplement, character 20); Xu and Norell (2004: supplement, character 20).

0395. Os premaxillare, corpus ossis premaxillare, processus frontalis, length relative to os maxillare, and (associated) os nasale, processus frontalis, length relative to os frontale, i.e., regio preorbitalis, forma definitivum:

a. os premaxillare less than half as long as os maxillare, os nasale considerably longer than os frontale;

b. os premaxillare more than half as long as os maxillare, os nasale subequal in length to os frontale—i.e., “nasomaxillary truncation.”

Note.—This character principally represents an alternative partitioning to preceding character based on relative caudal extents of primary elements of ossa faciei. See: Barsbold and Osmólska (1999); Rauhut (2003: character 71).

0396. Os premaxillare, corpus ossis premaxillare, processes frontales, persistence in adult of sutura interpremaxillaris rostrad to midpoint of apertura nasi ossea, status et forma definitivum (**ordered**):

a. present, entire sutura remains nonsynostotic throughout;

b. partial, sutura synostotic only caudally;

c. absent, entire sutura synostotic, except proximate to zona flexoria craniofacialis in some taxa.

Note.—Herein the elongation of ossa premaxillares—structurally the cause of medial separation of ossa nasales (i.e., fissura internasalis; **new term**)—was treated separately by Cracraft (1986: appendix, character 49). See: Cracraft (1986: appendix, character 49); Holdaway (1991: appendix 5.1, character 1); Norell and Clarke (2001: appendix I, character 1), treated similarly by J. A. Clarke (2002: appendix I, character 1), J. A. Clarke and Norell (2002: appendix 2, character 1), and J. A. Clarke (2004: appendix 1, character 1); Zhou and Zhang (2002: appendix III, character 1); Chatterjee (1991: character 23); Maryanska et al. (2002: appendix 1, character 13); Ji et al. (2005: supplement, part I, character 1).

0397. Os premaxillare, corpus ossis premaxillare, processus frontalis, et os nasale processus maxillaris, tumulus pneumaticus (**new term**)—abruptly raised segment of processes perforated by pori pneumatici et foramina neurovascularia—status:

a. absent; **b.** present.

Note.—See: Chu (1998: appendix 1, character 39); Maryanska et al. (2002: appendix 1, character 8).

0398. Os premaxillare, corpus ossis premaxillare, processus maxillaris, extension of caudal terminus as triangular flange ventral to sutura jugomaxillaris and free from arcus jugalis, emergence rostral to sutura jugomaxillaris, status:

a. absent; **b.** present, variably prominent.

Note.—Related in large part to abrupt dorsal angling of arcus jugalis immediately caudal to junctura with os maxillare, processus nasalis; comparatively small in *Megapodius*, *Ortalis*, and *Lophortyx*. See: Strauch (1978: character 13); Andors (1992: table 2, character 3); Livezey (1997a: appendix 1, character 28; *corrigenda*, Livezey 1998a); Chu (1998: appendix 1, character 40); Livezey (1998b: appendix A, character 23).

0399. Os premaxillare, rostrocaudal length (ventral to naris) relative to height below naris, expressed as ratio (**ordered**):

a. greater than 1.7;

b. 1.0–1.4; **c.** 0.7 or less.

Note.—See: Holtz (1994b: appendix 7.1, character 1); Maryanska et al. (2002: appendix 1, character 4).

0400. Os premaxillare, corpus ossis premaxillare, processus palatinus, status:

a. absent or narrow, and lacking junctura interpremaxillaris rostral to ossa vomera;

b. present and broad, and junctura interpremaxillaris rostral to os vomeris.

Note.—See: Holdaway (1991: appendix 5.1, characters 2–3); J. M. Clark et al. (1994); Russell and Dong (1994a [1993a]: table 2, character 3); Elzanowski (1995: character ?PG'1), also Elzanowski (1995: 38, character unindexed); Sues (1997: appendix 1, character 1); Makovicky and Sues (1998: appendix 1, character 9); Xu et al. (1999a: character 3); Holtz (2000 [1998]: appendix I, character 7); Rauhut (2003: character 3).

0401. Os premaxillare, corpus ossis premaxillare, crista tomialis, forma:

a. (sub)linear;

b. crenulate, i.e., having numerous minute protrusions or undulations;

x. noncomparable (Neornithes).

Note.—See: Norell et al. (2001: appendix 1, character 30); J. M. Clark et al. (2002a: appendix 2.2, character 23); Xu (2002: suite II, character 251); Xu et al. (2002a: supplement, character 196); Hwang et al. (2004: supplement, character 22); Xu and Norell (2004: supplement, character 22).

0402. Os premaxillare, corpus ossis premaxillare, processus supratomialis (**new term**), status:

a. absent; **b.** present.

Note.—See: Rauhut (2003: character 4). Processus supratomialis is the ventralmost portions of os premaxillare (ventral to pars subnarialis) and includes as margines ventrales the cristae tomiales and margines dorsales of the apertura nasales.

0403. Os premaxillare, corpus ossis premaxillare, pars subnarialis (**new term**), processus supratomialis (**new term**), forma *sensu* comparative depth:

a. depth low to moderate, at least as long as high;

b. depth substantial, significantly higher than long.

Note.—New term synonymous with "ramus ventralis" of some. See: Bonaparte (1991); Holtz (1994a: appendix 1, character 13); Holtz (1994b: appendix 7.1, character 1); Holtz (2000 [1998]: appendix I, character 5); Rauhut (2003: character 1).

0404. Os premaxillare, corpus ossis premaxillare, pars prenarialis (**new term**)—(*i*) length relative to that of pars subnarialis and (*ii*) associated angulus between planum medianum rostri et margo tomialis—forma:

a. (*i*) former less than latter, (*ii*) angulus at least 75°;

b. (*i*) former greater than latter, (*ii*) angulus less than 70°.

Note.—See: Rauhut (2003: character 2).

0405. Os premaxillare, corpus ossis premaxillare, canalis neurovascularis maxillae, foveae corpusculorum nervosorum within rostrum maxillae, status et forma (**ordered**):

a. present, densely distributed throughout pars prenasalis rostri (**new term**) and in some cases extending farther caudad;

b. present, limited to rostrum maxillae, apex rostri and (minority) limited distribution to margines tomiales rostri;

c. absent.

Note.—See: Livezey (1998b: appendix A, character 25).

Os Maxillare

0406. Ossa maxillare et premaxillare (dorsal perspective), constriction of former and rostral expansion of latter, status:

a. absent; **b.** present.

Note.—See: Rauhut (2003: character 8), with respect to contriction and "rosette" of articulated premaxillae.

0407. Ossa maxillares, angulus defined by intersection of rostrally extended tangent lines to ossa toward planum medialis, forma:

a. angulus acute;

b. angulus practically undefined, tangentia subparallel;

x. noncomparable (Aves, including Neornithes).

Note.—See: Madsen (1976); Sereno and Novas (1994 [1993]); J. A. Clarke et al. (1994); J. D. Harris (1998); Sereno et al. (1998); Rauhut (2003: character 10).

0408. Os maxillare, crista tomialis, angulus tomialis (**new term**)—extension of caudal terminus as distinct tuberculum or short processus caudal to sutura jugomaxillaris and lateral to, and variably free from, arcus jugalis, status (**unordered**):

a. absent;

b. present, composed entirely of os maxillare;

c. present, composed of os premaxillare or ossa maxillare et premaxillare.

Note.—See: Strauch (1978: character 13), reanalyzed by Björklund (1994: appendix) and Chu (1995); Livezey (1996a: appendix 1, characters 14–15), regarding variations within anserines; Livezey (1997a: appendix 1, character 37; *corrigenda*, Livezey 1998a); Chu (1998: appendix 1, character 43).

0409. Os maxillare, crista tomialis maxillaris, distinct, ventrally prominent discontinuity, differentiated basally as truncate or convex margines adjacent to angulus oris (lateral perspective), status:

a. absent; **b.** present.

Note.—Distinct from tomium maxillare within Anseriformes in which variably shear margines are evident along majority of rostrum maxillae (Livezey 1996a: character 12).

0410. Os maxillare, facies ventralis, margo caudalis medial to lateral limit of sutura maxillaropalatinus, conformation as distinct plica, continuous across the midline, and distinctly ventral to os palatinum, processus rostralis, status:

a. absent; **b.** present.

Note.—See: D. W. Thompson (1899).

0411. Os maxillare, ramus ascendens postnarialis (**new term**), forma *sensu* confluence with margo rostralis of corpus ossis maxillare, relative inclination and height of pars rostralis corporis (**unordered**):

a. confluent with margo rostralis, pars rostralis shallowly inclined caudodorsad;

b. displaced from margo rostralis, pars rostralis shorter than high;

c. displaced from margo rostralis, pars rostralis at least as long as high.

Note.—See: Sereno et al. (1996); Rauhut (2003: character 11).

0412. Os maxillare, pons maxillaro-jugalis (**new term**), status:

a. absent; **b.** present.

Note.—This character refers to "maxillopalatine strut(s)" defined by Strauch (1978: characters 14–17) and Strauch (1985: character 1) for many Charadriiformes, the former reanalyzed by Björklund (1994: appendix) and Chu (1995). Chu (1998: appendix 1, character 47) considered feature to be equivalent to "strut B" of Zusi and Jehl (1970: fig. 2). Fenestra ventrolateralis (**new term**), synonymous with the *accessorische Gamenlucken* of Höfer (1949) and treated elsewhere, corresponds to a subcircular enclosure delimited caudad by coplanar intersection of strut "A" (margo ventrolateralis of pars palatus maxillare to arcus jugalis) and strut "B" (arcus jugalis to margo dorsolateralis of pars palatus maxillare). The two struts can be so tightly coalesced in some taxa as to make differentiation problematic. After Chu (1998), the comparatively tenuous and uncommon strut "A"—pons maxillaro-jugalis dorsalis (**new term**)—is not considered here, instead focus is on the generally robust strut "B"—pons maxillaro-jugalis ventralis (**new term**).

0413. Os maxillare, processus jugalis, lamina palatina (**new term**), status and forma *sensu* terminus caudalis (**ordered**):

a. absent;

b. present, rostrocaudally abbreviate, extends moderately caudad processus palatus;

c. present, rostrocaudally elongate, extends markedly caudad to processus palatus.

Note.—New term refers to a medial shelf that extends caudad to processus palatus et os lacrimale. See: Livezey (1998b: appendix A, character 31), which related position of processus jugalis with apertura nasi ossea; Barsbold and Osmólska (1999), pertaining to caudal extent of processus nasalis relative to that of processus jugalis in *Velociraptor*.

0414. Os maxillare, corpus ossis et processus premaxillaris, pneumaticity—recesses, foramina, cellulae pneumatica related to sinus maxillaris rostralis of Witmer (1990)—status et forma (**unordered**):

a. absent;

b. present, large, shallow recessus;

c. present, large, deep recessus, latter penetrating most of processus premaxillaris;

d. present, variable combination of foramina and cellulae pneumaticae.

Note.—See: Witmer (1990: 372, character 15); Cracraft and Clarke (2001: appendix 2, character 16), regarding "recessus pneumatici [paranasales] maxillaris rostralis," provisionally considered synonymous with "rostral maxillary sinus," and considered present in avian outgroups and *Hesperornis*; Cracraft and Clarke (2001: appendix 2, character 17), considered "caudal maxillary sinus" synonymous and present in avian outgroups and *Hesperornis*; G. Mayr (2003a: appendix I, character 8).

0415. Os maxillare, processus palatus (**new term**), sectio caudolateralis, facies ventralis, single, large foramen pneumaticum rostral to junctura with arcus jugalis, status:

a. absent; **b.** present;

x. noncomparable (Dinornithiformes).

0416. Os maxillare, processus nasalis, foramen, status et forma (**unordered**):

a. present, single; **b.** present, double;

c. absent.

Note.—See: Witmer (1997), regarding *Archaeopteryx*; Chiappe et al. (1999: figs. 14–16), regarding *Confuciusornis*. Doubtful that foramen considered here is homologous with foramina antorbitales situated within suturae (e.g., fenestra antorbitalis externa or fenestra promaxillaris), but likely state "a" is homologous with the "fenestra maxillaris" of *Albertosaurus* (Witmer 1997: fig. 30)

0417. Os maxillare, processus nasalis, ramus dorsalis, prominence and lateromedial exposure, forma (repectively):

a. substantial, present;

b. reduced, slight or absent.

Note.—See: Chiappe (1996b: character 6), with respect to bifurcation of os maxillare, processus nasalis into rami dorsalis et ventralis (**new terms**); Livezey (1998b: appendix A, character 30); Chiappe (2001a: appendix 1, character 7); Norell and Clarke (2001: appendix I, character 10), treated similarly by J. A. Clarke (2002: appendix I, character 10), J. A. Clarke and Norell (2002: appendix 2, character 10), and J. A. Clarke (2004: appendix 1, character 10); Chiappe (2002: appendix 20.2, character 7); Chiappe and Lacasa-Ruiz (2002), regarding *Noguerornis*; Zhou and Zhang (2002: appendix III, character 10); Ji et al. (2005: supplement, part I, character 10).

0418. Os maxillare, processus nasalis, ramus ventralis (lateral perspective), involvement in margo rostralis of fenestra antorbitalis, status et forma (**ordered**):

a. present, extensive;

b. present, limited by small dorsal fragmentum of processus maxillaris of os nasale contacting os premaxillare and thereby excluding os maxillare;

c. absent, including absence of dorsal fragmentum of os maxillare.

Note.—See: Norell and Clarke (2001: appendix I, character 11), treated similarly by J. A. Clarke (2002: appendix I, character 11), J. A. Clarke and Norell (2002: appendix 2, character 11), and J. A. Clarke (2004: appendix 1, character 11); Zhou and Zhang (2002: appendix III, character 11); Ji et al. (2005: supplement, part I, character 11).

0419. Os maxillare, processus palatus (**new term**), breadth and contribution to palatum osseum, status:

a. present, broad and contributing significantly to palatum osseum;

b. present, but narrow.

Note.—Processus palatus of os maxillare formerly referred to as "the maxillopalatines" or "palatal shelf." See: Ostrom (1976a); Gauthier (1986: 13), as synapomorphy of Ornithurae; J. M. Clark et al. (1994); Elzanowski (1995: character ?PG'2); Elzanowski (1995: character ?PG'3); Sues (1997: appendix 1, character 19); Xu et al. (1999a: character 7); Xu et al. (1999a: character 3), with respect to "secondary bony palate"; Azuma and Currie (2000: appendix 1, character 78); Hughes (2000: appendix 2, characters 48–49); Xu (2002: suite II, character 74); also see: Norell et al. (2001: appendix 1, character 32); J. M. Clark et al. (2002a: appendix 2.2, characters 26 [contributions by ossa premaxillare, maxillare, et vomeris], 27 [midline ventral denticulate eminentia]); Maryanska et al. (2002: appendix 1, character 7), with respect to junctura interpremaxillaris; Hwang et al. (2004: characters 25–26); G. Mayr (2004b: appendix 1, character 8); G. Mayr and Ericson (2004: appendix I, character 7); Xu and Norell (2004: supplement, characters 25–26).

0420. Os maxillare, processus palatus (**new term**), ala caudalis (**new term**), status et forma (**unordered**):

a. present, simple blade, shell, or cone, with variable numbers (typically few) of exposed (typically coarse) trabeculae pneumaticum;

b. present, largely enclosed, variably inflated prominentia, containing numerous, typically fine, uniformly distributed trabeculae pneumaticum, producing spongiform internum;

c. present, largely open, variably inflated prominentia, composed of numerous, exposed, typically fine, uniformly distributed, trabeculae pneumaticum, producing spongiform corpus;

d. absent;

x. noncomparable by synostosis or component elements (*Apteryx*, *Sula*, *Pelecanus*, *Balaeniceps*, *Steatornis*).

Note.—See: Strauch (1978: character 13), reanalyzed by Björklund (1994: appendix) and Chu (1995); S. F. Simpson and Cracraft (1981: character 12); Cracraft (1985: character 10); Strauch (1985: character 2); Siegel-Causey (1997: table I, character 9); K. Lee et al. (1997: appendix 1, character 57), with respect to "maxillopalatine antrum" of some ratites; Chu (1998: appendix 1, character 44); Livezey (1998b: appendix A, character 28).

0421. Os maxillare, processus palatus (**new term**), synostosis medialis, status et forma (**unordered**):

a. absent;

b. present, excluding septum interorbitalis;

c. present, including septum interorbitalis.

Note.—See: Strauch (1978: character 12), reanalyzed by Björklund (1994: appendix) and Chu (1995); S. F. Simpson and Cracraft (1981: character 12); Cracraft (1985: characters 1, 8, and 10); J. M. Clark et al. (1994); K. Lee et al. (1997: appendix 1, character 57); Siegel-Causey (1997: table I, character 9); Livezey (1998b: appendix A, character 28); G. Mayr (2003b: appendix I, character 4), regarding "desmognathy"; G. Mayr and Clarke (2003: appendix A, character 11); Dyke and van Tuinen (2004: appendix 1, character 4); G. Mayr (2004a: appendix 1, character 4).

0422. Os maxillare, processus palatus (**new term**), pneumatic inflation, synostosis symphysialis medialis, broad lateral separation from ossa palatini, and caudad extension to (ventrally distinguishable) suturae palatinomaxillares, status:

a. absent; **b.** present.

Note.—See: S. F. Simpson and Cracraft (1981: character 12); Cracraft (1985: characters 1 and 10); Holdaway (1991: appendix 5.1, character 4); Ericson (1997: table 1, character 10); Livezey (1997a: appendix 1, character 38; *corrigenda*, Livezey 1998a); Siegel-Causey (1997: table I, character 9); Chu (1998: appendix 1, character 44); Livezey (1998b: appendix A, character 28); G. Mayr (2004a: appendix 1, character 3).

0423. Os maxillare, processus palatus (**new term**), elaboration as sinus maxillaris caudalis (**new term**), status:

a. absent; **b.** present.

Note.—Character formerly referred to as "cup-shaped caudal sinus." See: Witmer (1990: 371, characters 2 and 4); Chiappe et al. (1998: character 3); Ji et al. (1998: supplement, character 3); Chatterjee (1999: appendix II, character 24); Chiappe (2001a: appendix 1, character 8); Chiappe (2002: appendix 20.2, character 8); Chiappe and Lacasa-Ruiz (2002), regarding *Noguerornis*.

0424. Os maxillare, processus palatus (maxillopalatinus), hamulate prominentia medialis maxillaris (**new term**), status:

a. absent; **b.** present.

Note.—See: Xu et al. (2002a: supplement, character 19), regarding "palatal shelf of maxilla . . . with midline ventral 'toothlike' projection"; Maryanska et al. (2002: appendix 12, character 12), regarding "two longitudinal ridges and a toothlike process" in "palatal shelf of maxilla."

0425. Os maxillare, processus maxillaris, regio infra-orbitalis, bilateral medial compression, status:

a. absent; **b.** present.

Note.—See: Maryanska et al. (2002: appendix 1, character 10).

Os Palatinum

0426. Os palatinum, forma generalis (ventral perspective) related to partes rostralis et/aut jugalis:

a. both partes (including jugals) present, element "tetraradiate" (subrectangular or trapezoidal) in ventral aspect;

b. pars jugalis absent, element "triradiate" or triangular in ventral aspect.

Note.—See: Ligon (1967: fig. 1); Payne and Risley (1976: character 2), regarding Ardeidae; Cracraft (1982: series 4, character 1), regarding *Gestalt* of ossa palatini of Gaviidae and Podicipedidae; Cracraft (1988: series VII, character 5); Cracraft and Mindell (1989: table 1, character 31); Chatterjee (1991: character 27), regarding apparently apomorphic *Gestalt* combining short, complex os pterygoideum with elongate, narrow os palatinum in *Hesperornis*; Sereno (1991a: appendix), regarding fenestra pterygopalatina (**new term**) in Ornithosuchia; Elzanowski (1995: character ?N11); Ericson (1996: character 5); Chiappe et al. (1998: character 5); J. D. Harris (1998: appendix 2, character 29); Ji et al. (1998: supplement, character 5), with respect to processus "jugalis" (pars lateralis); Currie and Carpenter (2000: appendix 1, character 31); Holtz (2000 [1998]: appendix I, character 76); Chiappe (2001a: appendix 1, character 10); Cracraft and Clarke (2001: appendix 2, character 36); Norell et al. (2001: appendix 1, character 65); Chiappe (2002: appendix 20.2, character 10); J. M. Clark et al. (2002a: appendix 2.2, character 65); Maryanska et al. (2002: appendix 1, character 64); Xu (2002: suite I, suite II, character 103); Xu et al. (2002a: supplement, character 48); Currie et al. (2003: appendix, character 43); Rauhut (2003: character 65); Hwang et al. (2004: supplement, character 64); G. Mayr (2004b: appendix 1, character 11), regarding planar expanse; Xu and Norell (2004: supplement, character 64).

0427. Ossa premaxillare, maxillare et palatinum—palatum osseum—expansion rostrad of palatum rostral from choanae to crista tomialis largely by sutura ventromediana inter(pre)maxillaris and closure of fissura interpalatina, status:

a. present, palatum osseum (intertomialis) rostralis divided mediad by variably wide and conformed fissurae et/aut fenestrae;

b. absent, palatum intertomialis ventral to regio nasales obsolete.

Note.—Assessments confounded by a diversity of pneumatic expansions in pars rostralis palati ossium.

0428. Os palatinum, pars jugalis, distal expansion, status et forma (**ordered**):

a. absent; **b.** present, moderate;

c. present, extreme, effecting articulatio jugopalatina.

Note.—See: Payne and Risley (1976: character 2), regarding Ardeidae; Sereno et al. (1996: footnote 45, character 43), in reference to "flange-shaped process for lacrimale"; J. D. Harris (1998: appendix 2, character 32); Currie and Carpenter (2000: appendix 1, character 34); Holtz (2000 [1998]: appendix I, character 77) regarding distal expansion of "jugal process" of os palatinum.

0429. Os palatinum (especially pars lateralis), marked ventral angling relative to rostrum parasphenoidale, status:

a. absent; **b.** present.

Note.—See: D. W. Thompson (1899).

0430. Os palatinum, pars maxillaris, abrupt medial curvature caudally producing a rostral segment in which the paired elements are parallel and widely separated, and laminae choanales ventrales are parallel and narrowly separated, status (**unordered**):

a. absent; **b.** coplanar; **c.** present.

Note.—See: Livezey (1997a: appendix 1, character 39; *corrigenda*, Livezey 1998a).

0431. Os palatinum, processus rostralis, junctura palatinomaxillaris, position relative to junctura jugo(pre)maxillaris:

a. medioventral; **b.** mediodorsal.

Note.—See: Strauch (1978: character 13); Livezey (1997a: appendix 1, character 40; *corrigenda*, Livezey 1998a).

0432. Os palatinum, processus rostralis, union with os vomeris by suturae (sutura vomeropalatina) or fusion rostral to choana ossea, status:

a. absent; **b.** present.

Note.—See Zusi and Livezey (2006).

0433. Os palatinum, processus rostralis, prominent, obliquely oriented plica terminating rostrally at zona flexoria palatina, status:

a. absent; **b.** present.

Note.—Unlike some aspects of palatinum including rostralmost portions of element—e.g., uniformity of width to sutura palatinomaxillaris (Strauch 1978: character 13; Livezey 1998b: appendix A, character 32; Sereno 2001: table 2, character 41)—this autapomorphy evident despite synostosis as it characterizes a comparatively differentiable palatum osseum.

0434. Os palatinum, pars choanalis, lamella dorsalis, facies dorsolateralis, recessus pneumaticus opening rostrally and positioned at basis partis maxillaris, status:

a. absent; **b.** present.

Note.—See: Holdaway (1991: appendix 5.1, character 6).

0435. Os palatinum, pars choanalis, lamella dorsalis, facies dorsolateralis, dense fenestration permitting transverse penetration of paired elements immediately ventral to rostrum parasphenoidale, status:

a. absent, including taxa possessing few pori aut fenestrae;

b. present.

Note.—See: Heerwagen (1889).

0436. Os palatinum, pars choanalis, lamella dorsalis, margo choanalis, loss or severe reduction of dorsal component, margo nasalis essentially coplanar with facies ventralis of lamina, status:

a. absent; **b.** present.

Note.—See: Siegel-Causey (1988: characters 31–32).

0437. Os palatinum, pars choanalis, lamella dorsalis, margo choanalis, pronounced funnel-like conformation, including pronounced lateromedial constriction of lateral and medial surfaces of lamina choanalis dorsalis, resulting in almost complete, bilateral closure of aperturae choanae rostrally (associated with breadth of os vomeris medial to margo rostralis opposite point of constriction of lamina choanalis dorsalis), status:

a. absent; **b.** present.

Note.—See: G. Mayr (2003a: appendix I, character 9); G. Mayr (2004b: appendix 1, character 9).

0438. Os palatinum, pars choanalis, lamella dorsalis, margo choanalis, caudal elongation so as to reduce margo dorsalis to relatively short segment (bordered caudally by pars pterygoideus), status:

a. absent; **b.** present;

x. noncomparable because of unique complexus articulationum (palaeognathous Neornithes).

0439. Os palatinum, pars choanalis, lamella dorsalis, margo dorsalis, bilateral compression and synostosis forming prominent carina, status:

a. absent; **b.** present.

Note.—See following character.

0440. Os palatinum, pars choanalis, lamella dorsalis, margo medialis, synostosis interpalatina medialis, possibly including pars palatina pterygoidea et os vomeris, if present and interposed, status et forma (**ordered**):

a. absent, elements distinguishable, including at least as distinct sutura interpalatina;

b. present, but not forming prominent carina medialis;

c. present and producing ventrally prominent carina medialis.

Note.—See: Cracraft (1988: series VIII, character 2); Rowe and Gauthier (1990); J. D. Harris (1998: appendix 2, character 31); Currie and Carpenter (2000: appendix 1, character 33); Livezey (1998b: appendix A, character 37), regarding relative length of "fissura interpalatina"; Holtz (2000 [1998]: appendix I, character 75); G. Mayr (2003a: appendix I, character 10); G. Mayr and Clarke (2003: appendix A, character 15), emphasizing crista (carina medialis) and synostosis interpalatinus medialis, respectively; Dyke and van Tuinen (2004: appendix 1, character 8); G. Mayr (2004a: appendix 1, character 8); G. Mayr (2004b: appendix 1, character 10).

0441. Os palatinum, pars choanalis, lamella ventralis, status (**ordered**):

a. absent; **b.** rudimentary or vestigial;

c. prominent.

Note.—See: Ericson (1997: table 1, character 9; table 2, character 8); Zusi and Livezey (2006).

0442. Os palatinum, pars choanalis, lamella ventralis, medial synostosis to form a ventrally closed fossa choanalis, status:
a. absent; **b.** present.

0443. Os palatinum, pars choanalis, lamella ventralis, position of angulus caudomedialis relative to that of pars lateralis, margo caudalis, situs rostrocaudalis (**ordered**):
a. rostral; **b.** coincident; **c.** caudal;
x. noncomparable where pars lateralis absent, rudimentary, or extensively synostotic.
Note.—See: Livezey (1998b: appendix A, character 33); Hughes (2000: appendix 2, character 47); G. Mayr (2002a: appendix 1, character 2); Pascotto and Donatelli (2003); G. Mayr (2005b: appendix A, character 2).

0444. Os palatinum, pars choanalis, lamella ventralis, medial separation of bilateral lamellae, forma (**ordered**):
a. moderate; **b.** great; **c.** extreme.

0445. Os palatinum, pars choanalis, margo (ala) ventralis, processus rostromedialis (**new term**), status:
a. absent or minute; **b.** distinct;
x. noncomparable (Dinornithiformes).
Note.—See: Strauch (1985: character 3); Cracraft (1988: series XV, character 1); Livezey (1998b: appendix A, character 34).

0446. Os palatinum, pars choanalis, lamella ventralis, processus rostromedialis (if present), rostromedial convergence, status et forma (**ordered**):
a. absent;
b. present, separate throughout length;
c. present, synostotic rostrally.
Note.—See: Pascotto and Donatelli (2003: figs. 12–13), regarding "angulus caudomedialis of crista ventralis of lamina choanalis" after nomenclature of Zusi *fide* Baumel and Witmer (1993: annotation 64).

0447. Os palatinum, pars lateralis, status (**ordered**):
a. absent; **b.** rudimentary or vestigial;
c. well developed.
Note.—See: Payne and Risley (1976: characters 2 and 4), regarding Ardeidae; Livezey (1997a: appendix I, characters 41–42; *corrigenda*, Livezey 1998a); Zusi and Livezey (2006).

0448. Os palatinum, pars lateralis, tumulus ventralis (**new term**), status:
a. absent; **b.** present.
Note.—See: Stephan (1979), a comprehensive atlas of Spheniscidae.

0449. Os palatinum, pars lateralis, marked rostrocaudal foreshortening, in which rostrocaudal dimension is approximately equal to or less than lateromedial dimension, status:
a. absent; **b.** present.
Note.—See: Payne and Risley (1976: character 3), regarding Ardeidae.

0450. Os palatinum, pars lateralis, distinct dorsal sloping caudally toward facies articularis parasphenoidalis, resulting in apparent lateral torsion of pars lateralis about longitudinal axis, status:
a. absent; **b.** present.

0451. Os palatinum, pars lateralis, marked caudolateral orientation, status:
a. absent; **b.** present.
Note.—See: G. Mayr et al. (2003: appendix 1, character 10).

0452. Os palatinum, pars lateralis, margo lateralis broad and rounded, status:
a. absent; **b.** present.
Note.—See: G. Mayr (2002a: appendix 1, character 3), with respect to Caprimulgiformes; G. Mayr et al. (2003: appendix 1, character 10); G. Mayr (2005b: appendix A, character 3).

0453. Os palatinum, pars lateralis, margo lateralis, processus accessorius (**new term**), status:
a. absent; **b.** present;
x. noncomparable, pars lateralis absent (palaeognathous Neornithes).
Note.—The medial position of the spina relative to the angulus caudolateralis merits study. See: Livezey (1997a: appendix 1, character 42; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, character 35).

0454. Os palatinum, pars lateralis, angulus (processus) caudolateralis, status:
a. present; **b.** absent;
x. noncomparable (palaeognaths, Psittaciformes, *Opisthocomus*, Caprimulgiformes exclusive Steatornithidae).
Note.—See: Payne and Risley (1976: characters 2 and 4), regarding Ardeidae; Holdaway (1991: appendix 5.1, character 5); Livezey (1997a: appendix 1, characters 41–42; *corrigenda*, Livezey 1998a); G. Mayr (2002a: appendix 1, character 2), with respect to Caprimulgiformes; G. Mayr (2003a: appendix I, character 11); G. Mayr and Clarke (2003: appendix A, character 16); Dyke and van Tuinen (2004: appendix 1, character 9); G. Mayr (2004a: appendix 1, character 9); G. Mayr and Ericson (2004: appendix I, characters 8 [angulus] and 9 [pars *per se*]).

0455. Os palatinum, pars lateralis, fossa ventralis, continuity rostrad with choana ossea, and continuation of fossa to midline on lamina choanalis ventralis, status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes).
Note.—See: G. Mayr (2002a: appendix 1, character 4), with respect to Caprimulgiformes.

0456. Os palatinum, pars lateralis, immediately lateral to rostral terminus of fossa ventralis, prominentia muscularis (**new term**), status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes).

0457. Os palatinum, pars lateralis, fossa ventralis, crista obliqua (**new term**), a rostral, sharply defined, sloping crista that defines a second, smaller, rostral fossa in pars lateralis palatini, status:
a. absent; **b.** present.

0458. Os palatinum, pars pterygoideus, processus pterygoideus, status (**ordered**):
a. absent or rudimentary;
b. present, moderately developed;
c. present, extensively developed.
Note.—See: Cracraft (1985: character 1), referred to as "mediopalatine process"; Zusi and Livezey (2006).

0459. Os palatinum, pars pterygoideus, crista dorsalis (**new term**), status:
a. absent; **b.** present, variably developed.
Note.—In some taxa, lamella forms (bilaterally) amplexus rostri parasphenoidalis. Originally scored for prominence as well as status, varation within Rallidae (Livezey 1998b) and unacceptable subjectivity prompted a retreat to binary status. See: Holdaway (1991: appendix 5.1, character 8), in reference to prominent crista serving as amplexus rostri parasphenoidalis in some falconiforms; G. Mayr and Clarke (2003: appendix A, character 21); Dyke and van Tuinen (2004: appendix 1, character 14).

0460. Ossa palatinum et ectopterygoideum, interposed fenestra ectopterygopalatina (**new term**), status:
a. absent, sutura ectopterygopalatina continuous;
b. present; **x.** noncomparable (Neornithes).
Note.—Nomenclature for this lacuna or fenestra suturalis—between ossa within the junctura (syndesmosis) pterygopalatina—after Elzanowski (2001). See: Ostrom (1969); Gauthier (1986: text character 53); Sereno (1991a: appendix, ingroup-clades character 17); Russell and Dong (1994a [1993a]: table 2, character 13); Russell and Dong (1994b [1993b]: list A, character 1); Holtz (1994a: appendix 1, character 79); Currie (1995: appendix, character 18); Elzanowski (1995: 40, fig. 1, character unindexed), regarding "subsidiary fenestra"; Sues (1997: appendix 1, character 6); Forster et al. (1998: supplement, character 13); J. D. Harris (1998: appendix 2, character 30); Xu et al. (1999a: character 12); Xu et al. (1999b: character 12); Azuma and Currie (2000: appendix 1, character 86); Currie and Carpenter (2000: appendix 1, character 32); Holtz (2000 [1998]: appendix I, characters 79–80); Maryanska et al. (2002: appendix 1, characters 65 and 69); Elzanowski (2002), for *Archaeopteryx*; Norell et al. (2001: appendix 1, character 66); J. M. Clark et al. (2002a: appendix 2.2, character 64); Elzanowski (2002), for recent reconstruction of *Archaeopteryx*; Maryanska et al. (2002: appendix 1, character 68); Xu (2002: II, character 233); Xu et al. (2002b); Rauhut (2003: character 68). P. Currie (pers. comm.) concluded this feature corresponded to the "ventral fossa," and that tyrannosaurids lacked such a fenestra (*contra* Rauhut 2003) as os ectopterygoideum extends to os palatinum in this taxon; Hwang et al. (2004: supplement, character 63); Xu and Norell (2004: supplement, character 63).

Ossa Vomerae (synostotic pair of which forming "vomer")

Note.—In application to Reptilia *sensu lato*, including birds, the term "vomer" poses nomenclatural problems or points of potential confusion. First, paired primordia of the "vomer" occur in Aves and undergo variably complete synostosis during ontogeny (Hofer 1949; Baumel and Witmer 1993: annotation 68); i.e., the "vomer" is the collective term for the composite skeletal *structure* comprising bilaterally paired constituent subparts or **ossa vomeris sinistris et dextrus**. This composition is reflected in the terms "ossa prevomera" (Goodrich 1958), "the two vomers" (Romer 1956: 62), and less clearly "the vomer, which meets its partner anteriorly and extends back medial to the internal naris" (Romer 1956: 235). The distinct pair of broad palatal "vomera" in the seymouriaform *Kotlassia* (Romer 1956: fig. 34B) present an extreme example of separate vomerine elements. Dinosauria exclusive of the Theropoda retain separate, paired ossa vomerae (Gauthier 1986; Elzanowski and Galton 1991; Elzanowski and Wellnhofer 1996), and symphysis intervomeralis appears to be synapomorphic of Theropoda (Erdmann 1940). Extreme avian cases are afforded by the Dinornithiformes (*Pachyornis australis*; two specimens) and Picidae, in which the paired primordia remain separate throughout life. Second, the syntactical implication that "*the* vomer" is a single, medial element ontogenetically distinct from other paired cranial elements, seems to derive from the situation in Mammalia.

These issues prompt a clarification of nomenclatural usage, one that serves not only to clarify the vomer from its constituent ossa vomeris, but also to point out parallel instances in which skeletal "structures" (e.g., vomer, sternum, coracoideum, carpometacarpus, and tarsometacarpus) are explicitly distinguished from the variably synostotic bones that each comprise. Note that two distinct types of such structural constitution, coincident in some taxa, apply: (*i*) median union of bilateral pairs of the same element (e.g., ossa vomeris); (*ii*) unilateral union of formerly distinct elements (e.g., ossa procoracoideum, acrocoracoideum et sternocoracoideum, ossa carpi distalia et metacarpi) into a single bone-like structure (e.g., coracoideum and carpometacarpus, respectively); and (*iii*) unions involving both bilateral and unilateral pairs of homologous elements to form a single, variably synostotic structure, typically treated as a single "bone" (sternum).

Throughout this work, homologous elements or bones *sensu stricto* are distinguished by the antecedent os followed by a genitive singular modifier, whereas composite structures lack the foregoing biterminological form. This convention, if explicitly recognized and applied, clearly permits the biosseous composition (ossa vomeris) of the structure (vomer) in birds. As need for clarification and nomenclature of homologous structures expands taxonomically, the constituency of the clavicula, femur, tarsometatarsus, etc., will become necessary, requiring the explicit distinction of these skeletal "structures" from elemental "bones." Together with establishment of interclass homologies of the latter, these issues pose significant but essential challenges for phylogenetics of the highest orders.

Unfortunately, the comparably situated structure of mammals is of questionable homology to the bilaterally paired ossa that characterize Reptilia (Goodrich 1958). The nomenclature espoused above clarifies issues of structure and homology in Aves, but is not intended to imply a dubious homology with the apparently unipartite "vomer" of Mammalia.

For purposes of this analysis, we retain the *structurally composite term* **vomer** comprising variably synostotic *constituent elements* or **ossa vomeris**. We differ from the third-declension "ossa vomera" of Sereno (1991a: 14) on the basis of gender (vomer being masculine, not neuter). Should the need arise, the essential (third) declensions for the elemental constituents of the structure "vomer" are as follows: nominative singular, vomer; genitive singular, vomeris ("of the vomer"); nominative plural, vomeres ("vomers"); and genitive plural, vomerum ("of the vomers"). Only the structural or collective term "vomer" and the nominative singular for one of the bilateral constituents ("vomer") are identical. The adjectival form (singular) is "vomeralis."

All characters of ossa vomeris are noncomparable in numerous Neornithes evidently (or apparently) lacking distinguishable ossa vomeris (e.g., some Galliformes, Pelecaniformes, Columbiformes, Coraciiformes, Piciformes), and minority of others not codable if bilateral elements are not synostotic.

0461. Ossa vomeris, status modalis definitivum:

a. present, variably developed; **b.** absent.

Note.—See: Cracraft (1985: character 9); Holdaway (1991: appendix 5.1, character 7); J. M. Clark et al. (1994); Rotthowe and Starck (1998: appendix, character 30), who cited Cracraft (1988) as source; G. Mayr (2003a: appendix I, character 12); G. Mayr and Clarke (2003: appendix A, character 18); Dyke and van Tuinen (2004: appendix 1, character 11); G. Mayr (2004b: appendix 1, character 12); G. Mayr and Ericson (2004: appendix I, character 12), assigned apomorphic state for Columbidae and Pteroclidae.

0462. Vomer (synostotic ossa vomeris), corpus vomeris (ossa vomeris exclusive of extremitates rostralis et caudalis) in planum transversus, forma (**unordered**):

a. strutlike, variable;

b. bladelike, primary feature is bilateral compression with dorsoventral deepening, in Gruiformes and Charadriiformes the dorsal margin tending to "Y-shaped" caudally;

c. cruciate, ventral portion a dorsoventrally oriented blade, with dorsal portion perpendicular and bilaterally expanded;

d. laminate, primary feature is bilaterally broadening;

e. cylindrical.

Note.—See: Cracraft (1988: series XIII, character 3); G. Mayr and Clarke (2003: appendix A, character 20); Dyke and van Tuinen (2004: appendix 1, character 13).

0463. Vomer, corpus vomeris, marked pneumaticity throughout, status:

a. absent; **b.** present.

0464. Vomer (synostotic ossa vomerum), corpus vomeris, terminus rostralis, forma:

a. acuminate;

b. other, e.g., bifurcated, bilaterally divergent, or rounded.

Note.—States in Apodiformes (*Hemiprocne*, *Cypseloides*, *Apus*) require further study. See: Cracraft (1986: appendix, character 46); Livezey (1998b: appendix A, character 38); G. Mayr et al. (2003: appendix 1, character 9); G. Mayr and Ericson (2004: appendix I, character 13).

0465. Vomer, corpus vomeris, spina rostralis vomeris (**new term**; variably elongate rostral spine, distinguishable from basis of corpus proprius), status:

a. absent; **b.** present.

Note.—Apomorphy characterizes all Trochilidae except possibly *Colibri*.

0466. Vomer, facies articularis palatina, rostrocaudal extent relative to margo rostralis, pars maxillaris, os palatinum:

a. former rostral to latter;

b. former caudal to latter.

Note.—See: Maryanska et al. (2002: appendix 1, character 66).

0467. Vomer (synostotic ossa vomeris), processus pterygoideus, status (**ordered**):

a. present; **b.** vestigial; **c.** absent.

Note.—Assessment of *Phoenicopterus* requires examination of juvenile. See: Cracraft (1988); Livezey (1998b: appendix A, character 39); Rotthowe and Starck (1998: appendix, character 27), regarding incisura medialis processi.

0468. Vomer (synostotic ossa vomeris), processus pterygoideus, caudally elongated with pronounced lateral deflection, associated with lateral displacement of sutura vomeropalatina relative to rostrum parasphenoidale, status:

a. present; **b.** absent.

0469. Vomer (synostotic ossa vomeris), terminus caudalis relative to basis cranii externa and associated articulatio vomerosphenoidalis (**new term**), status:

a. terminating rostrad to basis cranii externa;

b. extending caudally to basis cranii externa, producing an articulatio vomerosphenoidalis.

Note.—See: Russell and Dong (1994a [1993a]: table 2, character 12); Xu et al. (1999a: character 11); Holtz (2000 [1998]: appendix I, character 74); G. Mayr and Ericson (2004: appendix I, character 14), emphasizing invaginationes mediales.

Os Pterygoideum

Note.—Herein we consider the os pterygoideum to comprise two parts—pars palatina (homologous to "os mesopterygoideum") and pars proprius, the latter corresponding to os pterygoideum in most adult birds (Zusi and Livezey 2006).

Synonyms include hemipterygoideum, anteropterygoideum; small element rostral to and associated with os pterygoideum (Baumel and Witmer 1993: 77). See: Pycraft (1901); Hofer (1945); Jollie (1957); Gauthier (1986); Livezey (1986: appendix 1, character 18); Livezey (1989: table 1, character 18); Baumel and Raikow (1993: annotation 18); Weber (1993); Elzanowski (1995: characters NG1, ?N12, and ?PG6), in the last he suggested that some taxa—Anseriformes, Galliformes, Falconidae, and Alcidae—lack a "hemipterygoideum" altogether; Kurochkin (1995b); Elzanowski and Wellnhofer (1996); Ericson (1997: table 2, character 7); Livezey (1997a: appendix 1, characters 44–46; *corrigenda*, Livezey 1998a); Rotthowe and Starck (1998: appendix, character 25); Holtz (2000 [1998]: appendix I, character 73); Manegold et al. (2004: characters 4–5), regarding sutura mesopterygopalatina in some Piciformes; G. Mayr and Clarke (2003: appendix A, character 19), limited to synostosis caudalis; Dyke and van Tuinen (2004: appendix 1, character 12); Zusi and Livezey (2006).

Where both partes palatina et proprius of os pterygoideum (i.e., partitioned homologues of primordial os pterygoideum) are divided in the adult, the resultant articulationes assume several forms, including a single vertically oriented articulatio of the caudal part with the rostral complex of os palatinum and pars palatina of the os pterygoideum, and others where there are both dorsal (horizontal) and caudal (vertical) facies; condition in anseriforms is elaborate and possibly should be treated as a separate state. The situation exemplified by the primordial os pterygoideum with respect to adult morphology is paralleled with others in the palatal-rostral part of the skull, in which primordia are partitioned during ontogeny to enable kinesis and synostosis among different elements (e.g., pars maxillaris palatini with os maxillare, with caudal zona flexoria, and portions of ossa nasales with ossa frontales caudad to zona flexoria craniofacialis).

0470. Os pterygoideum, corpus pterygoidei (**new term**), distinctly angular form and concave margo dorsalis, status:

a. present, with obtuse angulus between facies articularis para(basi)sphenoidalis and axis longus of processus palatinus pterygoidei;

b. absent, facies articularis para(basi)sphenoidalis aligned (defining straight angulus) with axis majoris of processus palatinus pterygoidei.

Note.—See: W. K. Parker (1891b: 55–56); McDowell (1948: 527–528); Jollie (1957: 420); Witmer and Martin (1987: character 3); Houde (1988: 20, 47); K. Lee et al. (1997: appendix 1, character 54); Norell and Clarke (2001: appendix I, character 24), in reference to "kinking" of element, treated similarly by J. A. Clarke (2002: appendix I, character 24), J. A. Clarke and Norell (2002: appendix 2, character 24), and J. A. Clarke (2004: appendix 1, character 24); Zhou and Zhang (2002: appendix III, character 24); G. Mayr and Ericson (2004: appendix I, character 11), who cited "inflated" os pterygoideum as uniting Columbidae and Pteroclidae; Ji et al. (2005: supplement, part I, character 24), in terms of "kinked" pterygoideum.

0471. Os pterygoideum, corpus pterygoidei (**new term**), facies dorsalis, recessus pneumaticus, status:

a. absent; **b.** present.

Note.—See: Chu (1998: appendix 1, character 50), with respect to foramen pneumaticum in "processus quadraticus, facies medialis adjacent to facies articularis dorsalis quadratica of Johnson (1984)" in modern larids.

0472. Os pterygoideum, corpus pterygoidei (**new term**), facies lateralis, ala lateralis (**new term**), status:

a. well developed; **b.** reduced or absent.

Note.—See: Norell et al. (2001: appendix 1, character 64); J. M. Clark et al. (2002a: appendix 2.2, character 63); Xu (2002: suite II, character 102); Xu et al. (2002a: supplement, character 47), who referred to "flange of pterygoid well developed . . . or reduced." Multiple examples are provided by Romer

(1956); Hwang et al. (2004: supplement, character 62); Xu and Norell (2004: supplement, character 62).

0473. Os pterygoideum, corpus pterygoidei (**new term**), facies ventralis, pronounced lateral curvature (convexitas) between facies articularis palatini et facies articularis basipterygoidea (if present), status:

a. absent; **b.** present.

Note.—See: Murray and Vickers-Rich (2004: fig. 143, character 1), regarding a "fossa on the ventromedial surface of shaft" of ossa pterygoidea in Dromornithidae, likely representing impressio insertii m. pterygoideus, pars medialis, caput caudale; Ji et al. (2005: supplement, part I, character 23).

0474. Os pterygoideum, facies articularis basipterygoidea, situs pterygoidei:

a. pes pterygoideus, opposite processus orbitalis quadrati;

b. corpus pterygoideus, facies articularis basipterygoidea.

0475. Os pterygoideum, corpus pterygoidei (**new term**), margo rostralis (ventral view), distinct bifurcation, status:

a. absent; **b.** present.

Note.—McDowell (1948) considered this feature unique to Apterygidae; see related, unique sutura pterygomaxillaris, in which contact is achieved by pars medialis of bifurcated margo rostralis. See also: Murray and Vickers-Rich (2004: fig. 143, character 4).

0476. Os pterygoideum, corpus pterygoidei (**new term**), pars rostralis, pronounced dorsoventral compression, typically associated with irregular fossa in facies dorsalis, status:

a. absent; **b.** present.

Note.—See: G. Mayr and Ericson (2004: appendix I, character 10), in terms of lateromedial expansion in *Aramus*, *Grus*, and *Opisthocomus*.

0477. Os pterygoideum, corpus pterygoidei (**new term**), pes pterygoidei, facies articularis palatina—lateromedial separation of bilaterally paired extremitates caudales (ventral view), and corresponding junctura (articulatio) interpterygoidea—forma (**ordered**):

a. widely separated, juncturae well lateral from rostrum parasphenoidale;

b. moderately or slightly separated, juncturae only slightly lateral to rostrum or barely reaching planum of rostrum parasphenoidale;

c. not separated, articulatio aut sutura interpterygoidea present.

Note.—Character concerns os pterygoideum exclusive of pars palatina pterygoidei (mesopterygoideum), whether continuous or partitioned by articulatio intrapterygoidea. In most neognathous birds, this character concerns the expanded, ventrally exposed terminus rostralis pterygoidei, i.e., "pes pterygoidei" (Johnson 1984); synonyms include "antepterygoideum" (Jollie 1957; Bock 1964). Homologous locus in palaeognathous birds is caudalmost segment of sutura pterygopalatina.

0478. Os pterygoideum, facies articularis quadratica relative to calvaria, situs:

a. significantly separated;

b. contact or overlapping.

Note.—See: Maryanska et al. (2002: appendix 1, character 57). Also related regarding forma in Dromornithidae, see Murray and Vickers-Rich (2004: fig. 143, fig. 1, character 2).

0479. Os pterygoideum, pes pterygoidei, lamella dorsalis (**new term**), status:

a. absent; **b.** present, variably prominent.

Note.—New term refers to lamella incorporating facies articularis parasphenoidalis and associated with os palatinum, pars pterygoideus, crista dorsalis (if latter also present). See: Hughes (2000: appendix 2, character 45); Maryanska et al. (2002: appendix 1, character 58), relative to "basal processus for a contact with the basisphenoid."

0480. Os pterygoideum, facies articularis palatina, situs dorsoventralis (ventral perspective) of junctura pterygopalatina relative to rostrum parasphenoidale, situs dorsoventralis (**ordered**):

a. markedly ventral, articulatio pterygo-rostroparasphenoidalis absent;

b. slightly ventral, articulatio pterygo-rostroparasphenoidalis absent;

c. on rostrum, articulatio pterygo-rostroparasphenoidalis present.

Note.—Placements of *Podargus* and strigids comparatively troublesome (Zusi and Livezey 2006). The character concerns whether pars proprius of os pterygoideum continuous with the former or partitioned by an articulatio intrapterygoidea. In the Galliformes and Anseriformes, it is especially critical to avoid confusion between the homologous point in question (caudalmost point of facies articularis palatina of "pes pterygoidei") from the more-dorsal facies articularis basipterygoidea; note that taxa in both states "a" and "b" are characterized by an articulatio pterygobasipterygoidea but lack an articulatio pterygoparasphenoidalis. In most neognathous birds, this character concerns the expanded rostral end of os pterygoideum that is visible ventrally ("pes pterygoidei"). The homologous locus in palaeognathous birds is the caudalmost part of the sutura pterygopalatina. See: Livezey (1997a: appendix 1, character 47; *corrigenda*, Livezey 1998a).

0481. Os pterygoideum, facies articularis basipterygoideus (parasphenoidalis), forma:

a. simple, sessile; **b.** elevated, marginate;

x. noncomparable where processus basipterygoideus lacking.

Note.—See: Chatterjee (1991: character 26); Ericson (1997: table 1, character 7; table 2, character 5); Chu (1998: appendix 1, character 49); Hughes (2000: appendix 2, character 46); Norell and Clarke (2001: appendix I, character 23), in reference to "pterygoid, articular surface for basisphenoid"; treated similarly by J. A. Clarke (2002: appendix I, character 23), J. A. Clarke and Norell (2002: appendix 2, character 23), and J. A. Clarke (2004: appendix 1, character 23); G. Mayr and Clarke (2003: appendix A, character 24); G. Mayr (2004a: appendix 1, character 13); Murray and Vickers-Rich (2004: fig. 143, character 3).

0482. Os pterygoideum, facies articularis basipterygoideus (parasphenoidalis), lamella faciei lateralis (**new term**) overlapping processus basipterygoideus ossis parasphenoidale laterad, status:
a. absent; **b.** present.

0483. Os pterygoideum, extremitas quadratica pterygoideus, facies articularis quadratica, forma:
a. only moderately enlarged relative to corpus pterygoidei, subcondylar;
b. markedly broadened and dorsally elongate.
Note.—Extreme apomorphy manifested by Cracidae, in which facies articularis quadratica ossis pterygoidei approximates in depth os quadratum.

0484. Os pterygoideum, processus dorsalis, forma in which processus constitutes rectilinear jugum on caudal one-third of facies caudodorsalis, and terminus assuming form of rostrally directed tuberculum, status:
a. absent; **b.** present.
Note.—Tuberculum terminalis continued by aponeurosis ossificans in Picidae. See: Hughes (2000: appendix 2, character 44), who mistakenly considered the processus unique and uniformly present to Cuculidae. Processus, distinct from lamella dorsalis, serves as ancora insertii m. protractor pterygoidei *sensu stricto*.

Os Jugale

0485. Os jugale, status (at least with respect to arcus jugalis):
a. present;
b. absent, arcus jugalis composed entirely of ossa maxillare et quadratojugale.

0486. Os jugale, terminus rostralis relative to apertura nasi ossea, margo caudalis, situs proximodistalis:
a. separated, distinctly caudal;
b. proximate, approximately aligned.
Note.—See: Chiappe and Calvo (1994: appendix I, character 7); Chiappe (1995b: character 7); Sanz et al. (1995, 1997: character 7); Chiappe (1996: character 7); Chiappe et al. (1996b: appendix 1, character 7); Chiappe (2001a: appendix 1, character 9); Chiappe (2002: appendix 20.2, character 9); Chiappe and Lacasa-Ruiz (2002), regarding *Noguerornis*; Novas et al. (2004: appendix, character 32), regarding "caudal process" in Ornithischia.

0487. Os jugale, sectio sublacrimalis (**new term**), forma:
a. tapering rostrad; **b.** rectangular, blunt;
c. expanded.
Note.—Although variable, this segment of arcus gives rise, where present, to tuberculum lacrimale jugalis. See: Rauhut (2003: character 23).

0488. Os jugale, foramen (cavitas) pneumaticum, status:
a. absent; **b.** present, on margo caudalis.
Note.—See: Houde (1988: table 27, character 11), in reference to "foramen jugulare spurium"; Sereno et al. (1994: footnote 12), as synapomorphy of Tetanurae; Sereno et al. (1996: footnote 45, character 4); J. D. Harris (1998: appendix 2, character 12), Azuma and Currie (2000: appendix 1, character 65), and Currie and Carpenter (2000: appendix 1, character 15), regarding pneumaticity; Rauhut (2003: character 26).

0489. Os jugale, facies medialis, foramen jugalis medialis, status (**new term**):
a. absent; **b.** present.
Note.—See: J. D. Harris (1998: appendix 2, character 13); Currie and Carpenter (2000: appendix 1, character 16), in reference to "jugal, foramen on medial surface"; Norell et al. (2001: appendix 1, character 36); J. M. Clark et al. (2002a: appendix 2.2, character 36); Xu (2002: suite II, character 82); Xu et al. (2002a: supplement, character 27), in reference to "medial jugal foramen present on medial surface ventral to postorbital bar"; Hwang et al. (2004: supplement, character 35); Xu and Norell (2004: supplement, character 35).

0490. Os jugale, processus dorsalis (**new term**), status:
a. present; **b.** absent;
x. noncomparable (Avialae).
Note.—In Mesozoic taxa, variably treated in terms of structural vestiges of a direct junctura (articulatio or sutura) or ligamentous connection between a "postorbital process" (whether of os postorbitale or os laterosphenoidale) and the arcus jugalis (either of os jugale or os quadratojugale); this is distinct from more-rostral tuberculum lacrimale. Here the Neornithes are treated as noncomparable based on dubious homology of either or both of the dorsal and ventral ossa involved.

See: Chatterjee (1991: character 10); J. M. Clark et al. (1994); Forster et al. (1998: supplement, character 12, modified); Chatterjee (1999: appendix II, characters 2 and 10, modified); Currie and Carpenter

(2000: appendix 1, character 18); Holtz (2000 [1998]: appendix I, character 59). New character with respect to Neornithes, present in some modern taxa (e.g., Bucerotidae). Refers to tuberculum for ligamentum laterospheno-jugale (e.g., in Bucerotidae; D. Starck 1940); in *Balaeniceps*, the ligamentum "postorbitale" encloses at least one os sesamoideum.

0491. Os jugale, processus dorsalis (**new term**), contribution to pila postorbitalis (**new term**) relative to that of dorsal processus postorbitalis (where present) of os postorbitale, status:

a. former approximately equal to latter;

b. former significantly less than latter, i.e., processus dorsalis of os jugale reduced and processus postorbitalis of os postorbitale elongated ventrally;

x. noncomparable because os postorbitale and/or processus postorbitalis of os postorbitale lacking (Neornithes).

Note.—New term synonymous with "postorbital bar" of some authors. See: Norell et al. (2001: appendix 1, character 33); J. M. Clark et al. (2002a: appendix 2.2, character 33); Xu (2002: suite II, character 79); Xu et al. (2002a: supplement, character 24); Hwang et al. (2004: supplement, character 32); Xu and Norell (2004: supplement, character 32).

0492. Os jugale, facies lateralis, jugum jugalis lateralis (**new term**), status:

a. absent; **b.** present.

Note.—See: Sereno and Novas (1992: appendix, character 5), in reference to rostrocaudally oriented "jugal ridge."

0493. Os jugale, corpus ossis jugale, especially pars subtemporalis (**new term**), forma:

a. laminar—twice as high dorsoventrally as wide mediolaterally;

b. essentially cylindrical—height and width approximately equal.

Note.—See: Norell et al. (2001: appendix 1, character 34); J. M. Clark et al. (2002a: appendix 2.2, character 34); Xu (2002: suite II, character 80); Xu et al. (2002a: supplement, character 25); Maryanska et al. (2002: appendix 1, character 33); Rauhut (2003: character 27); Hwang et al. (2004: supplement, character 33); Xu and Norell (2004: supplement, character 33).

0494. Os jugale (processus quadratojugalis), facies lateralis, terminus caudalis (**new term**), rami dorsalis et ventralis of bifurcation (terminus bifurcated), length of former relative to latter (**ordered**; state "b" basal):

a. former less than latter; **b.** subequal;

c. former greater than latter.

Note.—See: Elzanowski and Wellnhofer (1996); J. D. Harris (1998: appendix 2, character 15); Currie and Carpenter (2000: appendix 1, character 18).

0495. Os jugale, facies lateralis, terminus caudalis (**new term**), forma:

a. tapered; **b.** bifurcate;

x. noncomparable by synostosis with os quadratojugale (Neornithes).

Note.—See: Sereno and Novas (1992: appendix, character 17); Sereno et al. (1993: legend for fig. 3a); Novas (1994 [1993]: appendix, character 25); Maryanska et al. (2002: appendix 1, character 35).

Os Quadratojugale

0496. Os quadratojugale (lateral perspective), ramus caudoventralis (**new term**), status and associated aspect of element (**ordered**):

a. absent, aspect hamulate, craniocaudally *reversed* "L-shaped," lacking ramus caudoventralis;

b. present, aspect cruciate, dorsoventrally inverted "T-shaped," ramus caudoventralis in some taxa enclosing margo lateroventralis quadratici.

Note.—See: Sereno and Novas (1992: appendix, character 8), configurations diagrammed for basal theropods by Sereno and Novas (1992: figs. 9–10); J. M. Clark et al. (1994); Currie (1995: appendix, character 11); Elzanowski and Wellnhofer (1996: figs. 7B, 12); Holtz (2000 [1998]: appendix I, character 63); Norell et al. (2001: appendix 1, character 37); J. M. Clark et al. (2002a: appendix 2.2, character 37); Xu (2002: suite I, characters 5 and 43; suite II, character 83); Xu et al. (2002a: supplement, character 28); Rauhut (2003: character 47); Hwang et al. (2004: supplement, character 36); Xu and Norell (2004: supplement, character 36).

0497. Os quadratojugale, ramus dorsalis (**new term**), status:

a. present; **b.** absent.

Note.—Ramus dorsalis refers to "ascending" or "squamosal" process, that typically coincides with articulatio quadrato-quadratojugalis. See: Maryanska et al. (2002: appendix 1, character 37, part).

0498. Os quadratojugale, ramus dorsalis (**new term**), forma *sensu* robustness and situs relative to fenestra "infratemporalis" (**unordered**):

a. massive, bordering approximately the ventral half of fenestra;

b. slender, bordering at least the ventral two-thirds of fenestra;

c. slender, bordering no more than ventral half of fenestra;

x. noncomparable (Neornithes).

Note.—Ramus dorsalis refers to "ascending" or "squamosal" process at terminus of arcus jugalis at articulatio quadrato-quadratojugalis. See: Maryanska et al. (2002: appendix 1, character 37).

0499. Os quadratojugale, condylus quadraticus, status:

a. present, variably distinguishable from corpus;

b. absent.

0500. Os quadratojugale, facies articularis quadratica et adjacent arcus jugalis, forma (**unordered**):

a. planar aut depressio, effecting articulatio planum aut sellaris;

b. (sub)condylus, centrally positioned within facies lateralis processi mandibularis quadrati;

c. subcondylus, arcus quadratojugalis angled mediad at terminus to effect articulatio at terminus of facies lateralis processi mandibularis quadrati;

d. subplanaris cum solum perpendicularoventralis, typically with arcus quadratojugalis angled mediad to rest obliquely at terminus.

Note.—See: Ji et al. (2005: supplement, part I, character 34); Bourdon (2006: character 5).

0501. Os quadratojugale, fenestra quadratojugalis (**new term**), comparative size:

a. small, a foramen; **b.** large, a fenestra;

x. noncomparable (Neornithes).

Note.—See: Currie (1995: appendix, character 12); Xu (2002: suite I, character 6).

Os Quadratum

0502. Os quadratum, corpus ossis quadrati (partes incertae), pneumaticitas (cf. foramina pneumatica), status:

a. absent or rudimentary;

b. present and extensive.

Note.—See: M. L. Walker (1888); Lowe (1926a); Siegel-Causey (1988: character 36); Witmer (1990: 372, characters 11 and 16); Chiappe and Calvo (1994: appendix I, character 12); Sereno et al. (1994: footnote 12); Chiappe et al. (1996: appendix 1, character 11); Sereno et al. (1996: footnote 45, character 36); Forster et al. (1998: supplement, character 24); Makovicky and Sues (1998: appendix 1, character 12); Sereno et al. (1998: footnote 22, character 28); Xu et al. (1999b: character 21); Chatterjee (1999: appendix II, character 14); Holtz (2000 [1998]: appendix I, character 71 [“pneumaticity”]); Norell et al. (2000: appendix 1, character 21); Chiappe (2001a: appendix 1, character 19); Currie and Chen (2001: 1709), in reference to *Sinosauropteryx*; Norell and Clarke (2001: appendix I, character 38), treated similarly by J. A. Clarke (2002: appendix I, characters 38–40) and J. A. Clarke and Norell (2002: appendix 2, character 38); Norell et al. (2001: appendix 1, character 56); Chiappe (2002: appendix 20.2, character 19); J. M. Clark et al. (2002a: appendix 2.2, character 54); Maryanska et al. (2002: appendix 1, character 40); Vickers-Rich et al. (2002), concerning *Avimimus*; Xu (2002: suite II, character 96); Xu et al. (2002a: supplement, character 41), in reference to “hollow” state and “posterior” depressio; Zhou and Zhang (2002: appendix III, characters 38–40); Rauhut (2003: character 48); Hwang et al. (2004: supplement, character 53); Xu and Norell (2004: supplement, character 53); Ji et al. (2005: supplement, part I, character 38).

0503. Ossa quadratum et quadratojugale, foramen within or proximate to junctura quadrato-quadratojugalis, status et situs (**unordered**):

a. present, enclosed almost entirely within os quadratum;

b. present, interposed between ossa, i.e., as foramen suturalis;

c. absent, condylus lateralis, cotyla quadratojugalis quadrati articulates with os quadratojugale unobstructed.

Note.—See: J. D. Harris (1998: appendix 2, character 17); Currie and Carpenter (2000: appendix 1, character 21), a trinary treatment of fenestrae; Holtz (2000 [1998]: appendix I, with character 67); Rauhut (2003: character 49).

0504. Os quadratum, corpus ossis quadrati, margo dorsalis corporis (**new term**), forma:

a. sublinear or only shallowly concave;

b. distinctly concave, margo thereby delimiting incisura dorsalis quadrati.

Note.—See: Livezey (1986: appendix I, character 15).

0505. Os quadratum, corpus ossis quadrati, facies lateralis, lamina rostrolateralis quadrati (**new term**), status:

a. absent; **b.** present.

Note.—New term refers to “large rostrolateral flange” of some authors. See: Barsbold and Osmolska (1999); Xu (2002: suite I, character 7). Probably homologous are: Norell et al. (2001: appendix 1, character 55); J. M. Clark et al. (2002a: appendix 2.2, character 55); Xu (2002: suite II, character 228), about “lateral tabs” and “enlarged quadrate foramen”; Hwang et al. (2004: supplement, character 54); Xu and Norell (2004: supplement, character 54).

0506. Os quadratum, corpus ossis quadrati, facies lateralis, tuberculum articularis zygomaticus, status et forma (**unordered**):

a. absent;

b. present, subsessile, indistinct facies articularis quadrato-zygomaticus (**new term**) on facies lateralis of processus oticus, capitulum squamosa quadrati or margo dorsalis immediately cranial to processus;

c. present, pedicillate, separate processus zygomaticus (**new term**) on facies lateralis quadratica.

Note.—Rarely results in articulatio quadrato-squamoso-zygomatica. See: Elzanowski (1995: character PG3); Weber and Hesse (1995); K. Lee et al. (1997: appendix 1, character 53); Livezey (1998b: appendix A, character 48); Cracraft and Clarke (2001: appendix 2, character 10).

0507. Os quadratum, corpus ossis quadrati, facies rostromedialis, foramen pneumaticum dorsomedialis (**new term**) et sulcus (arcus aut pons) medialis (**new terms**), status et forma (**unordered**):

a. present, without associated arcus medialis or sulcus;

b. present, within pronounced sulcus;

c. present, at basis dorsalis arcus (pontis) medialis;

d. absent.

Note.—New term refers to arcus or pons serving as osseous ostium for small arteria aut vena, typically with foramina pneumatica at both bases arcuales.

0508. Os quadratum, corpus ossis quadrati et processus oticus quadrati, facies rostromedialis, foramen pneumaticum ventromedialis (**new term**), status:

a. absent; **b.** present.

Note.—Dinornithiformes typified by comparatively prominent foramen pneumaticum within sulcus. See: Elzanowski and Galton (1991: character 14), in regard to neurocranial corollary; Chatterjee (1995: character 4, part); Chiappe (1995b: character 12); Sanz et al. (1995, 1997: character 11); Chiappe (1996b: character 2); Chu (1998: appendix 1, character 51); Livezey (1998b: appendix A, character 49); Holtz (2000 [1998]: appendix I, character 67), combining size and situs of foramen; Norell and Clarke (2001: appendix I, character 40), similarly by J. A. Clarke (2002: appendix I, character 40), J. A. Clarke and Norell (2002: appendix 2, character 40), and J. A. Clarke (2004: appendix 1, character 40); Ji et al. (2005: supplement, part I, character 40).

0509. Os quadratum, corpus ossis quadrati et processus oticus quadrati, facies caudomedialis, foramen pneumaticum centralis (**new term**), status:

a. absent; **b.** present.

Note.—Dinornithiformes typified by comparatively prominent foramen pneumaticum within sulcus. See: Elzanowski and Galton (1991: character 14), in regard to neurocranial corollary; Chatterjee (1995: character 4, part); Chiappe (1995b: character 12); Sanz et al. (1995, 1997: character 11); Chiappe (1996b: character 2); Chu (1998: appendix 1, character 51); Livezey (1998b: appendix A, character 49); Holtz (2000 [1998]: appendix I, character 67), combining size and situs of foramen; Norell and Clarke (2001: appendix I, character 40), similarly by J. A. Clarke (2002: appendix I, character 40) and J. A. Clarke and Norell (2002: appendix 2, character 40).

0510. Os quadratum, processus mandibularis quadrati, condylus caudalis (typically associated with an opposing fossa articularis quadratica, sulcus intercotylaris of mandibula), status:

a. obsolete or absent; **b.** present, distinct.

Note.—See: Dzerzhinsky (1995); Ericson (1996); Cracraft (1988); Livezey (1998b: appendix A, characters 52 and 54), concerning sulcus intercondylaris; Elzanowski et al. (2000); Hughes (2000: appendix 2, character 27), regarding condylus caudalis in cuculiforms; Chiappe (2001a: appendix 1, character 21); Cracraft and Clarke (2001: appendix 2, character 38), in reference to size and form of "external (lateral) mandibular condyle of quadrate"; Cracraft and Clarke (2001: appendix 2, characters 39–40), in reference to facies and lamina of condylus; Chiappe (2002: appendix 20.2, character 21), regarding essentially bicondylar or tricondylar processus; G. Mayr (2002a: appendix 1, character 9), with respect to Caprimulgiformes; Zhou and Zhang (2002: appendix III, character 37); G. Mayr et al. (2003: appendix 1, character 16); G. Mayr (2004a: appendix 1, characters 22–23).

0511. Os quadratum, processus mandibularis quadrati, facies articularis quadratojugalis, status et typus (**unordered**):

a. absent;

b. present, fovea aut cotyla, comparatively shallow and with variably deep rostral incisura and processus subcotylaris (**new term**) to accommodate os quadratorjugale;

c. present, fovea aut cotyla—concave, orbiculate, with rima variably raised by comparatively prominent, defining essentially complete margo;

d. present, incisura—concave, troughlike, raised margo lacking entirely or at least in two, geometrically opposing points;

e. present, tuberculum—convex, knoblike.

Note.—See: Cracraft (1985: character 46); Sereno et al. (1996: footnote 45, character 42); Hughes (2000: appendix 2, character 29); Chiappe (2001a: appendix 1, character 17); Chiappe (2002: appendix 20.2, character 17).

0512. Os quadratum, processus mandibularis quadrati, (condylus lateralis), cotyla quadratojugalis, processus supracotylaris lateralis (**new term**), status:

a. absent; **b.** present.

Note.—Consult Jollie (1957) for alternative name for this feature.

0513. Os quadratum, processus mandibularis quadrati, (condylus lateralis), cotyla quadratojugalis, situs caudolateralis relative to processus mandibularis quadrati, condylus lateralis:

a. lateral; **b.** caudal.

0514. Os quadratum, processus mandibularis quadrati, condylus rostralis (condylus lateralis, subcondylus rostralis), status:

a. absent; **b.** present.

Note.—Condylus opposed by cotyla rostralis of fossa articularis quadratica. See: Zusi (1987).

0515. Os quadratum, processus mandibularis quadrati, condylae lateralis, medialis et caudalis, forma principalis condylarum fossae articularis:

a. bicondylar; **b.** tricondylar.

Note.—See: Thulborn (1984: 126–127, character 1); Gauthier (1986: 14, unindexed synapomorphy of Aves); Chatterjee (1991: character 21); Andors (1992: table 2, character 16); Chiappe (1995a: legend for fig. 1); Chiappe et al. (1996: appendix 1, character 82); Elzanowski (1995: character N'4); Chatterjee (1999: appendix II, character 18); Cracraft and Clarke (2001: appendix 2, character 19); Norell and Clarke (2001: appendix I, character 37), treated similarly by J. A. Clarke (2002: appendix I, character 37), J. A. Clarke and Norell (2002: appendix 2, character 37), and J. A. Clarke (2004: appendix 1, character 37); G. Mayr (2004a: appendix 1, character 23); Ji et al. (2005: supplement, part I, character 37).

0516. Os quadratum, processus mandibularis quadrati, condylus medialis, conformation as elongate, lateromedially compressed discus, distinctly larger than condylus lateralis quadrati and with distinctly oblique orientation in which rostral terminus is medial to the caudal terminus, paralleling os pterygoideum, status:

a. absent; **b.** present.

Note.—See: D. W. Thompson (1899), illustrating diversity of ossa quadrati of Psittaciformes; Burton (1984) and Prum (1988: character 26), with respect to "shelflike" shape in some piciforms; Chu (1998: appendix 1, character 55), regarding general proportions within the element.

0517. Os quadratum, facies articularis pterygoidei relative to processus mandibularis et corpus ossis quadrati, situs (**ordered**):

a. processus orbitalis, facies medialis et margo ventralis proximal (dorsal) to processus mandibularis, condylus pterygoideus;

b. margo mediocaudalis corporis ossis quadrati, typically extending over most or all of margo mediocaudalis corporis ossis quadrati, terminating dorsal to processus mandibularis quadrati, and terminus processi quadratici pterygoidei variably bilobate;

c. processus mandibularis, condylus pterygoideus.

Note.—Anseriformes characterized by an incisura supportive of facies articularis quadratopterygoidea on os quadratum dorsal to processus mandibularis quadrati.

0518. Os quadratum, processus mandibularis quadrati, condylus medialis, facies articularis, forma superficialis (**ordered**):

a. convex;

b. concave, ventral aspect bilobate;

c. concave, enclosing obliquely oriented sulcus, ventral aspect trochlear;

x. noncomparable because of indistinguishable condylae (*Aptornis*) or inclusion of nonhomologous features within condylus medialis (*Podargus*).

Note.—See: Strauch (1978: character 11); Andors (1992: table 2, characters 16–18, fig. 10), with respect to Galloanseres, *Diatryma*; Livezey (1998b: appendix A, characters 51, 54); G. Mayr (2004a: appendix 1, character 21); G. Mayr (2004b: appendix 1, character 19).

0519. Os quadratum, processus mandibularis quadrati, condylus medialis, dorsoventral position relative to os quadratum, processus mandibularis, condylus lateralis (caudal perspective), normal to planum defined by condylus occipitalis and margo rostralis of lamina parasphenoidalis, angulus:

a. ventral; **b.** coplanar or dorsal.

Note.—See: Cracraft (1985: character 7); Hesse (1990: 33, fig. 8); Andors (1992: table 2, characters 16–18) with respect to Galloanseres and *Diatryma*; Livezey (1997a: appendix 1, characters 51–52; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, character 53); Hughes (2000: appendix 2, character 28); G. Mayr (2002a: legend fig. 9, node 4, character 1); G. Mayr (2003a: appendix I, character 18); G. Mayr and Clarke (2003: appendix A, character 37), in terms of "marked, rostrally projecting, concave articular surface"; Dyke and van Tuinen (2004: appendix 1, character 24).

0520. Os quadratum, processus mandibularis quadrati, planum condyli occipitalis, situs rostrocaudalis (**ordered**):

a. caudal; **b.** coplanar; **c.** rostral;

x. noncomparable by kinesis of complex (Neornithes).

Note.—See: Maryanska et al. (2002: appendix 1, character 43).

0521. Os quadratum, processus mandibularis (condylus medialis), (sub)condylus pterygoideus (lateral perspective) relative to cotyla quadratojugalis, situs:

a. distinctly ventral or coplanar;

b. distinctly dorsal.

Note.—See: Holtz (1994a: appendix 1, character 26) regarding "enlarged insertion area for the pterygoideus muscle below the mandibular condyle"; also Gauthier (1986), whereas latter work emphasized "depth of quadrate articulation." See: Cracraft (1988: series VII, character 7); Cracraft and Mindell (1989: table 1, character 33); Andors (1992: table 2, characters 16–18, fig. 10), with respect to Galloanseres and *Diatryma* (Gastornithiformes); Livezey (1997a: appendix 1, character 53; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, character 55); Chiappe (2001: appendix 1, character 18); Xu (2002: suite I, character 45; suite II, character 13).

0522. Os quadratum, processus mandibularis quadrati, facies articularis pterygoidea, forma et situs:

a. broad, on facies medialis of processus;

b. narrow, on margo rostromedialis of processus.

Note.—See: Norell and Clarke (2001: appendix I, character 30), incorrectly attributed with processus orbitalis quadrati; treated similarly by J. A. Clarke (2002: appendix I, character 30), J. A. Clarke and Norell (2002: appendix 2, character 30), and J. A. Clarke (2004: appendix 1, character 30); Ji et al. (2005: supplement, part I, character 30).

0523. Os quadratum, processus mandibularis quadrati, facies articularis pterygoidea (facies ventralis in those taxa having two), typus (**unordered**):

a. facies articularis, with slight anteromedial eminentia on basis;

b. cotylar, largely concave;

c. condylar, tubercular, or jugo-sublinear.

Note.—See: Norell and Clarke (2001: appendix I, character 32), treated similarly by J. A. Clarke (2002: appendix I, character 32), J. A. Clarke and Norell (2002: appendix 2, character 32), and J. A. Clarke (2004: appendix 1, character 32); Xu (2002: suite I, character 45); Ji et al. (2005: supplement, part I, character 32).

0524. Os quadratum, processus mandibularis quadrati, facies articularis pterygoidea relative to processus orbitalis, situs (**ordered**):

a. reaches terminus of processus orbitalis and properly could be attributed to that processus;

b. extends distad at least one-half length of processus orbitalis;

c. basally positioned on processus mandibularis.

Note.—See: Norell and Clarke (2001: appendix I, character 31), questionably identified with processus orbitalis quadrati; treated similarly by J. A. Clarke (2002: appendix I, character 31), J. A. Clarke and Norell (2002: appendix 2, character 31), and J. A. Clarke (2004: appendix 1, character 31); G. Mayr and Ericson (2004: appendix I, character 20), emphasizing concavity of rostral extremity; Ji et al. (2005: supplement, part I, character 31).

0525. Os quadratum, processus mandibularis quadrati, facies articularis pterygoidea, forma (**unordered**):

a. elongate with broad articulatio quadratopterygoidea, facies articularis single or bipartite, facies ventralis typically predominant;

b. restricted, a single, distinct, subcircular facies;

c. single, well defined, continuous, facies uniquely parabolic.

Note.—See: Hughes (2000: appendix 2, character 26).

0526. Os quadratum, processus mandibularis quadrati, (condylus lateralis), (sub)condylus pterygoideus, status et forma (**unordered**):

a. absent, junctura quadratopterygoidea (if any) a sutura;

b. present, typically a subcircular facies or tuberculum;

c. present, typically comprising a sublinear or concave jugum articularis (including or tending toward tuberculum in some) along margo rostroventralis quadrati, enforced by ligamenta.

Note.—See: Houde (1988: table 27, character 8); Chatterjee (1991: character 28); Chatterjee (1999: appendix II, character 17), with respect to "ventral condylar articulation with pterygoid."

0527. Os quadratum, processus mandibularis quadrati, condylus lateralis, cotyla quadratojugalis, status et situs:

a. absent; **b.** present, lateral;

c. present, distal.

Note.—Junctura quadrato-quadratojugalis typically an articulatio synovialis among most Neornithes, with a minority (e.g., Caprimulgidae) being a syndesmosis involving enclosed ligamentum interosseum (Bühler 1970; Baumel and Witmer 1993: annotation 24).

See: Thulborn (1984: 126–127, character 2); Chatterjee (1991: character 15); Chatterjee (1999: appendix II, characters 16 and 18); Sanz et al. (1995, 1997: character 10); Chiappe (1996b: character 10); Forster et al. (1998: supplement, character 23); Maryanska et al. (2002: appendix 1, characters 41–42); Vickers-Rich et al. (2002), concerning *Avimimus*.

0528. Os quadratum, processus mandibularis quadrati, condylus lateralis, sulcus intercondylaris, foramina pneumatica, status:

a. absent; **b.** present.

Note.—See: Lowe (1926a); Chu (1998: appendix 1, character 54); Holtz (2000 [1998]: appendix I, character 67), which confounded size and position of foramen.

0529. Os quadratum, processus mandibularis quadrati, condylus lateralis, sulcus intercondylaris, conformation as deep, parabolic ("U-shaped") channel with sides (craniocaudal perspective) subdiagonal (typically parallel) and directly opposite each other and dorsally foveate (ventral perspective), status:

a. absent; **b.** present.

Note.—See: Livezey (1998b: appendix A, characters 52 and 54) in reference to structural obfuscation of sulcus intercondylaris.

0530. Os quadratum, processus mandibularis quadrati, tuberculum caudalis (**new term**), status:

a. absent; **b.** present.

Note.—New feature is situated on margo caudalis quadrati, dorsal to condylis caudalis; a superficially similar structure (below), associated with sesamoideum quadratico-parasphenoidalis, occurs in most

Psittaciformes. See: Ericson (1996: character 7); Ericson (1997: table 1, character 17; table 2, character 12).

0531. Os quadratum, processus mandibularis quadrati, sesamoideum quadratico-parasphenoidalis (**new term**), status:
a. absent;
b. present, interposed between processus mandibularis quadrati, condylus medialis, and os parasphenoidale, tuba auditiva (pharyngotympanica) communis.
Note.—Variable, possibly a derivation of os siphonium.

0532. Os quadratum, processus orbitalis quadrati, status et forma relative to (*i*) processus oticus quadrati aut (*ii*) orbita (**ordered**):
a. present, longer than orbita;
b. present, shorter than orbita;
c. present, of comparable length to processus oticus;
d. present, distinctly shorter than processus oticus;
e. absent.
Note.—See: Cracraft (1982: fig. 2); Cracraft (1985: character 13); Cracraft (1986: appendix, character 52); Livezey (1986: appendix 1, character 15); Cracraft (1988: series II, character 19); Siegel-Causey (1988: character 37); Livezey (1989: table 1, character 15); Chatterjee (1991); Chiappe and Calvo (1994: appendix I, character 9), including aspects of shape; Chatterjee (1995: character 3); Chiappe et al. (1996: appendix 1, character 9); Ericson (1997: table 2, character 11); Siegel-Causey (1997: table I, character 11); Chatterjee (1999: appendix II, character 19); Elzanowski et al. (2000); Holtz (2000 [1998]: appendix I, character 68), for "quadrate dorsal ramus" relative to orbita; Dyke and Gulas (2002: appendix 1, character 52); G. Mayr (2002a: appendix 1, character 8), with respect to Caprimulgiformes; Vickers-Rich et al. (2002), concerning *Avimimus*; Dyke et al. (2003: appendix 1, character 22); G. Mayr (2003a: appendix I, character 19); G. Mayr (2004b: appendix 1, character 20); G. Mayr et al. (2003: appendix 1, character 15); Bourdon et al. (2005: appendix 1, character 40); G. Mayr (2005b: appendix A, character 8).

0533. Os quadratum, processus orbitalis quadrati, markedly thin, attenuated, spiculate or subfilamentous forma:
a. absent; **b.** present.

0534. Os quadratum, processus orbitalis, inordinate elongation of processus, status et forma (**unordered**):
a. absent;
b. present, processus also markedly robust;
c. present, processus also markedly slender, subacuminate.
Note.—See: Bourdon et al. (2005: appendix 1, character 41).

0535. Os quadratum, processus orbitalis quadrati, elongation (exceeding processus oticus in length) and rostral expansion into spatulate terminus (latter at least as broad as any other part of the processus orbitalis) in which rostral margin is rounded, status et forma (**unordered**):
a. absent;
b. present, terminus spatulate with margo rostralis rounded;
c. present, terminus subrectangular with margo rostralis flat.
Note.—See: Sereno et al. (1996: footnote 45, character 46), concerning position of "head" relative to orbita; Livezey (1998b: appendix A, character 50); Sereno et al. (1998: footnote 22, character 27), for shape of "head."

0536. Os quadratum, processus orbitalis, terminus processi, margo apicalis broadly blunt and subtly convex, status:
a. absent; **b.** present.

0537. Os quadratum, processus orbitalis quadrati, forma apicalis:
a. blunt; **b.** (sub)acuminate.
Note.—See: Chatterjee (1991: character 16); Chiappe (1995a: legend for fig. 1); Chiappe (1995b: character 9); Sanz et al. (1995, 1997: character 9); Chiappe (1996b: character 9); Hughes (2000: appendix 2, characters 22–23); Chiappe (2002: appendix 20.2, character 18).

0538. Os quadratum, processus orbitalis, terminus processi, margo apicalis markedly slender, subspinous, status:
a. absent; **b.** present.
Note.—See: Bourdon et al. (2005: appendix 1, character 41).

0539. Os quadratum, processus orbitalis, subobsolescence processi, status:
a. absent; **b.** present.
Note.—See: Bourdon et al. (2005: appendix 1, character 40).

0540. Os quadratum, processus orbitalis, articulatio pterygoideus marginalis ventralis, status:
a. absent; **b.** present.
Note.—See: Bourdon et al. (2005: appendix 1, character 41).

0541. Os quadratum, processus orbitalis quadrati, facies lateralis, tuberculum m. adductor mandibulae ossis quadrati, status:
a. absent or indistinct;
b. prominent, ventrorostrally positioned, marking vertex of medial deflection of processus orbitalis.

Note.—See: Weber and Hesse (1995); Ericson (1996: character 6); Livezey (1997a: appendix 1, character 50; *corrigenda*, Livezey 1998a), after Davids (1952); possibly related to Livezey (1997a: appendix 1, character 49; *corrigenda*, Livezey 1998a), attributed to tuberculum m. adductor mandibulare externum, pars profundus; Andors (1992: table 2, character 15, fig. 10); Hughes (2000: appendix 2, character 25), in reference to "mesial inflection"; Cracraft and Clarke (2001: appendix 2, character 37); Norell and Clarke (2001: appendix I, character 33), treated similarly by J. A. Clarke (2002: appendix I, character 33), J. A. Clarke and Norell (2002: appendix 2, character 33), and J. A. Clarke (2004: appendix 1, character 33), judged synonymous with "spina 6" of A. Fuchs (1954a–b); Zhou and Zhang (2002: appendix III, character 33), regarding "tubercle on anterior surface of dorsal process"; G. Mayr and Clarke (2003: appendix A, character 35); Dyke et al. (2003: appendix 1, character 4); G. Mayr (2004a: appendix 1, character 20), in reference to "eminentia articularis" of Weber and Hesse (1995); G. Mayr and Ericson (2004: appendix I, character 21); Ji et al. (2005: supplement, part I, character 33).

0542. Os quadratum, processus oticus quadrati, pronounced lateromedial compression, resulting in narrowing of incisura intercapitularis and reduction in size and comparative juxtaposition of capitulum (condylus) oticum et capitulum (condylus) squamosum, status:

a. absent;

b. present, facies articularis a single tuberculum.

0543. Os quadratum, processus oticus ("head") quadrati, rostrocaudal position relative to that of processus mandibularis et articulatio quadratomandibularis, situs ventrocaudalis (**ordered**):

a. ventrocaudal; **b.** directly ventral;

c. ventrorostral.

Note.—See: Ostrom (1976a); Forster et al. (1998: supplement, character 16); Xu et al. (1999b: character 14, modified); Xu et al. (2000: supplement, character 10, modified); Norell et al. (2001: appendix 1, character 54); J. M. Clark et al. (2002a: appendix 2.2, character 53); Maryanska et al. (2002: appendix 1, character 38); Xu (2002: suite II, character 95); Rauhut (2003: character 51); Hwang et al. (2004: supplement, character 52); Xu and Norell (2004: supplement, character 52).

0544. Cotylae quadratici squamoso-otici (articulatio quadrato-squamoso-otica), planum transversum cotylarum, relative to extremitas caudalis of condylus occipitalis, situs rostrocaudalis (**ordered**):

a. well caudal; **b.** slightly caudal;

c. rostral.

Note.—See: Azuma and Currie (2000: appendix 1, character 97); Holtz (2000 [1998]: appendix I, character 70), contrasted relative rostrocaudal position of articulatio quadrati with extremitas caudalis condyli occipitalis; Hughes (2000: appendix 2, character 24); Holtz (1994a: appendix 1, character 49), cited "deeply posteroventrally projected articulation of the quadrate."

0545. Os quadratum, processus oticus quadrati, status et numerus capitulorum (**ordered**):

a. one;

b. two, distinguishable but lacking distinct incisura intercapitularis;

c. two, separated by variably distinct incisura intercapitularis.

Note.—See: Cracraft (1986: appendix, character 8); Gauthier (1986: 12), as synapomorphy of Avialae; Cracraft (1988: 345); Cracraft and Mindell (1989: table 1, character 21); Witmer (1990); Chatterjee (1991, 1999: character 18); Andors (1992: table 2, character 14); Elzanowski (1995: character PG2); Elzanowski (1995: character ?N13); J. M. Starck (1995); Ericson (1997: table 1, character 16); K. Lee et al. (1997: appendix 1, character 55); Novas (1997: appendix, character 62); Novas and Puerta (1997), identically by Novas (1997); Forster et al. (1998: supplement, character 15); Rotthowe and Starck (1998: appendix, character 1), regarding Cracraft (1988); J. A. Clarke and Chiappe (2001: character 60); Norell and Clarke (2001: appendix I, characters 35 [cotylae] and 36 [incisura intercondylaris]), treated similarly by J. A. Clarke (2002: appendix I, characters 35–36), J. A. Clarke and Norell (2002: appendix 2, characters 35–36), and J. A. Clarke (2004: appendix 1, characters 35–36); Norell et al. (2001: appendix 1, character 53); J. M. Clark et al. (2002a: appendix 2.2, character 52); Xu (2002: suite II, character 94); G. Mayr and Clarke (2003: appendix A, character 34); Rauhut (2003: character 50); Dyke and van Tuinen (2004: appendix 1, character 22); Hwang et al. (2004: supplement, character 51); Xu and Norell (2004: supplement, character 51); Ji et al. (2005: supplement, part I, character 36).

0546. Os quadratum, processus oticus quadrati, capitulum (condylus) oticum, basis condyli (**new term**), forma:

a. sessile;

b. pedunculate, having columna proötica.

Note.—Distinct from pila (pro)ötica, a pedunculate support for facies articularis cranii. See: Elzanowski and Galton (1991: character 13); Andors (1992: fig. 10); Elzanowski (1995: character Nb'4); Rotthowe and Starck (1998: appendix, character 16), as synapomorphy of gallo-anseriforms.

0547. Os quadratum, processus oticus, pronounced elongation and curvature distal to cotyla, status:

a. absent; **b.** present.

0548. Os quadratum, processus oticus quadrati, capitulum (condylus) oticum, marked elongation and uniquely caudomedial orientation, directed approximately perpendicularly to processus oticus, status:

a. absent; **b.** present.

Note.—See: Cracraft (1988: series XVI, character 1); Cracraft and Mindell (1989: table 1, character 32).

0549. Os quadratum, processus oticus quadrati, conformation in which capitulum (condylus) oticum is markedly ventral to capitulum (condylus) squamosum and partitioned by a pronounced, subangular sloping profile (anteromedial perspective), status:

a. absent; **b.** present.

Note.—In Falconiformes, the derived state associated with robust triangular *Gestalt*. See: Livezey (1998b: appendix A, character 56).

0550. Os quadratum, processus oticus quadrati, capitulum (condylus) squamosum, partitioning into two distinct subcapitula by complete incisura, status:

a. absent; **b.** present.

Note.—Rudimentary incisura present in *Otus* (Strigidae).

0551. Os quadratum, processus oticus quadrati, capitulum (condylus) squamosum et capitulum (condylus) oticus, marked separation at least as great as that between condyli medialis et lateralis of processus mandibularis quadrati, status:

a. absent; **b.** present.

Note.—*Archaeopteryx* is noncomparable by absence of condylus oticus.

0552. Os quadratum, processus oticus quadrati, margo dorsalis, tuberculum insertii m. adductor mandibulae externus (pars articularis, caput internus), status et forma (**ordered**):

a. absent; **b.** present, subtle;

c. present, marked.

Note.—See: Cracraft (1988: series VII, character 6), regarding "dorsally projecting process immediately anterior to quadrate-proötic articulation"; Livezey (1998b: appendix A, character 49); Zusi and Livezey (2000).

0553. Os quadratum, processus oticus quadrati, incisura intercapitularis, status:

a. absent, capitulum oticum et capitulum squamosum indistinct from each other and intervening bone;

b. present, capitulum oticum et capitulum squamosum distinct.

Note.—See: Andors (1992: table 2, character 14); Chiappe and Calvo (1994: appendix I, character 11), in reference to processus oticus of os quadratum having articulation with os proöticum; Chiappe et al. (1999); Cracraft and Clarke (2001: appendix 2, character 18).

0554. Os quadratum, processus oticus quadrati, margo caudalis quadrati, typically encroaching on incisura intercondylaris or immediately ventral to capitulum cristae tympanica, foramen (sulcus) pneumaticum, status:

a. absent; **b.** present.

Note.—Cuculiformes typified by double foramina, with ventral foramen deeply recessed in sulcus pneumaticus, and crista tympanica prominent. See: Chu (1998: appendix 1, characters 52–54); Elzanowski et al. (2000); Holtz (2000 [1998]: appendix I, character 67, part), comprising three states confounding size and position; Norell and Clarke (2001: appendix I, character 39), treated similarly by J. A. Clarke (2002: appendix I, characters 38–40), J. A. Clarke and Norell (2002: appendix 2, character 39), and J. A. Clarke (2004: appendix 1, characters 38–40); Xu et al. (2002a: supplement, character 173), referred to "lateral border of quadrate shaft straight . . . or [sparsely distributed apomorphy] with lateral tab that touches squamosal and quadratojugal above an enlarged quadrate foramen"; G. Mayr (2002a: appendix 1, character 10), with respect to Caprimulgiformes; G. Mayr and Clarke (2003: appendix A, character 36); G. Mayr et al. (2003: appendix 1, character 17); Dyke and van Tuinen (2004: appendix 1, character 23); Ji et al. (2005: supplement, part I, character 39); G. Mayr (2005b: appendix A, character 9).

0555. Os quadratum, processus oticus, facies articularis parasphenoidalis et articulatio (accessoria) quadrato-parasphenoidalis (**new terms**), status:

a. absent;

b. present, lateromedially elongate junctura between facies lateralis processi otici quadrati et ala parasphenoidalis, apex alae parasphenoidalis proximate to cotyla quadratojugalis.

Note.—Articulatio accessoria ossis quadrati related in part to unusual angulus between os quadratum et rostrum parasphenoidalis, form of processus paroccipitalis, and partial dorsal enclosure of os quadratum thereby.

Suturae Faciei Maxillaris

Note.—See: Erdmann (1940) regarding development of ossa faciei et palati. Sereno (1991a: appendix, p. 52) attributed reduction or loss of junctura prefrontonasalis (**new term**) to Ornithosuchidae; D. A. Winkler et al. (1997: appendix 1, character 3); Novas et al. (2004: appendix, character 1) for junctura premaxillaro-lacrimalis (**new term**).

0556. Sutura frontonasalis, bilateral pair of fonticuli frontonasales (**new term**), enclosed immediately rostral to zona flexoria craniofacialis, status:

a. absent; **b.** present.

Note.—Limited polymorphism of status within Apodidae. Among Neornithes, junctura frontonasalis is a sutura retaining variable discernability into adulthood.

0557. Sutura lacrimo-postorbitalis, status:
a. absent, by dorsal interposition of os frontale;
b. present.
Note.—See: Sampson et al. (1998); Rauhut (2003: character 39).

0558. Junctura lacrimo-ectethmoidalis, status et typus (**ordered**):
a. absent;
b. present, as articulatio simplex or limited sutura aut synostosis lacrimo-ectethmoidalis;
c. present, as extensive sutura or synostosis lacrimo-ectethmoidalis;
x. noncomparable where ossa lacrimale et/aut ectethmoidale absent.
Note.—See: Holdaway (1991: appendix 5.1, character 10); Ericson (1997: table 1, character 6); Chu (1998: appendix 1, character 26); Livezey (1998b: appendix A, character 64); G. Mayr and Ericson (2004: appendix I, character 6), including sutura fronto-ectethmoidalis; Bourdon et al. (2005: appendix, character 9), in terms of status of sutura.

0559. Junctura prefronto-frontalis (**new term**), typus:
a. sutura plana or articulatio sellaris;
b. gomphosis;
x. noncomparable by way of absence of os prefrontale (Avialae).
Note.—See: Sereno et al. (1994: footnote 12); Sereno et al. (1996: footnote 45, character 5); J. D. Harris (1998: appendix 2, character 6); Azuma and Currie (2000: appendix 1, character 91); Holtz (2000 [1998]: appendix I, character 38).

0560. Sutura lacrimo-frontalis *vs.* sutura lacrimo-prefrontalis, status:
a. absent, by interposition of os prefrontale;
b. present, by regression or absence of os prefrontale.
Note.—See: Rauhut (2003: character 35).

0561. Junctura lacrimo-frontalis et lacrimo-nasalis (**new term**), combined length:
a. moderate or truncate, length approximately equal to or less than that of processus orbitalis lacrimalis;
b. elongate, length exceeding that of processus orbitalis lacrimalis;
x. noncomparable (Dinornithiformes).
Note.—See: Hughes (2000: appendix 2, character 9).

0562. Sutura lacrimo-frontalis, status via situs:
a. present;
b. absent, entirely replaced by sutura lacrimo-nasalis (**new term**), related to rostrad shift of os lacrimale on rostrum maxillae;
x. noncomparable (Podargidae).
Note.—See: Cracraft (1968a).

0563. Sutura lacrimo-frontalis, margo caudalis, forma:
a. linear; **b.** incisurate;
x. noncomparable, sutura obscure (Neornithes).
Note.—See: Norell et al. (2001: appendix 1, character 46); J. M. Clark et al. (2002a: appendix 2.2, character 46); Xu (2002: suite I, character 3; suite II, character 231); Hwang et al. (2004: supplement, character 45); Xu and Norell (2004: supplement, character 45).

0564. Sutura lacrimo-(facialis)nasofrontalis (**new term**), typus definitivum:
a. sutura or synostosis;
b. articulatio or syndesmosis;
x. noncomparable in absence or vestigial status of os lacrimale.
Note.—See: Cracraft (1968a); Payne and Risley (1976: character 7), regarding Ardeidae; Livezey (1986: appendix 1, character 10); Andors (1992: table 2, character 5); Livezey (1996a: appendix 1, character 6); Livezey (1997a: appendix 1, character 15; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, character 60); Bourdon et al. (2005: appendix 1, character 9); Bourdon (2006: supplement, character 54).

0565. Suturae lacrimo-frontalis, lacrimo-prefrontalis et fronto-prefrontalis, segmenta laterales, dorsales, et ventrales, typus:
a. suturae typical—serratae, squamosae foliatae aut planae—in all segmenta;
b. suturae typical in lateral segmenta, whereas dorsal and ventral juncturae fissuriform or "slotted";
x. noncomparable (Neornithes).
Note.—See: Sereno et al. (1994: footnote 12); Currie (1995: appendix, character 8); Xu et al. (1999b: character 87); Xu et al. (2000: supplement, character 67).

0566. Suturae lacrimo-frontalis et lacrimo-nasalis, situs relative to zona flexoria craniofacialis:
a. at least partly coincident or caudal;
b. completely rostral, completely synostotic with ossa nasales et frontales throughout length.
Note.—At least among Neornithes, most or all of juncturae lacrimo-frontalis et lacrimo-nasalis remain discernable suturae.

0567. Junctura (sutura) nasopremaxillaris, status et forma (**ordered**):
a. absent;
b. present, limited, ventral to apertura nasalis et/aut os nasale;
c. present, extensive, ventral to apertura nasalis et/aut os nasale.
Note.—See: Russell and Dong (1994a [1993a]: table 2, character 1); Russell and Dong (1994b [1993b]: troödontid character 3); Xu et al. (1999a:

character 2); Currie and Carpenter (2000: appendix 1, character 2); Holtz (2000 [1998]: appendix I, character 10, polarity reversed).

0568. Junctura lacrimo-premaxillaris, status:
a. absent, os lacrimale caudal to os premaxillare;
b. present.
Note.—See: Novas et al. (2004: appendix, character 1).

0569. Sutura nasomaxillaris externa (**emended term**), status modalis definitivum:
a. present and distinct;
b. obsolete or absent;
x. noncomparable because junctura nasomaxillaris interrupted (ratites, Dromornithidae).
Note.—Important to distinguish true sutura from plica supratomialis and processus maxillaris ossis premaxillare (e.g., *Psophia*, *Heliornis*, *Rostratula*, *Cursorius*, and *Uria*). See: Cracraft (1986: appendix, character 61) and Cracraft (1988: series II, character 20).

0570. Sutura aut synostosis internasalis, status et forma (**ordered**):
a. absent, margines medialis typically separated by pars nasalis ossis premaxillare;
b. present, variably extensive, typically synostotic definitively, concealing coaligned margines mediales ossium nasales ranging virtually to junctura along entire ossa to significantly limited extent.
Note.—Presence restricted to sutura significantly rostral to zona flexoria craniofacialis. Character essentially represents bilateral juxtaposition of margines mediales of processes premaxillares of ossa nasales dorsal to other components of pila supranasalis, and related status of a sutura internasalis dorsal to processes frontales of ossa premaxillares (dorsal perspective) in dorsoventrally compressed rostum maxillae.

See: Hofer (1945); Cracraft (1988: series II, character 17); Baumel and Raikow (1993: annotation 14); Holtz (1994b: appendix 7.1, character 3); Currie and Carpenter (2000: appendix 1, character 8); Holtz (2000 [1998]: appendix I, character 28); Currie et al. (2003: appendix, character 42).

0571. Junctura interfrontalis (**new term**), typus:
a. sutura plana or serrata; **b.** synostosis.
Note.—See: Holtz (2000 [1998]: appendix I, character 41).

0572. Junctura interpremaxillaris, typus definitivum:
a. articulatio aut sutura plana;
b. synostosis (symphysis), processus frontales indistinguishable.
Note.—See: Gauthier (1986: 13, unindexed synapomorphy of Ornithurae); Chiappe and Calvo (1994: appendix I, character 1); J. M. Clark et al. (1994); Chiappe (1995b: character 1); Elzanowski (1995: characters N'9, ?PG4); Sanz et al. (1995, 1997: character 1); Chiappe (1996b: character 1); Chiappe et al. (1996: appendix 1, character 1); Chiappe et al. (1998: character 1); Ji et al. (1998: supplement, character 1); Sereno et al. (1998: footnote 22, character 10); Chatterjee (1999: appendix II, character 29); Chiappe (2001a: appendix 1, character 1); Chiappe (2002: appendix 20.2, character 1); Chiappe and Lacasa-Ruiz (2002), regarding *Noguerornis*; Zhou and Zhang (2002: appendix III, character 1).

0573. Junctura interpremaxillaris (symphysis premaxillaris), forma (ventral perspective) or angulus symphysialis premaxillaris:
a. angular, chevroniform or "V-shaped";
b. rounded, parabolic or "U-shaped."
Note.—See: Bakker et al. (1988); Holdaway (1991: appendix 5.1, character 1); Holtz (1994a: appendix 1, character 104); J. D. Harris (1998: appendix 2, character 1); Azuma and Currie (2000: appendix 1, character 92); Currie and Carpenter (2000: appendix 1, character 1); Holtz (2000 [1998]: appendix I, character 17); Norell et al. (2001: appendix 1, character 29); J. M. Clark et al. (2002a: appendix 2.2, character 25); Xu (2002: suite II, character 72); Xu et al. (2002a: supplement, character 31), in which only first two states recognized; Hwang et al. (2004: supplement, character 24); Xu and Norell (2004: supplement, character 24).

0574. Junctura (sutura) maxillaropremaxillaris (**revised term**), fenestrae maxillaris et "promaxillaris," situs:
a. latter rostral to former;
b. latter dorsal to former.
Note.—See: Witmer (1997); Holtz (2000 [1998]: appendix I, character 19).

0575. Junctura maxillaropremaxillaris (**revised term**), fenestrae maxillaris et "promaxillaris," forma *sensu* relative size:
a. former larger than latter;
b. former smaller than latter.
Note.—See: Witmer (1997); Holtz (2000 [1998]: appendix I, character 20).

0576. Sutura vomeropremaxillaris (**new term**), status:
a. absent; **b.** present.
Note.—See: Cracraft (1974: cranial character 1, part); Cracraft (1986: appendix, character 40); Witmer and Martin (1987: characters 5 and 7); Houde (1988: table 27, character 5); Cracraft and Mindell (1989: table 1, character 23); Elzanowski (1995: character ?N10); Cracraft and Clarke (2001: appendix 2, character 9); Norell and Clarke (2001: appendix I, character 17), treated similarly by J. A. Clarke (2002: appendix I, character 17), J. A. Clarke and Norell (2002: appendix 2, character 17), and J. A. Clarke (2004: appendix 1, character 17); Zhou and Zhang

(2002: appendix III, character 17); Ji et al. (2005: supplement, part I, character 17).

0577. Sutura (synostosis) vomeromaxillaris, status:
a. present; **b.** absent.
Note.—See: Cracraft (1974: cranial character 1, part); Cracraft (1988: series VI, character 4); Witmer and Martin (1987: character 7).

0578. Junctura palatinopremaxillaris, status et typus:
a. absent, contact limited to palatinomaxillaris;
b. present, sutura aut synostosis;
c. present, syndesmosis.
Note.—Syndesmosis also occurs in some large-billed cardeulines. See: D. W. Thompson (1899); Witmer and Martin (1987: character 4); Cracraft and Clarke (2001: appendix 2, character 8), contrasting plesiomorphic articulatio palatinomaxillaris; Norell and Clarke (2001: appendix I, character 16, part), treated similarly by J. A. Clarke (2002: appendix I, character 16), J. A. Clarke and Norell (2002: appendix 2, character 16), and J. A. Clarke (2004: appendix 1, character 16); Zhou and Zhang (2002: appendix III, character 16, part); Ji et al. (2005: supplement, part I, character 16).

0579. Junctura interpalatina et articulatio palatino-rostroparasphenoidalis (“palatorostralis”), preclusion by medial interposition of ossa vomera throughout length of palatum osseum, status:
a. present; **b.** absent.
Note.—Indiscernability of ossa vomera et palatina in sectio medialis juncturae vomeropalatina precludes determination of typus juncturae (e.g., sutura *vs*. synostosis) or precise quantification of interposition of ossa vomera between the ossa palatini, an imprecision exacerbated by variable and indiscernable incorporation of os mesopterygoideum with extremitas caudalis palatini. See: Cracraft (1986: appendix, character 42); Witmer and Martin (1987: character 2); Cracraft (1988: series VI, character 5); Elzanowski (1991), in which the os vomeris is considered absent in *Hesperornis*; Currie (1995: fig. 1c); Cracraft and Clarke (2001: appendix 2, character 7); G. Mayr and Clarke (2003: appendix A, character 17); Dyke and van Tuinen (2004: appendix 1, character 17); G. Mayr (2004a: appendix 1, character 8); Bourdon et al. (2005: appendix 1, character 5).

0580. Sutura pterygomaxillaris (**new term**), status:
a. absent; **b.** present.
Note.—See: McDowell (1948); Zusi and Livezey (2006). Contact is achieved by the lateral portion of bifurcated margo rostralis of os pteryogoideum in *Apteryx*.

0581. Articulatio pterygopalatino-rostroparasphenoidalis, extreme restriction of articulatio and pronounced angulus palatino-rostroparasphenoidalis, status:
a. absent; **b.** present.
Note.—Derived state includes a marked gap between edge of rostrum parasphenoidale and os palatinum rostral to articulatio. Occurs in confamilials (e.g., *Ceryle*) of exemplary Alcedinidae.

0582. Junctura (sutura aut synostosis) intervomeralis, status definitivum:
a. absent, paired elements remain separate and on opposite sides of the os mesethmoidale;
b. present, paired primordia united in adult, with some taxa retaining vestigium suturae;
x. noncomparable where element absent or vestigial or presence unconfirmed.

0583. Junctura—articulatio aut sutura—vomeropterygoidea, status et forma (**ordered**):
a. present, moderately extensive;
b. present, short; **c.** absent;
x. noncomparable (*Struthio*).
Note.—Cracraft (1988) stated *Struthio* as having undergone reversal.
See: Cracraft (1974: cranial character 1, part); Cracraft (1986: appendix, character 39); Witmer and Martin (1987: character 1); Cracraft (1988: series V, character 1); Cracraft and Mindell (1989: table 1, character 12); Livezey (1997a: appendix 1, character 43; *corrigenda*, Livezey 1998a); J. A. Clarke and Chiappe (2001: character 58); Cracraft and Clarke (2001: appendix 2, character 5); Norell and Clarke (2001: appendix I, character 14), treated similarly by J. A. Clarke (2002: appendix I, character 14), J. A. Clarke and Norell (2002: appendix 2, character 14), and J. A. Clarke (2004: appendix 1, character 14); Zhou and Zhang (2002: appendix III, character 14); Ji et al. (2005: supplement, part I, character 14).

0584. Sutura jugolacrimalis, continuous (e.g., sine ossa suturales aut uncinatum) and accompanied by structural modification of os lacrimale, processus orbitalis, terminus ventralis, status:
a. present; **b.** absent;
x. noncomparable by absence of os lacrimale (Nyctibiidae, Podargidae, Trochilidae, Bucerotidae).
Note.—See: Payne and Risley (1976: character 8), regarding Ardeidae; Sereno et al. (1994: footnote 12), as synapomorphy of Tetanurae.

0585. Junctura jugo-quadratojugalis, typus:
a. remains distinguishable, sutura jugo-quadratojugalis persistent;
b. indistinguishable in adult, synostosis jugo-quadratojugalis complete.
Note.—See: Norell et al. (2001: appendix 1, character 38); J. M. Clark et al. (2002a: appendix 2.2, character 38); Xu (2002: suite II, character 84); Xu et al. (2002a: supplement, character 29); Hwang et al. (2004: supplement, character 37); Xu and Norell (2004: supplement, character 37).

0586. Junctura—sutura aut articulatio—lacrimo-postorbitalis (**new term**), status:
a. absent; **b.** present, typically broad;
x. noncomparable by absence of os postorbitale (Neornithes).
Note.—See: J. D. Harris (1998: appendix 2, character 8); Azuma and Currie (2000: appendix 1, character 90); Currie and Carpenter (2000: appendix 1, character 11); Holtz (2000 [1998]: appendix I, character 50).

0587. Junctura lacrimo-palatina, status:
a. absent; **b.** present, articulatio.
Note.—*Fide* P. J. Currie.

0588. Junctura jugo-postorbitalis (**new term**), status:
a. present, complete, involving both os postorbitale, processus jugalis, and os jugale, processus postorbitalis;
b. absent; **x.** noncomparable (Neornithes).
Note.—See: Chatterjee (1991, 1999: character 12); J. M. Clark et al. (1994); Chiappe et al. (1996: appendix 1, character 95); Sanz et al. (1997: footnote 29, character *i*); Chiappe et al. (1998: character 6, modified); Ji et al. (1998: supplement, character 6, modified); Forster et al. (1998: supplement, character 12, modified); Chatterjee (1991, 1999: characters 2 and 10, modified); Holtz (2000 [1998]: appendix I, character 51, modified); Norell and Clarke (2001: appendix I, character 50), treating character solely in terms of "contact," treated similarly by J. A. Clarke (2002: appendix I, character 50), J. A. Clarke and Norell (2002: appendix 2, character 50), and J. A. Clarke (2004: appendix 1, character 50); Chiappe (2001a: appendix 1, character 14); Chiappe (2002: appendix 20.2, character 14); J. M. Clark et al. (2002a: appendix 2.2, character 33); Maryanska et al. (2002: appendix 1, character 34); Xu (2002: suite II, character 79); Zhou and Zhang (2002: appendix III, character 50); Xu and Norell (2004: 840); Hwang et al. (2004: supplement, character 32); Xu and Norell (2004: supplement, character 32); Ji et al. (2005: supplement, part I, character 50).

Synchondroses Facies

Note.—Consistent with nomenclatural proposals made for palatum osseum (Zusi and Livezey 2006), synchondrosis mesethmo-rostroparasphenoidalis replaces synchondrosis rostromesethmoidalis. Also, the following terms are noted: synchondrosis mesethmo-ectethmoidalis, junctura (articulatio) jugo-ectopterygoidea (**new term**).

0589. Juncturae maxillaro-ectopterygoidea (**new term**) et lacrimo-ectopterygoidea (**new term**), status:
a. absent; **b.** present;
x. noncomparable by absence of os ectopterygoideum (Ornithurae).
Note.—See: Maryanska et al. (2002: appendix 1, character 60).

0590. Synchondrosis (articulatio) pterygo-ectopterygoidea (**new term**), status:
a. absent; **b.** present;
x. noncomparable by absence of os ectopterygoideum (Ornithurae).
Note.—Polarity and even occurrence uncertain. See: J. M. Clark et al. (1994); Currie (1995: appendix, character 16), regarding contributions of ossa pterygoideum et ectopterygoideum; Xu et al. (2002a: supplement, character 47); Maryanska et al. (2002: appendix 1, character 62).

0591. Synchondrosis (articulatio) pterygo-ectopterygoidea (**new term**), sitae dorsoventrales ossium:
a. os ectopterygoideum ventral to os pterygoideum;
b. os ectopterygoideum dorsal to os pterygoideum;
x. noncomparable by absence of os ectopterygoideum (Ornithurae).
Note.—See: Novas (1994 [1993]: appendix, character 13).

0592. Synchondrosis (articulatio) ectopterygo-palatina, status:
a. absent, junctura precluded by interposition of os pterygoideum;
b. present;
x. noncomparable by absence of os ectopterygoideum (Ornithurae).
Note.—See: Chatterjee (1991, 1999: character 20); Currie (1995: appendix, character 17); Forster et al. (1998: supplement, character 14); Xu et al. (1999b: character 13, part); Xu et al. (2002a: supplement, character 178).

Articulationes Maxillae et Palati

0593. Syndesmosis jugo-maxillaris, status:
a. absent; **b.** present.
Note.—Some large-billed cardeulines (unrepresented) also apomorphic. See: D. W. Thompson (1899); Lamanna et al. (2002: appendix 1, character 10), regarding extent in Abelisauridae.

0594. Articulatio vomero-rostroparasphenoidalis (**new term**), status et forma (**ordered**):
a. present and extensive, composing majority of dorsomedial contact between palatum osseum et rostrum parasphenoidalis;
b. present, limited to rostral segment and supplemented by ligamentum mesethmovomerale;
c. present, limited to rostral segment or absent.

Note.—See: Hofer (1949); Cracraft (1974: cranial character 1, in part).

0595. Junctura (articulatio) quadrato-quadratojugalis, typus (**unordered**):

a. sutura; **b.** syndesmosis;

c. articulatio synovialis, typically a gomphosis, i.e., "ball-and-socket."

Note.—Bracketed taxa correspond to "unfused sutura" listed by Holtz (2000 [1998]), presumably suturae possessed of weak ankylosis or even kinesis. See: Gilmore (1920); Ostrom (1969); Cracraft (1986: appendix, character 9); Gauthier (1986: 13, unindexed synapomorphy of Ornithurae); Cracraft (1988: series II, character 3); Andors (1992: table 2, character 11); Chiappe and Calvo (1994: appendix I, character 10); J. M. Clark et al. (1994); Holtz (1994a: appendix 1, character 50); Chiappe et al. (1996: appendix 1, character 10); Novas (1996: appendix, character 61), regarding articulationes quadrato-squamoso-otica aut postorbitosquamosa; Chiappe et al. (1998: character 7, modified); Ji et al. (1998: supplement, character 7, modified). Note subdivision of state "b" to include as alternative the true articulatio (with cotyla articularis quadratum) noted by Chatterjee (1991, 1999: character 16); Holtz (2000 [1998]: appendix I, character 66); Chiappe (2001a: appendix 1, character 15); Norell and Clarke (2001: appendix I, character 34), treated similarly by J. A. Clarke (2002: appendix I, character 34), J. A. Clarke and Norell (2002: appendix 2, character 34), and J. A. Clarke (2004: appendix 1, character 34); Chiappe (2002: appendix 20.2, character 15); Maryanska et al. (2002: appendix 1, characters 41–42); Zhou and Zhang (2002: appendix III, character 34), regarding "overlapping" *vs*. "peg and socket" articulatio; Ji et al. (2005: supplement, part I, character 34).

0596. Articulatio quadratojugo-squamosa, and presence of incorporated processus ventralis of os squamosum and processus dorsalis of os quadratojugale, status:

a. present, comprising both processus ventralis of os squamosum and processus dorsalis of os quadratojugale;

b. absent, by absence of one or both processus ventralis of os squamosum et/aut processus ascendens of os quadratojugale.

Note.—See: Thulborn (1984: 126–127, character 3); Cracraft (1986: character 60); Cracraft (1988: series I, character 9); J. M. Clark et al. (1994); Chiappe et al. (1996: appendix 1, character 68), purporting absence-presence of any contact between elements; Novas (1996: appendix, character 61), regarding articulationes between os quadratum and os squamosum or latter and "postorbital"; Sanz et al. (1997: footnote 29, character *iii*), for which matrix must be acquired from author; Chiappe et al. (1998: character 8); Ji et al. (1998: supplement, character 8); J. A. Wilson and Sereno (1998: appendix, character 23), regarding mere status among Sauropoda; Holtz (2000 [1998]: appendix I, character 64); Norell et al. (2001: appendix 1, character 52); Chiappe (2001a: appendix 1, character 16); Chiappe (2002: appendix 20.2, character 16); J. M. Clark et al. (2002a: appendix 2.2, character 50); Maryanska et al. (2002: appendix 1, character 36); Xu (2002: suite I, character 40; suite II, character 93), the last three references pertaining to articulatio quadratojugo-squamosa (via processus descendens of os squamosum); Xu et al. (2002a: supplement, character 38); Rauhut (2003: character 46); Xu and Norell (2004: 840); Hwang et al. (2004: supplement, character 49); Xu and Norell (2004: supplement, character 49).

0597. Junctura quadratojugo-squamosa, forma ventralis:

a. narrow and tapering;

b. uniformly wide or broadening;

x. noncomparable (Neornithes).

Note.—See: Chatterjee (1999: appendix II, characters 6–7), described "descending process" of os squamosum and "ascending process" of os quadratojugale; Rauhut (2003: character 45), presented in terms of ventral change in breadth of "ventral process" of os squamosum.

0598. Articulatio quadrato-cranii (**new term**), typus (**unordered**):

a. articulatio quadrato-squamosa, wherein os squamosum typically if not uniformly involved in junctura postorbito-squamosa, but articulatio quadrato-proötica (*sensu lato*) absent in any form;

b. articulatio quadrato-squamoso-proötica present and structurally united;

c. articulationes quadrato-squamosa et quadrato-proötica present and distinct;

d. articulatio quadrato-squamoso-proötica-exoccipitalis (**new term**) present;

e. articulatio quadrato-squamoso-proötica-exoccipito-laterosphenoidalis.

Note.—Palaeognathous taxa (states "b" and "c"), in which facies articularis in question uniquely involves os exoccipitale, manifest a pila exoccipitalis (**new term**), although superficially resembling the widely recognized "pila otica" of neognathous birds. Likely redundant incarnation of previously scripted character.

See: Cracraft (1986: appendix, character 54); Cracraft (1988: series IV, character 3; series VI, character 2); Cracraft and Mindell (1989: table 1, character 3); Witmer (1991); Chiappe and Calvo (1994: appendix I, character 11), in reference to articulatio between processus oticus quadrati and os proöticum; Chiappe (1995b: character 11); Chiappe et al. (1996: character 68, part); Chiappe et al. (1998: character 9, modified); Ji et al. (1998: supplement, character 9, modified); Chatterjee (1991, 1999: character 27);

Chatterjee (1999: appendix II, character 30); Holtz (2000 [1998]: appendix I, character 65); Chiappe (2001a: appendix 1, character 20); Norell and Clarke (2001: appendix I, character 35); Chiappe (2002: appendix 20.2, character 20); J. M. Clark et al. (2002a: appendix 2.2, character 52); Maryanska et al. (2002: appendix 1, character 39); Xu (2002: suite II, character 94); Xu et al. (2002a: supplement, character 39); Zhou and Zhang (2002: appendix III, characters 35–36), in reference to cranial elements and subcondylae; Hwang et al. (2004: supplement, character 51); Xu and Norell (2004: supplement, character 51); Ji et al. (2005: supplement, part I, character 35).

0599. Articulatio quadrato-(latero)sphenoidalis (**new term**), including facies articularis laterosphenoidalis on corpus quadrati, facies medialis, status:

a. absent; **b.** present.

Note.—Articulatio weakly syndesmotic.

0600. Junctura quadratopterygoidea, typus et forma (**ordered**):

a. sutura;

b. articulatio complex, involving both broad contact on facies medialis of processus orbitalis supplementary to condylus pterygoideus quadraticum;

c. articulatio duplex, moderate dorsal extension on facies medialis of processus orbitalis combined with condylus pterygoideus;

d. articulatio simplex, retaining vestigial contact on basis of processus orbitalis in addition to primary articulatio with condylus pterygoideus;

e. articulatio simplex, virtually limited to condylus pterygoideus.

Note.—See: Cracraft (1974: cranial character 5); Chatterjee (1991: character 17); Zhou and Zhang (2002: appendix III, characters 30–32).

0601. Junctura pterygopalatina, typus (**ordered**):

a. syndesmosis aut sutura pterygo-palatina propria, extensive rostrocaudally, caudal terminus approaching processus quadraticus pterygoidei;

b. articulatio pterygo-palatina simplex;

c. articulatio mesopterygo-palatina, with rudimentary gomphosis intrapterygoidea;

d. articulatio mesopterygo-palatina, with complete gomphosis intrapterygoidea.

Note.—Use of “simplex” to describe articulationes of most Neornithes serves to distinguish the variably derived gomphoses of Galloanseres. Where syndesmosis pterygo-palatina is present, as in ratites, junctura involves margo lateralis ossis pterygoidei, and the latter element is interposed between rostrum parasphenoidalis et os palatinum. Apparently unusual condition characterizes the moas, in which junctura resembles sutura foliata or articulatio trochlearis.

See: Huxley (1867); W. K. Parker (1864); T. J. Parker (1895: plates 56 and 57); Pycraft (1900); H. J. Müller (1961a: fig. 2); Cracraft (1974: cranial character 3); Cracraft (1986: appendix, character 43); Cracraft (1988: series VI, character 6); Livezey (1986: appendix 1, character 18), subsequently refined; Cracraft and Mindell (1989: table 1, character 25); J. M. Clark et al. (1994); Livezey (1997a: appendix 1, character 44; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, character 40); Chatterjee (1999: appendix II, character 31, modified), with respect to mobility; Rotthowe and Starck (1998: appendix, characters 3 and 13), latter after Dzerzhinsky (1995); J. A. Clarke and Chiappe (2001: character 57); Cracraft and Clarke (2001: appendix 2, character 6); Manegold et al. (2004: character 5), regarding sutura mesopterygoideopalatina; Norell and Clarke (2001: appendix I, character 15), treated similarly by J. A. Clarke (2002: appendix I, character 15), J. A. Clarke and Norell (2002: appendix 2, character 15), and J. A. Clarke (2004: appendix 1, character 15); Zhou and Zhang (2002: appendix III, character 15); G. Mayr and Clarke (2003: appendix A, character 22); Dyke and van Tuinen (2004: appendix 1, character 15); G. Mayr (2004d: appendix I, character 5); Ji et al. (2005: supplement, part I, character 15); G. Mayr (2005a: appendix 1, character 5); G. Mayr (2005b: appendix A, character 4).

0602. Articulatio simplex et/aut zona flexoria pterygopalatina, typus et forma (**unordered**):

a. articulatio pterygopalatina et intrapterygoidea both present, processus palatinus pterygoidei synostotic with os palatinum;

b. articulatio intrapterygoidea only, processus palatinus pterygoidei synostotic with os palatinum;

c. articulatio pterygopalatina only, processus palatinus pterygoidei lacking;

d. articulatio pterygopalatina et zona flexoria pterygoidea both present, processus palatinus pterygoidei synostotic with os palatinum;

e. zona flexoria pterygoidea et sutura pterygopalatina present;

x. noncomparable by presence of synostosis pterygopalatinus (ratites) or gomphosis pterygopalatinus (Galliformes, Anseriformes), and in many absence of articulatio intrapterygoidea (Rheidae, Galloanserae).

Note.—Syndesmoses and articulationes synoviales are not reliably distinguishable in this junctura. Purportedly, syndesmosis pterygopalatina of Rheidae includes detail unique among ratites (Jollie 1957), the absence of articulatio intrapterygoidea (H. J. Müller 1963; Baumel and Raikow 1993: annotation 28). See: Zusi and Livezey (2006).

Zonae Flexoriae Ossium Faciei

Note.—Synonymous with ginglymae craniofaciales aut frontonasales (Bühler 1970), these zonae permit enhanced flexion or kinesis within ossa through thinning of bone in transverse bands. Analogous kinesis within cranii of mosasaurs was described by Russell (1964).

0603. Zonae flexoriae craniofaciales, zonae flexoriae lateralis et medialis, rostrocaudal alignment, status:

a. absent, zona medialis rostral to zonae laterales, not forming a continuous, lateromedial axis transversus flexoria;

b. present, forming axis transversus flexoria.

Note.—Functionally, closely related to maxillary kinensis (Thulborn 1984: 126–127, character 3). Plesiomorphic state results in akinesis or (rarely) prokinesis, and apomorphic state associated with rhynchokinesis; rhynchokinesis in a variety of taxa is accompanied by zonae flexoriae maxillares, rostrodorsales, rostroventrales, dorsomedialis et/aut arcus jugalis (Zusi 1984; Baumel and Raikow 1993: annotation 47). Apterygidae and some other probe-feeding groups have lost zona medialis; some Trochilidae and "higher" passeriforms (e.g., Furnariidae and Acanthisittidae) manifest polymorphism of states (Zusi 1984).

See: Chatterjee (1991: character 19); Elzanowski (1995: character ?PG7); Livezey (1998b: appendix A, character 24), including amphikinesis in Rallidae; Chatterjee (1999: appendix II, character 8); Ericson (1997: table 1, character 12); Livezey (1997a: appendix 1, character 36; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, character 43); Maryanska et al. (2002: appendix 1, character 70), regarding distance of "jaw joint" from cranial midline; reference to rostrocaudal motion being primary in mandibulae of Oviraptorosauria (J. M. Clark et al. 2001); G. Mayr (2003b: appendix I, character 1); G. Mayr and Clarke (2003: appendix A, character 5); Dyke and van Tuinen (2004: appendix 1, character 2); Xu and Norell (2004: 840).

0604. Zona flexoria craniofacialis, conformation as variably distinct transverse linea(e), often buttressed by margines rostrales et/aut caudales by eminentia of ossa frontales, status et forma:

a. absent, an indistinct jugum, angulus, or depressio;

b. present, a distinct lamina or sulcus;

c. present, a deep fissura with bordering eminentiae.

Note.—See: Andors (1992: table 2, character 4); Livezey (1997a: appendix 1, character 35; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, character 44); Hughes (2000: appendix 2, character 2); G. Mayr (2002a: legend fig. 9, node 5, character 1); G. Mayr (2004b: appendix 1, character 2).

0605. Zona flexoria palatina, status et forma (**unordered**):

a. absent;

b. present, zona simplex, restricted by ligamentum palatomaxillare;

c. present, including syndesmosis of processus premaxillaris palatini.

Note.—See: van Gennip (1986); Baumel and Raikow (1993: annotation 47).

Mandibula

Note.—Where possible, aspects of the mandibula were treated by ossa involved, however, many features characterizing parts or the whole of the structure—likened to a structural girder (Bock and Kummer 1968)—may have comprised several, often undifferentiable elements.

See: Lebedinsky (1920); de Kock (1955); Jollie (1957); Romanoff (1960); H. J. Müller (1963), the last being critical to assessments of ratites and perhaps galloanseres.

Os Mentomandibulare

0606. Os mentomandibulare (ossa interdentales), status et forma definitivum (**unordered**):

a. present, ossa dentales separate;

b. present, ossa dentales joined by cartilagines;

c. rudimentary, not extending dorsad to margo dorsalis of os dentale and typically appearing to be absent entirely.

Note.—Romanoff (1960) reported cartilagines symphysiales of birds are distinct cartilagines mentomandibulares (**new term**) or "mentomandibular elements" and later ossify to produce the definitive symphysis, replacing primordial cartilago symphysialis.

See: Siegel-Causey (1988: character 54) concerning "accessory bone" in symphysis; J. M. Clark et al. (1994); Holtz (1994a: appendix 1, character 114); Pérez-Moreno et al. (1994: legend for fig. 3, character 5); Russell and Dong (1994b [1993b]: troödontid character 10); Currie (1995: appendix, character 6); Forster et al. (1998: supplement, character 25, modified); Makovicky and Sues (1998: appendix 1, character 29); Sereno et al. (1998: footnote 22, character 14), referring to "paradental laminae"; Xu et al. (1999a: character 30, modified); Xu et al. (1999b: character 22); Azuma and Currie (2000: appendix 1, character 62); Holtz (2000 [1998]: appendix I, character 135); Xu et al. (2000: supplement, character 15); Norell et al. (2001: appendix 1, character 91); J. M. Clark et al. (2002a: appendix 2.2, character 93); Xu (2002: suite I, character 10; suite II, character 124); Hwang et al. (2004: supplement, character 90); Xu and Norell (2004: supplement, character 90).

Os Predentale

0607. Os predentale, status:

a. absent;

b. present, on planum medianum of apex rostralis mandibulae.

Note.—See: Benton (1990a: 24).

Os Dentale

0608. Os dentale, ramus dentalis (**new term**) in planum transversus (craniocaudal perspective), forma:

a. lateromedially broad relative to dorsoventral height, with deep sulcus Meckelii ("Meckelian groove") and distinct pluteus dentalis (**new term**);

b. lateromedially thin relative to dorsoventral height, with shallow "Meckelian groove" and pluteus dentalis;

x. noncomparable (Neornithes).

Note.—Commonly held that vestigium of cartilago Meckelii is incorporated within the definitive os dentale (de Kock 1955), whereas the "Meckelian groove" may be absent in Aves, and the pluteus dentale (**new term**)—synonymous with "dental shelf"—may correspond to the rostrum (symphysis) mandibulae. See: J. M. Clark et al. (1994); Currie (1995: appendix, character 19); Xu et al. (1999a: character 21); Xu et al. (1999b: character 95); Azuma and Currie (2000: appendix 1, character 32); Xu et al. (2000: supplement, character 75); Maryanska et al. (2002: appendix 1, character 73); Xu (2002: suite I, characters 8 and 47; suite II, character 16); Zhou and Zhang (2002: appendix III, character 48); J. A. Clarke (2004: fig. 32).

0609. Os dentale, ramus dentalis (**new term**), facies medialis (lingualis), sulcus Meckeli (**new term**), exposure:

a. comparatively great, open medially, conspicuous;

b. comparatively limited, not exposed medially.

Note.—See: Norell and Clarke (2001: appendix I, character 48), treated similarly by J. A. Clarke (2002: appendix I, character 48), J. A. Clarke and Norell (2002: appendix 2, character 48), and J. A. Clarke (2004: appendix 1, character 48); Ji et al. (2005: supplement, part I, character 48).

0610. Os dentale, ramus dentalis (**new term**), facies lateralis (labialis), forma superficialis:

a. laminar;

b. with jugum lateralis and enclosed sulcus accommodating dentes;

x. noncomparable by edentuly (Neornithes).

Note.—See: Norell et al. (2001: appendix 1, character 71); J. M. Clark et al. (2002a: appendix 2.2, character 71); Xu (2002: suite II, character 253); Hwang et al. (2004: supplement, character 70); Xu and Norell (2004: supplement, character 70).

0611. Os dentale, pars symphysialis, forma (**ordered**):

a. straight or weakly recurved; **b.** decurved.

Note.—See: J. M. Clark et al. (1994); Livezey (1997a: appendix 1, character 17; *corrigenda*, Livezey 1998a); Sues (1997: appendix 1, character 17); Livezey (1998b: appendix A, character 8); Xu et al. (1999a: character 24); Norell et al. (2001: appendix 1, character 70); J. M. Clark et al. (2002a: appendix 2.2, character 68); Maryanska et al. (2002: appendix 1, character 74); Xu (2002: suite II, character 252); Xu et al. (2002a: supplement, character 197); Hwang et al. (2004: supplement, character 67); Xu and Norell (2004: supplement, character 67).

0612. Os dentale (occlusal perspective), ramus dentalis (**new term**) immediately caudal to pars symphysialis, medial (re)curvature, status:

a. absent, almost straight; **b.** present.

Note.—See: J. M. Clark et al. (1994); Russell and Dong (1994a [1993a]: table 2, character 14) and Russell and Dong (1994b [1993b]: troödontid character 6), regarding "symphyseal region of dentary medially recurved"; Currie (1995: appendix, character 20); Sues (1997: appendix 1, character 15); Makovicky and Sues (1998: appendix 1, character 28), terming it "medially inflected symphyseal region"; Xu et al. (1999b: character 96); Holtz (2000 [1998]: appendix I, character 107), evidently following Russell and Dong (1994b [1993b]); Norell et al. (2000: appendix 1, character 24); Xu et al. (2000: supplement, character 76); Norell et al. (2001: appendix 1, character 67); J. M. Clark et al. (2002a: appendix 2.2, character 67); Vickers-Rich et al. (2002), concerning *Avimimus*; Xu (2002: suite II, characters 105 and 252); Rauhut (2003: character 76); Hwang et al. (2004: supplement, character 66); Xu and Norell (2004: supplement, character 66).

0613. Os dentale (lateral perspective), ramus dentalis (**new term**), rostrocaudal profile, forma marginalis:

a. margines dorsalis et ventralis mandibulae subparallel, profile rhomboid;

b. margines dorsalis et ventralis divergent caudad (convergent distad), profile subtriangular.

Note.—See: Currie (1995); Azuma and Currie (2000: appendix 1, character 33); Norell et al. (2000: appendix 1, character 23); Norell et al. (2001: appendix 1, character 69); J. M. Clark et al. (2002a: appendix 2.2, character 72); Xu (2002: suite II, character 234); Xu et al. (2002a: supplement, character 179); Hwang et al. (2004: supplement, character 71); Xu and Norell (2004: supplement, character 71).

0614. Os dentale (dorsal perspective), ramus dentalis (**new term**), caudal alignment of rami, forma:

a. subparallel;

b. widely divergent, including both lateral and medial curvature.

Note.—See: Makovicky and Sues (1998: appendix 1, character 25); Holtz (2000 [1998]: appendix I, character 109); Maryanska et al. (2002: appendix 1, characters 81–82).

0615. Os dentale (lateral perspective), pars rostralis, margo ventralis (relative to margo dorsalis), forma marginalis:

a. convex or linear; **b.** concave.

Note.—See: Russell and Dong (1994b [1993b]: troödontid character 6); Holtz (2000 [1998]: appendix I, character 108).

0616. Os dentale (lateral perspective), pars rostralis, distinct ventral angulus, effecting failure of occlusion with rostrum maxillae, margo tomialis, status:

a. absent; **b.** present.

Note.—See: Makovicky and Norell (2004: character 212); Xu and Norell (2004: supplement, character 212).

0617. Os dentale, margo caudalis (**new term**), bifurcatio marginalis, status:

a. absent, margo entire, typically oblique (rarely slightly concave), processus caudodorsalis lacking;

b. present, variable in length and depth, frequently (in nonavialians) including processus caudodorsalis to pars rostralis of fenestra mandibularis.

Note.—See: Cracraft (1986: appendix, characters 63–64); Cracraft (1988: series IV, character 5; series V, character 8); Cracraft and Mindell (1989: table 1, characters 5 and 19); Barsbold et al. (1990); Elzanowski (1995: 38, character unindexed); Chiappe et al. (1999); Cracraft and Clarke (2001: appendix 2, character 4); Norell and Clarke (2001: appendix I, character 42), treated similarly by J. A. Clarke (2002: appendix I, character 42), J. A. Clarke and Norell (2002: appendix 2, character 42), and J. A. Clarke (2004: appendix 1, character 42); J. M. Clark et al. (2002a: appendix 2.2, character 70); Maryanska et al. (2002: appendix 1, character 83); Xu (2002: suite I, characters 33 and 48; suite II, character 107); Zhou and Zhang (2002: appendix III, character 42); Rauhut (2003: character 77); Hwang et al. (2004: supplement, character 69); Xu and Norell (2004: supplement, character 69); Ji et al. (2005: supplement, part I, character 42).

0618. Os dentale, margo caudalis, processus caudodorsalis, forma:

a. long and shallow; **b.** short and deep.

Note.—See: Maryanska et al. (2002: appendix 1, character 84).

0619. Os dentale, margo caudalis, processus caudodorsalis, caudal extent (**ordered**):

a. terminus cranial to margo caudalis of fenestra (caudalis) mandibulae;

b. terminus caudalis minimally beyond (dorsal to) margo caudalis of fenestra (caudalis) mandibulae;

c. terminus caudalis distinctly beyond (dorsal to) majority of margo caudalis of fenestra (caudalis) mandibulae.

Note.—See: Norell et al. (2001: appendix 1, character 72); J. M. Clark et al. (2002a: appendix 2.2, character 70); Maryanska et al. (2002: appendix 1, character 85); Xu (2002: suite I, characters 33 and 48; suite II, character 107); Hwang et al. (2004: supplement, character 69); Xu and Norell (2004: supplement, character 69).

Os Angulare

0620. Os angulare, processus retroarticularis, dorsal recurvature, evidently produced by caudal elongation and dorsal drawing of dorsocaudal vertex of ramus mandibulae, status et forma (**unordered**):

a. absent, regio typically undistinguished or at most tubercular;

b. present, processes cuneate;

c. present, a small but distinct hamulus;

d. present, moderately large, lateromedially compressed, with margo ventralis angular, and length less than that of rostrocaudal dimension of fossa articularis quadratica mandibulae;

e. present, typically very large, lateromedially compressed, with margo ventralis monotonically curved, and length at least as great as that of rostrocaudal dimension of fossa articularis quadratica mandibulae.

Note.—The partitioning of curved structures in this region, at least those considered to be homologous based on arthrological and myological relationships, necessitated a departure from the simplistic, traditional term "retroarticular process" perpetuated by the *Nomina* (Baumel et al. 1993) and elsewhere.

See: Livezey (1986: appendix 1, character 14); Cracraft (1988: series VII, character 11); Houde (1988: table 27, character 15); Cracraft and Mindell (1989: table 1, character 37); Livezey (1989: table 1, character 14); Andors (1992: table 2, characters 22–23); Currie et al. (1994 [1993]); J. M. Clark et al. (1994); Sereno et al. (1994: footnote 12); Currie (1995: appendix, character 23); Ericson (1996: character 11); Sereno et al. (1996: footnote 45, character 25); Ericson (1997: table 1, character 19); Livezey (1997a: appendix 1, character 20; *corrigenda*, Livezey 1998a); Chu (1998: appendix 1, character 57); J. D. Harris (1998: appendix 2, characters 43–44); Livezey (1998b: appendix A, characters 17–18); Makovicky and Sues (1998: appendix 1, character 23); Rotthowe and Starck (1998: appendix, character 21); Xu et al. (1999b: character 99); Currie and Carpenter (2000: appendix 1, character 40), pertaining to breadth and caudal exposure; Holtz (2000 [1998]: appendix I, characters 123 [orientation], 124 [elongation], and 125); Xu et al. (2000: supplement, character 79); Cracraft and Clarke (2001: appendix 2, character 42); Dyke (2001b: appendix 1, character 20); Norell et al. (2001: appendix 1, character 80); J. M. Clark et al.

(2002a: appendix 2.2, character 80); Xu (2002: suite II, character 114); Xu et al. (2002a: supplement, character 59); G. Mayr and Clarke (2003: appendix A, character 44); Dyke and van Tuinen (2004: appendix 1, character 26); G. Mayr (2004a: appendix 1, characters 24–25); Hwang et al. (2004: supplement, character 79); Xu and Norell (2004: supplement, character 79); Makovicky and Norell (2004: character 219) and Xu and Norell (2004: supplement, character 219), regarding caudal orientation.

0621. Os angulare, processus rostralis, irruptio processi lacunis dento-angularis (**new term**), status:
a. present; **b.** absent.
Note.—New term refers to penetration by "anterior prong of the angular" into "dentary-splenial cavity." See: Bakker et al. (1988); J. M. Clark et al. (1994); Holtz (1994a: appendix 1, character 111); Holtz (2000 [1998]: appendix I, character 117).

0622. Os angulare, planum superficialis retroarticulare—dorsally rotated, roughly triangular flange caudal to fossa articularis quadratica, defined ventrolaterally on facies lateralis mandibulae by marked depressio m. pterygoideus—evidently produced by dorsocaudal elongation of ventrocaudal vertex of ramus mandibulae, status et forma (**ordered**):
a. absent;
b. present, comparatively short, blunt, and oriented caudoventrally;
c. present, elongate, pointed, and caudally oriented, with depressio m. pterygoideus extremely well developed.
Note.—Gaviidae possess both this planum and, rostrolateral to planum, a small, hamulate processus articularis proper. See: Stephan (1979), regarding Spheniscidae.

0623. Os angulare, processus retroarticularis (if present), forma as rounded flange, coplanar with facies lateralis mandibulae, and lacking both depressio m. pterygoideus laterally and incisura retroarticularis dorsally, status:
a. absent; **b.** present.

Os Articulare

0624. Os articulare, ramus mandibulae, processus medialis mandibulae, status:
a. absent; **b.** present.
Note.—See: Cracraft (1988); Ericson (1996); Livezey (1997a: appendix 1, character 25; *corrigenda*, Livezey 1998a) and Livezey (1998b: appendix A, character 19); Cracraft and Clarke (2001: appendix 2, character 41); Norell et al. (2001: appendix 1, character 79); J. M. Clark et al. (2002a: appendix 2.2, character 79); Xu (2002: suite II, character 113); Xu et al. (2002a: supplement, character 58), with reference to "articular . . . elongate slender medial, posteromedial, or mediodorsal process from retroarticular process"; G. Mayr and Clarke (2003: appendix A, character 45); Dyke and van Tuinen (2004: appendix 1, character 27); Hwang et al. (2004: supplement, character 78); Xu and Norell (2004: supplement, character 78).

0625. Os articulare, ramus mandibulae, processus medialis mandibulae, long and narrow, approximately perpendicular to mandibula at rostrocaudal position of cotyla medialis of fossa articularis quadratica, status:
a. absent; **b.** present;
x. noncomparable (Psittaciformes).

0626. Os articulare, ramus mandibulae, processus medialis mandibulae, forma in which processus short, facies caudalis supports medial portion of extensive, flattened, roughly triangular or semilunate impressio insertii m. depressor mandibulae, status:
a. present; **b.** absent;
x. noncomparable (Psittaciformes).

0627. Os articulare, pneumaticitas, status:
a. absent; **b.** present.
Note.—Strong association between this character and status of foramen pneumaticum of articulating os quadratum. See: Norell and Clarke (2001: appendix I, character 41), treated similarly by J. A. Clarke (2002: appendix I, character 41), J. A. Clarke and Norell (2002: appendix 2, character 41), and J. A. Clarke (2004: appendix 1, character 41); Ji et al. (2005: supplement, part I, character 41).

Os Coronoideum

0628. Os coronoideum, status:
a. present, small to moderately large, forming laminae interdentales;
b. absent or not discernable.
Note.—Element considered to be absent in most other Aves (de Kock 1955). Extreme elongation of this element results in distinctive bilateral longitudinal laminae along the medial aspects of the rami mandibulae is widespread and presumably plesiomorphic for Reptilia (Romer 1956).

See: W. K. Parker (1869a); J. T. Gregory (1952); de Kock (1955); Nemeschkal (1983); Cracraft (1986: appendix, character 3); Gauthier (1986: 14, unindexed synapomorphy of Aves); Cracraft (1988: series IV, character 2); Houde (1988: table 27, character 9); Cracraft and Mindell (1989: table 1, character 2); Baumel and Witmer (1993: 75); Sereno et al. (1993: legend for fig. 3a); J. M. Clark et al. (1994); Russell and Dong (1994a [1993a]: table 2, character 15); Elzanowski and Wellnhofer (1996); Sues (1997: appendix 1, character 16); Chiappe et al. (1998: character 11, modified); Forster et al. (1998: supplement, character 26, modified); Ji et al. (1998: supplement, character 11, modified); Makovicky and Sues (1998: appendix 1, character 27); Xu et al. (1999a: character 20, modified); Xu et al. (1999b: character 23); Holtz (2000 [1998]: appendix I, character 121); Xu et al. (2000: supplement, character 20); Chiappe (2001a: appendix 1, character 25); Cracraft and Clarke (2001: appendix 2, character 2); Norell and Clarke (2001: appendix I, character 18), treated similarly by J. A. Clarke (2002: appendix I, character 18), J. A. Clarke and Norell (2002: appendix 2, character 18), and J. A. Clarke (2004: appendix 1, character 18); Norell et al. (2001: appendix 1, character 78); Chiappe (2002: appendix 20.2, character 25); J. M. Clark et al. (2002a: appendix 2.2, character 69 [presence] and 78 [size]); Lamanna et al. (2002: appendix 1, character 3); Maryanska et al. (2002: appendix 1, character 94); Xu (2002: suite I, character 65; suite II, character 112); Xu et al. (2002a: supplement, character 57); Xu et al. (2002b); Zhou and Zhang (2002: appendix III, character 94); G. Mayr and Clarke (2003: appendix A, character 41); Rauhut (2003: character 80); Hwang et al. (2004: characters 68 and 77); Xu and Norell (2004: supplement, characters 68 and 77); Ji et al. (2005: supplement, part I, character 18).

0629. Os coronoideum, eminentia coronoidei (**new term**), status:

a. absent; **b.** present.

Note.—See: J. M. Clark et al. (2002a: appendix 2.2, character 69); Maryanska et al. (2002: appendix 1, character 86), in reference to “coronoid eminence” in Oviraptorosauria; Xu (2002: suite II, character 106); Xu et al. (2002a: supplement, character 51); Xu et al. (2002b); Rauhut (2003: character 72); Hwang et al. (2004: supplement, character 68); Xu and Norell (2004: supplement, character 68).

Os Intercoronoideum

0630. Os intercoronoideum, status:

a. present; **b.** absent.

Note.—Potential for confusion with os supradentale and lamina on medial aspects of dentes, as well as a derivative of os spleniale. See: Madsen et al. (1995: 31).

Os Prearticulare

0631. Os prearticulare, processus prearticularis (**new term**)—tuberculum (dorsale) insertii m. pseudotemporalis superficialis—status et forma (**unordered**):

a. absent or rudimentary (tuberositas), typically on dorsal surface of basis prearticularis, or proximate to tomium caudal to or within fossa aditus canalis mandibulae;

b. present and prominent (tuberculum verae), on margo dorsalis of processus rostralis prearticulare and at approximate midpoint of margines ventralis et dorsalis mandibulae, typically medial to fenestra caudale mandibulae within fossa aditus canalis mandibulae;

c. present and prominent (tuberculum verae), on apex of processus dorsalis prearticulare, subparallel with tomium and with planar facies dorsalis.

Note.—See: Hughes (2000: appendix 2, character 53).

0632. Os prearticulare, pars rostralis (**new term**), abrupt dorsal expansion resulting in (medial perspective) lamina dorsalis ossis prearticulare (**new term**), status:

a. absent; **b.** present;

x. noncomparable where synostotic.

0633. Os prearticulare, pars rostralis (**new term**), slender processus dorsalis (**new term**) and slender, comparatively elongate extension of corpus ossis combining to produce (medial perspective) a deep bifurcatio ossis prearticulare (**new term**), status:

a. absent; **b.** present;

x. noncomparable by synostosis (*Aptornis*).

0634. Os prearticulare, pars rostralis (**new term**), slender processus dorsalis (**new term**) and comparatively truncate extension of corpus ossis combining to produce (medial perspective) a shallow bifurcatio ossis prearticulare (**new term**), status et forma (**unordered**):

a. absent;

b. present, processus dorsalis extending rostrad to corpus;

c. present, processus dorsalis subtriangular, failing to extend rostrad to corpus;

x. noncomparable where synostotic.

Os Spleniale

0635. Os spleniale, exposure of element on facies lateralis mandibulae, status et forma:

a. absent, obsolete, or rectangular and not proximate to margo dorsalis mandibulae;

b. substantial, subtriangular area framed by ossa dentale et angulare, and approaching margo dorsalis mandibulae.

Note.—See: Houde (1988: table 27, character 4); J. M. Clark et al. (1994); Currie (1995: appendix, character 21); Makovicky and Sues (1998: appendix 1, character 26); Xu et al. (1999b: character 97); Holtz (2000 [1998]: appendix I, character 119); Norell et al. (2000: appendix 1, character 25); Xu et al. (2000: supplement, character 77); Norell et al. (2001: appendix 1, character 77); J. M. Clark et al. (2002a: appendix 2.2, character 77); Norell and Clarke (2001: appendix I, character 43), similarly by J. A. Clarke (2002: appendix I, character 43), J. A.

Clarke and Norell (2002: appendix 2, character 43), and J. A. Clarke (2004: appendix 1, character 43); Maryanska et al. (2002: appendix 1, character 92); Xu (2002: suite I, character 65; suite II, character 111); Xu et al. (2002a: supplement, character 56); Hwang et al. (2004: supplement, character 76); Xu and Norell (2004: supplement, character 76); Ji et al. (2005: supplement, part I, character 43).

0636. Os spleniale, incisura caudalis (**new term**) marginis rostralis fenestrae rostralis mandibulae, status:
a. absent, margo linear;
b. present, margo bifurcate.
Note.—See: J. M. Clark et al. (1994); Sereno et al. (1994: footnote 12); Sereno et al. (1996: footnote 45, character 24); J. D. Harris (1998: appendix 2, character 40); Currie and Carpenter (2000: appendix 1, character 39); Holtz (2000 [1998]: appendix I, character 120); Rauhut (2003: character 79).

0637. Os spleniale, margo rostroventralis, incisura aut foramen n. hyomandibularis (ramus caudalis), ramulus hyoideus, status et forma (**unordered**):
a. absent, sutura angulosplenialis completa;
b. present, incisura, foramen completed by lacuna in os angulare;
c. present, foramen completely enclosed within os spleniale.
Note.—See: Sereno (1991b); Currie and Zhao (1994b [1993b]); Rauhut (2003: character 78). Provisional identification of nervus served by structure proposed by Currie and Zhao (1994b [1993b]) as n. mylohyoideus.

Os Supraangulare (Surangulare)

0638. Os supraangulare, pronounced, lateral pneumatic inflation, status:
a. absent; **b.** present.

0639. Os supraangulare, pars rostralis, comparative dorsoventral height:
a. shallow, os supraangulare less than half mandibular height dorsal to fenestra mandibulae rostralis;
b. deep, os supraangulare more than half mandibular height dorsal to fenestra mandibulae rostralis.
Note.—See: Gauthier (1986); J. M. Clark et al. (1994); Holtz (1994a: appendix 1, character 105); Sereno et al. (1996); J. D. Harris (1998: appendix 2, character 37); Azuma and Currie (2000: appendix 1, character 101); Currie and Carpenter (2000: appendix 1, character 37); Holtz (2000 [1998]: appendix I, character 115); Rauhut (2003: character 75).

0640. Os supraangulare, foramina rostrale et/aut caudale, status et situs (**unordered**):
a. both foramina absent or minute;
b. foramen rostrale substantial;
c. foramen caudale substantial;
d. both foramina rostrale et caudale substantial.
Note.—See: Sereno and Novas (1992: appendix, character 10), with respect to "slotted surangular"; Holtz (1994a: appendix 1, character 89); Russell and Dong (1994a [1993a]: table 2, character 17); J. D. Harris (1998: appendix 2, character 39), with respect to foramen caudale; Makovicky and Sues (1998: appendix 1, character 24), merely with respect to presence of "surangular foramen"; Azuma and Currie (2000: appendix 1, character 102), with respect to foramen caudale; Holtz (2000 [1998]: appendix I, character 113), in reference to "rostral surangular foramen"; Holtz (2000 [1998]: appendix I, character 114), coded taxa in reference to "caudal surangular foramen"; J. M. Clark et al. (2002a: appendix 2.2, character 76); Maryanska et al. (2002: appendix 1, character 87); Xu (2002: suite II, character 110); Xu et al. (2002a: supplement, character 55), with reference to "foramen in lateral surface of surangular rostral to mandibular articulation" and provisionally treated as informative only regarding the rostral feature; Brochu (2003); Hwang et al. (2004: supplement, character 75); Xu and Norell (2004: supplement, character 75).

0641. Os articulare (supraangulare), ramus mandibulae, processus lateralis mandibulae, status et forma (**unordered**):
a. absent or limited to a faint impressio;
b. present, variably conformed, modest tuberculum or boss;
c. present as prominent, laterally oriented tuberculum;
d. present as prominent, "pendant" tuberculum.
Note.—See: Sereno et al. (1994: footnote 12); Sereno et al. (1996: footnote 45, character 45), in reference to a "pendant medial process" that was attributed to os articulare; Ericson (1997: table 2, character 16), who mistakenly coded the feature as absent in four families of Aves; Livezey (1997a: appendix 1, character 24; *corrigenda*, Livezey 1998a); Holtz (2000 [1998]: appendix I, character 116); Makovicky and Norell (2004: character 209) and Xu and Norell (2004: supplement, character 209), concerning lateral flange articulating with os quadratum. Variation is subtle and limited among Neornithes, in part because the processus may serve as lateral part of cotyla quadratica and/or ancora ligamentum postorbitale (Baumel and Witmer 1993: annotation 49d).

0642. Ramus mandibulae, processus lateralis mandibulae, hamulus lateralis (**new term**), status:
a. absent; **b.** present.

0643. Ramus mandibulae, facies dorsalis, sulcus aut planum paratomialis (**new terms**), status:
a. absent;
b. present, caudal to symphysis;
c. present, extends onto symphysis.

Partes mandibulae

0644. Rostrum (symphysis) mandibulae, facies dorsalis, decurvature relative to margo tomialis, status:
a. absent, symphysis planar and parallel to tomia;
b. present.
Note.—See: J. M. Clark et al. (2002a: appendix 2.2, character 68); Zhou and Zhang (2002: appendix III, character 44); Hwang et al. (2004: supplement, character 67); Xu and Norell (2004: supplement, character 67).

0645. Rostrum (symphysis) mandibulae, facies dorsalis, forma superficialis (**unordered**):
a. concave; **b.** planar;
c. convex, along symphysis medialis.
Note.—See: Gadow (1877); Jenkin (1957); Norell and Clarke (2001: appendix I, character 44), treated similarly by J. A. Clarke (2002: appendix I, character 44), J. A. Clarke and Norell (2002: appendix 2, character 44), and J. A. Clarke (2004: appendix 1, character 44); Ji et al. (2005: supplement, part I, character 44).

0646. Rostrum (symphysis) mandibulae, margo rostrodorsalis, forma:
a. sublinear or weakly concave;
b. strongly concave.
Note.—See: Maryanska et al. (2002: appendix 1, character 82).

0647. Rostrum (symphysis) mandibulae, facies ventralis, narrow and bilaterally paired sulci passing from margo caudalis to terminus, status:
a. absent;
b. present, typically forming chevroniform eminentia.
Note.—See: Chiappe (2001a: appendix 1, character 24); Norell and Clarke (2001: appendix I, character 7), treated similarly by J. A. Clarke (2002: appendix I, character 7), J. A. Clarke and Norell (2002: appendix 2, character 7), and J. A. Clarke (2004: appendix 1, character 7); Maryanska et al. (2002: appendix 1, character 75); Zhou and Zhang (2002: appendix III, character 7); Ji et al. (2005: supplement, part I, character 7).

0648. Rostrum (symphysis) mandibulae, facies ventralis, distinctly convex, bulbous shape, status:
a. absent; **b.** present.
Note.—See: Livezey (1997a: appendix 1, character 22; *corrigenda*, Livezey 1998a).

0649. Rostrum (symphysis) mandibulae, pronounced bilateral expansion into rounded, dorsoventrally flattened, rostrocaudally extensive lamina, status:
a. absent; **b.** present.

0650. Rostrum (symphysis) mandibulae, "scoop-like" conformation involving truncate apical margin, flattened and angular facies ventralis, status:
a. absent; **b.** present.
Note.—See: Sereno et al. (1996: footnote 45, character 50); J. D. Harris (1998: appendix 2, character 36); Holtz (2000 [1998]: appendix I, character 105), regarding "squared" terminus of rostrum (symphysis) mandibulae in Theropoda.

0651. Rostrum (symphysis) mandibulae, incisura symphysialis rostrale, status:
a. absent; **b.** present.
Note.—See: Chiappe (2002: appendix 20.2, character 24).

0652. Rostrum (symphysis) mandibulae, margo caudalis, foramina neurovascularia, numerus modalis:
a. one, formed by two superficially coalescent into single, exposed medial foramen;
b. two, both remaining separate to surface.
Note.—States exclude proximate, unrelated foramina or exposed septa (cf. Otididae, Cariamidae, Heliornithidae, and Burhinidae). Primitive falconids (e.g., *Poliohyrax*, *Spiziapteryx*) remain bilaterally paired. See: Stidham (1998), with respect to premature assessment of fragmentary fossil; Norell and Clarke (2001: appendix I, characters 45–46), treated similarly by J. A. Clarke (2002: appendix I, characters 45–46), J. A. Clarke and Norell (2002: appendix 2, characters 45–46), and J. A. Clarke (2004: appendix 1, characters 45–46); Zhou and Zhang (2002: appendix III, characters 45–46); Ji et al. (2005: supplement, characters 45–46).

0653. Rostrum (symphysis) mandibulae, margo caudalis, foramina neurovascularia (if paired), forma et numerus modalis (**unordered**):
a. bilaterally paired; **b.** dorsoventrally paired;
c. singular, central;
x. noncomparable (Falconidae).
Note.—See: Livezey (1997a: appendix 1, character 16; *corrigenda*, Livezey 1998a).

0654. Rostrum (symphysis) mandibulae, foramina neurovascularia, situs caudodorsalis:
a. margo caudalis symphysialis;
b. facies dorsalis symphysialis.
Note.—See: Norell and Clarke (2001: appendix I, character 47), treated similarly by J. A. Clarke (2002: appendix I, character 47), J. A. Clarke and Norell (2002: appendix 2, character 47), and J. A. Clarke (2004: appendix 1, character 47); Zhou and Zhang (2002: appendix III, character 47); Ji et al. (2005: supplement, part I, character 47).

0655. Rostrum (symphysis) mandibulae (dorsal perspective), rostrocaudal elongation, bilateral compression, and marked convergence of rami (in some taxa become parallel) well caudal to rostrum, producing distinctly "Y-shaped" mandibula, status et forma (**ordered**):

a. absent;

b. present, rami remain distinguishable;

c. present, rami indistinguishable and distally form a unified, apical carina.

Note.—See: G. Mayr et al. (2003: appendix 1, character 19).

0656. Rostrum (symphysis) mandibulae, pars symphysialis and anteriormost segment of pars intermedia, dorsoventral compression of rami producing essentially flat apex (especially obvious in rostral perspective), associated with virtual absence of crista tomialis rostrally, status:

a. absent; **b.** present.

Note.—See: Livezey (1996a: appendix 1, characters 11–12); G. Mayr and Clarke (2003: appendix A, character 43).

0657. Rostrum (symphysis) mandibulae, facies ventralis, pair of elongated depressiones revealing os spongiosum, with margo caudalis of symphysis involucral, status:

a. absent; **b.** present.

Note.—See: Jenkin (1957).

0658. Ramus mandibulae, pronounced, monotonic curvature producing continuous lateral convexity, status:

a. absent; **b.** present.

0659. Ramus mandibulae, partes symphysialis et intermedia, shallow sulci indicative of rhamphothecal patterns, status:

a. absent; **b.** present.

Note.—See: Ericson (1997: table 1, character 21), coded this feature for ratites, after Parkes and Clark (1966), S. L. Olson (1985), and Houde (1988).

0660. Ramus mandibulae, pars intermedia, facies lateralis, foramina neurovascularia, situs:

a. dispersed superficially;

b. confined within deep sulcus.

Note.—See: Russell and Dong (1994b [1993b]: troödontid character 11); Norell et al. (2001: appendix 1, character 73); J. M. Clark et al. (2002a: appendix 2.2, character 73); Xu (2002: suite II, character 108); Hwang et al. (2004: supplement, character 72); Xu and Norell (2004: supplement, character 72).

0661. Ramus mandibulae, pars intermedia, facies lateralis, sulcus crescentiformis (**new term**), characterized rostrally by pori neurovascularia and caudally by lateromedial compression, status:

a. absent; **b.** present.

0662. Ramus mandibulae, moderate, continuous, ventral curvature of both facies dorsales et ventrales, in which angulus dorsalis mandibulae, angulus ventralis mandibulae, zona flexoria intramandibularis caudalis, or processus coronoideus is distinguishable, status:

a. absent; **b.** present.

0663. Ramus mandibulae, pars intermedia, facies lateralis, elongate sulcus paralleling margo dorsalis, tuberculum ovalis on facies dorsalis, status:

a. absent; **b.** present.

Note.—Both structures accommodate arcus jugalis with mandibula adducted. See: Jenkin (1957).

0664. Ramus mandibulae, pars intermedia, facies lateralis, longitudinal striae mandibulae (**new term**) and insetting recessi alveolae (**new term**) of dentes (if present), forma:

a. facies lateralis flat and lacking inset dentes;

b. facies lateralis with longitudinal cristula, and dentes (if present) arranged as inset row;

x. noncomparable (Neornithes).

Note.—See: Sereno (1999: character 142); Suzuki et al. (2002: character 5); Xu et al. (2002a: supplement, character 198).

0665. Ramus mandibulae, pars intermedia, angulus mandibulae dorsalis (**new term**), status et forma (**ordered**):

a. absent;

b. present, but limited to terminus rostralis fenestralis;

c. present, but elongate, extending over majority of fenestra.

Note.—See: Xu et al. (2002a: supplement, character 52), in reference to "posterodorsal process dorsal to mandibular fenestra."

0666. Ramus mandibulae, pars intermedia, pronounced dorsoventral deepening, achieving maximal depth at margo caudalis symphysialis mandibulae, status:

a. absent; **b.** present.

Note.—See: Jenkin (1957).

0667. Ramus mandibulae, pars intermedia, facies lateralis, fossa lateralis mandibulae, deep recessus rostralis enclosing a large, rostrally directed foramen neurovascularium, status:

a. absent; **b.** present.

0668. Ramus mandibulae, pars intermedia, facies medialis, fossa medialis (**new term**) conformed as lateromedially deep, dorsoventrally broad (occupying majority of depth of ramus), and rostrocaudally extensive (occupying essentially all of pars intermedia) longitudinal sulcus, status:

a. absent; **b.** present.

Note.—A smaller fossa medialis occurs in many other Neornithes; this feature appears to act to preclude dorsoventral flexion of pars intermedia. See: Livezey (1997a: appendix 1, character 23; *corrigenda*, Livezey 1998a).

0669. Ramus mandibulae, pars intermedia, facies medialis, sulcus tomialis (**new term**)—deep, caudally broadening sulcus on margo dorsalis of facies medialis—status:
a. absent; **b.** present.

0670. Ramus mandibulae, all partes, maximal dorsoventral height as ratio to total mandibular length:
a. approximately 0.2; **b.** approximately 0.1;
x. noncomparable (Neornithes).
Note.—See: Maryanska et al. (2002: appendix 1, character 77); J. M. Clark et al (2001); Murray and Vickers-Rich (2004: table 9, character 2).

0671. Ramus mandibulae, pars caudalis, dorsoventral depth relative to that of ramus mandibulae, pars symphysialis (**ordered**):
a. approximately 120%;
b. approximately 150–200%;
c. greater than 220%.
Note.—See: Holtz (2000 [1998]: appendix I, character 112); Murray and Vickers-Rich (2004: table 9, character 2), regarding Dromornithidae.

0672. Ramus mandibulae, all partes, length of fenestra (rostralis) mandibulae as ratio to total mandibular length (**ordered**):
a. 0.10 or less; **b.** 0.15–0.20;
c. 0.25 or more.
Note.—See: Maryanska et al. (2002: appendix 1, character 79).

0673. Ramus mandibulae, pars intermedia and segment of pars caudalis rostral to fossa articularis quadratica, margo ventralis, curvature (lateral perspective), status et forma (**unordered**):
a. present, variably but distinctly decurved;
b. obsolete, i.e., virtually straight;
c. present, strongly recurved;
x. noncomparable (Rynchopidae).
Note.—Decurvature so to exclude that attributable entirely to angulus ventralis mandibulae (if present). Decurvature in at least Threskiornithidae formed comparatively late in ontogeny and is composed virtually entirely of ossa premaxillares et dentales.

0674. Ramus mandibulae, pars intermedia and symphysialis, margo dorsalis, pronounced medial deflection of tomium (approaching perpendicularity with facies medialis), especially pronounced rostral to margo proximalis symphysialis mandibulae, status:
a. absent; **b.** present.
Note.—See: Jenkin (1957). Ventral angulation develops relatively late in ontogeny, and during much of craniofacial development the rostrum maxillae is comparatively truncate and virtually straight.

0675. Ramus mandibulae, partes intermedia et symphysialis, pronounced, abrupt ventral curvature, effecting perpendicularity of apex and pars intermedia of tomia, status definitivum:
a. absent; **b.** present.
Note.—Corresponding curvature reflected by rostrum maxillae. Rostra during early ontogeny are essentially straight, similar to that of Ciconiidae, as are those of extremely apomorphic taxon (Jenkin 1957).

0676. Ramus mandibulae, pars symphysialis, length as proportion of total length of mandibula (**ordered**):
a. short, less than one-fifth;
b. medium, between one-fifth and one-third;
c. long, between one-third and one-half;
d. very long, more than one-half.
Note.—Intervals defined after method of Thiele (1993). See: Cracraft (1971a); Livezey (1998a: character 16).

0677. Ramus mandibulae, pars symphysialis, facies ventralis, deep, narrow sulcus medialis along entire symphysis, status:
a. absent; **b.** present.

0678. Ramus mandibulae, pars symphysialis, extreme dorsoventral attenuation and tenuous aspectus, status:
a. absent; **b.** present.
Note.—See: G. Mayr (2002a: appendix 1, character 11), with respect to Caprimulgiformes. Related kinetic properties of symphysis mandibulae considered under arthrologia rostri.

0679. Ramus mandibulae, angulus dorsalis mandibulae (**new term**), distinctly deeper dorsoventrally than remainder of ramus mandibulae, emphasizing sharp angulus ventralis of pars rostralis cristae tomialis (margo caudalis of pars symphysialis), status:
a. absent; **b.** present.
Note.—Position and depth varies within Psittaciformes. See: D. W. Thompson (1899).

0680. Ramus mandibulae, angulus dorsalis mandibulae, dorsolaterally oriented flange, status:
a. absent; **b.** present.

0681. Ramus mandibulae, angulus ventralis mandibulae (**new term**), status:
a. absent or indistinct; **b.** distinct.
Note.—Functionally associated with streptognathism. See: Livezey (1997a: appendix 1, character 19; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, character 9).

0682. Ramus mandibulae, tuberculum m. adductor mandibulae externus, pars articularis (**new term**), status:
a. absent or indistinct;
b. prominent, a distinct tuberculum located on facies lateralis ventrocaudal to angulus mandibulae.
Note.—Distinct from processus coronoideus (si-

tus insertii m. adductor mandibulae externus, pars coronoideus). See: Cracraft and Mindell (1989: table 1, character 36); Livezey (1996a: appendix 1, character 5); Livezey (1997a: appendix 1, character 18; *corrigenda*, Livezey 1998a), incorrectly identified.

0683. Ramus mandibulae, fenestra caudalis mandibulae—variably large fenestra transversa (os surangulare)—typically located in pars caudalis of fossa aditus canalis neurovascularis, status:

a. absent or appearing as foramen neurovascularia;

b. present, dorsoventral dimension at least one-fourth the height of ramus mandibulae at that point.

Note.—See: Livezey (1998b: appendix A, character 11); Chiappe (1999: fig. 13); Norell et al. (2001: appendix 1, character 76); J. M. Clark et al. (2002a: appendix 2.2, character 76); Xu (2002: suite II, character 110); G. Mayr and Ericson (2004: appendix I, character 22); Hwang et al. (2004: supplement, character 75); Xu and Norell (2004: supplement, character 75).

0684. Ramus mandibulae, fenestra rostralis mandibulae, status:

a. substantial and transverse; **b.** absent.

Note.—Typically occurs within or in proximity to zona flexoria intramandibularis caudalis (Baumel and Witmer 1993: annotation 46). Status and conformation somewhat problematic as both are composite result of forms and positional interrelationships of several elements—e.g., ossa spleniale, angulare, et supraangulare—in two overlapping plana. Herein the fenestra is deemed present where fenestrae lateralis et medialis (regardless of coalignment of fenestrae) are present in ramus mandibulae.

See: Lebedinsky (1920), regarding Aves; Benton (2004: 18), regarding "lateral mandibular fenestra" as synapomorphy of Archosauria.

0685. Ramus mandibulae, fenestra rostralis mandibulae, forma:

a. large and orbiculate;

b. small and fissuriform;

x. noncomparable (Neornithes).

Note.—See: Currie (1995: fig. 7); Norell et al. (2001: appendix 1, character 75); J. M. Clark et al. (2002a: appendix 2.2, character 75); Xu (2002: suite II, character 235). Also referred to as "internal mandibular fenestra"; Hwang et al. (2004: supplement, character 74); Xu and Norell (2004: supplement, character 74).

0686. Ramus mandibulae, canalis (cavum) neurovascularis mandibulae, status, lateromedial volume, and rostral extent (**ordered**):

a. present, broad, rostrally extensive;

b. present, breadth and rostral extent intermediate;

c. present, breadth obsolete (lamina medialis et lateralis largely adherent), and rostral extent limited, e.g., comparatively robust fossa aditus canalis neurovascularis;

d. obsolete or absent, remaining homologues limited to vestigial fossa aditus canalis neurovascularis immediately rostral to (if present) fenestrae mandibulae et foramina neurovascularia.

Note.—Considered to represent, at least in substantial part, the spatium evacuated through chondroclasty cartilaginis Meckelii, in extreme cases among dentulous taxa, canalis surrounding alveoli dentalia in pars rostralis. Hence this spatium is homologous to an apomorphous reductive elaboration of Meckel's groove. Vestigial condition frequent among Neornithes—fossa aditus canalis neurovascularis—was traditionally termed "adductor fossa." Evidently, canalis increasingly serves as conduit for nervii, venae, arteriae, et musculi—e.g., insertio m. inframandibularis (Elzanowski 1987)—the latter evidently manifesting general evolutionary reduction throughout stem Theropoda. See: Ji et al. (2005: supplement, part I, character 48).

0687. Ramus mandibulae, fenestra rostralis mandibulae, partial or complete division by spina (processus) rostralis of os surangulare, status:

a. absent, conserving oval fenestra;

b. present; **x.** noncomparable (Neornithes).

Note.—See: J. D. Harris (1998: appendix 2, character 38); Livezey (1998b: appendix A, character 10); J. A. Wilson and Sereno (1998: appendix, character 77); Azuma and Currie (2000: appendix 1, character 68); Currie and Carpenter (2000: appendix 1, character 38); Norell and Clarke (2001: appendix I, character 49); Norell et al. (2001: appendix 1, character 74); J. A. Clarke (2002: appendix I, character 49); J. A. Clarke and Norell (2002: appendix 2, character 49); J. M. Clark et al. (2002a: appendix 2.2, character 74); Xu (2002: suite II, character 109); Xu et al. (2002a: supplement, character 55); Zhou and Zhang (2002: appendix III, character 49); J. A. Clarke (2004: appendix 1, character 49); Hwang et al. (2004: supplement, character 73); Xu and Norell (2004: supplement, character 73); Ji et al. (2005: supplement, part I, character 49).

0688. Ramus mandibulae, fossa aditus canalis neurovascularis, status:

a. absent or merely a small fissura;

b. present, relatively large and triangular or subcircular;

x. noncomparable (Neornithes).

Note.—Not homologous with the "internal mandibular fenestra" of Currie (1995), in which the fossa aditus canalis neurovascularis was referred to as "adductor fossa" (Currie 1995: fig. 7). See: Gauthier (1986); Russell and Dong (1994a [1993a]: table 2, character 16); Holtz (1994a: appendix 1, character

29); Currie (1995: appendix, character 22); Livezey (1998b: appendix A, character 12); Xu et al. (1999b: character 98); Holtz (2000 [1998]: appendix I, character 118); Xu et al. (2000: supplement, character 78); Xu et al. (2002a: supplement, character 180).

0689. Ramus mandibulae, pars caudalis, fossa aditus canalis neurovascularis, status et forma (**unordered**):
a. absent;
b. present, variably developed, often delimited rostrad by rostral expansion of os prearticulare;
c. present, a short, narrow, horizontal fossa;
d. present, a shallow, horizontal fossa extending rostrad to prominent, orbiculate ostium neurovascularis.

0690. Ramus mandibulae, fossa lateralis mandibulae, elemental composition:
a. formed both by ossa supraangulare et articulare;
b. formed solely by os articulare.
Note.—See: Maryanska et al. (2002: appendix 1, character 88). Consult J. M. Clark et al. (2001), regarding unique crania of Oviraptorosauria.

Fossa articularis quadratica

Note.—For characters of fossa articularis quadratica, cotylae fossae articularis, cotylae caudalis, lateralis, rostralis, et medialis, see corresponding characters of os quadratum, processus mandibularis, condyli caudalis, lateralis, rostralis, et medialis. For example, reference to essentially bicotylar and tricotylar fossa articularis quadratica of the mandibula by Ericson (1997: table 1, character 18; table 2, character 13) is a structural "mirror-homologue" of the corresponding characters of the condylae quadraticum. Similarly, several characters of os articulare listed by Hughes (2000: appendix 2, characters 50–52, 54) presumably are reflected by corresponding features of os quadratum.

0691. Fossa articularis quadratica, length relative to processus mandibularis of os quadraticum:
a. approximately equal;
b. former approximately twice that of latter, allowing for rostrocaudal kinesis of mandibula.
Note.—See: Norell et al. (2001: appendix 1, character 81); J. M. Clark et al. (2002a: appendix 2.2, character 81); Xu (2002: suite II, character 115); Hwang et al. (2004: supplement, character 80); Xu and Norell (2004: supplement, character 80).

0692. Fossa articularis quadratica, dorsoventral position relative to that of margo dorsalis of ramus mandibulae, pars caudalis:
a. former ventral to latter;
b. former dorsal to latter.
Note.—See: Maryanska et al. (2002: appendix 1, character 90). Consult J. M. Clark et al. (2001) regarding unique crania of Oviraptorosauria.

0693. Fossa articularis quadratica, shelflike conformation in which facies articularis is positioned on dorsoventrally compressed lamina (i.e., completely excavated both above and below) that is oriented perpendicularly with respect to facies medialis of pars caudalis, status:
a. absent; **b.** present.
Note.—See: Ericson (1996: character 10); Livezey (1997a: appendix 1, character 26; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, characters 14–15).

0694. Fossa articularis quadratica, distinctness (depth) and delimitation by caudomedial and lateral laminae, forma:
a. distinct, laminae delimiting, resulting in a deeply concave fossa articularis;
b. indistinct, laminae obsolete, resulting in a craniocaudally elongate and shallow fossa articularis.
Note.—See: Cracraft (1988: series VII, character 9); Cracraft and Mindell (1989: table 1, character 35); Andors (1992: table 2, characters 19–21); J. M. Clark et al. (1994); Ericson (1996: character 9); J. D. Harris (1998: appendix 2, character 41), with respect to "ridge dividing mandibular glenoid"; Makovicky and Sues (1998: appendix 1, character 22); Rotthowe and Starck (1998: appendix, characters 25 and 29); Holtz (2000 [1998]: appendix I, character 122); Cracraft and Clarke (2001: appendix 2, character 40); Maryanska et al. (2002: appendix 1, character 93), regarding rostral delimitation; Xu et al. (2002a: supplement, character 60); G. Mayr and Clarke (2003: appendix A, character 38).

0695. Fossa articularis quadratica, cotylae fossae articularis, extreme rostrocaudal compaction (especially cotyla lateralis et processus medialis), status:
a. absent; **b.** present.
Note.—See: G. Mayr (2002a: appendix 1, character 12), with respect to Caprimulgiformes; G. Mayr (2005b: appendix A, character 10).

0696. Fossa articularis quadratica, sulcus intercotylaris, foramina pneumatica, status:
a. absent; **b.** present.
Note.—See: Ericson (1997: table 2, character 15), regarding foramina pneumatica in cotylae fossae articularis of Anseriformes. Distinct from foramen pneumaticum articulare, a structure connected to the cavum tympanicum, recessus pneumatici paratympanici by os siphonium, and perhaps synapomorphic for Neornithes.

0697. Fossa articularis quadratica, cotylae fossae articularis, foramen pneumaticum articulare, status:
a. absent; **b.** present.

Note.—See: Witmer (1990: 372, characters 6, 8–9); Molnar (1991); Chiappe and Calvo (1994: appendix I, character 13); Chatterjee (1995: character 4, part); Chiappe (1995b: character 13); Sanz et al. (1995, 1997: character 12); Chiappe (1996b: character 12); Chiappe et al. (1996: appendix 1, character 12); Ericson (1997: table 2, character 15); Chu (1998: appendix 1, character 58); J. D. Harris (1998: appendix 2, character 42); Chatterjee (1999: appendix II, character 15); Chiappe (2001a: appendix 1, character 26); Norell and Clarke (2001: appendix I, character 41), treated similarly by J. A. Clarke (2002: appendix I, character 41), J. A. Clarke and Norell (2002: appendix 2, character 41), and J. A. Clarke (2004: appendix 1, character 41); Chiappe (2002: appendix 20.2, character 26); Zhou and Zhang (2002: appendix III, character 41).

0698. Fossa articularis quadratica, cotylae fossae articularis, tuberculum intercotylare, forma:

a. variably tuberculate with intervening depressiones;

b. single, centrally positioned, rostrocaudally oriented jugum;

x. noncomparable by absence of tuberculum (Dromornithidae).

Note.—See: Cracraft (1988: series VII, characters 8 and 10); Cracraft and Mindell (1989: table 1, character 34); Andors (1992: table 2, characters 19–21); Ericson (1996: character 8); Livezey (1998b: appendix A, character 13); Rotthowe and Starck (1998: appendix, character 25); Cracraft and Clarke (2001: appendix 2, character 39); G. Mayr and Clarke (2003: appendix A, character 38).

0699. Processus retroarticularis mandibulae, forma generalis et situs insertii m. depressor mandibulae:

a. narrow and rodular, situs insertii m. depressor mandibulae a tumulus;

b. broad, situs insertii m. depressor mandibulae a sulcus transversus.

Note.—Situs insertii m. depressor mandibulae posssibly homologous with incisura retroarticularis aut crista transversa fossae caudalis mandibulae. See: Sereno et al. (1996); J. D. Harris (1998); Rauhut (2003: character 73).

0700. Processus retroarticularis mandibulae, situs insertii m. depressor mandibulae, forma *sensu* caudodorsal orientation:

a. dorsal;

b. essentially caudal, i.e., caudal, caudodorsal, or caudoventral.

Note.—See: Sereno et al. (1996); Rauhut (2003: character 74).

0701. Fossa articularis quadratica, incisura postcotylaris (**new term**), status:

a. absent; **b.** present.

Note.—Distinct from small sulci immediately rostral to processus or hamulus retroarticularis in some taxa. See: Jenkin (1957); G. Mayr (2004a: appendix 1, character 24).

0702. Ramus mandibulae, pars caudalis, recessus conicalis caudalis (**new term**), status:

a. absent; **b.** present.

Note.—See: Ericson (1997: table 2, character 14); Livezey (1997a: appendix 1, character 21; *corrigenda*, Livezey 1998a); Dyke (2001b: appendix 1, character 21).

0703. Ramus mandibulae, pars caudalis, fossa caudalis aut recessus insertii m. depressor mandibulae (**new term**), status:

a. absent; **b.** present.

Note.—See: Lebedinsky (1920); Baumel and Witmer (1993: annotations 50 and 51).

0704. Pseudodentes maxillae et mandibulae (**new term**), status:

a. absent; **b.** present.

Note.—Apomorphy diagnostic of single terminal taxon, odontopterygiformis. See: Zusi and Warheit (1992); Livezey (1996a: appendix 1, character 11); Bourdon (2006: supplement, character 52), regarding superficially similar condition in some anseriforms, the latter constituting comparatively small tuberculae largely composed of rhamphotheca with minimal mandibular or maxillar osseous substructures.

Suturae Facium Mandibulae

0705. Sutura (articulatio) angulosplenialis (lateromedial perspective), sectio rostralis (**new term**), forma:

a. os angulare straight and os spleniale with vertically oriented processus;

b. os angulare hamulate and os spleniale spatulate and ventral to os angulare, permitting articulatio synovialis.

Note.—See: Novas (1994 [1993]: appendix, character 39), referring to "posteroventral process of splenial."

0706. Junctura supraangularis, typus:

a. articulatio aut sutura; **b.** synostosis.

Note.—See: Maryanska et al. (2002: appendix 1, character 80). Consult J. M. Clark et al. (2001) regarding unique crania of Oviraptorosauria.

0707. Suturae dentosplenialis, dentoangularis, et dentosupraangularis, typus:

a. sutura squamata, with overlap of os dentale onto externa of more-caudal mandibular elements substantial;

b. sutura plana aut squamosa, with overlap of os dentale onto externa of more-caudal mandibular elements minimal or absent.

Note.—See: Gauthier (1986); Holtz (2000 [1998]: appendix I, character 110).

0708. Symphysis mandibularis, typus definitivum:
a. articulatio aut junctura ligamentosus;
b. synchondrosis; **c.** synostosis.
Note.—See: Cracraft (1986: appendix, character 31); Gauthier (1986: 14); Cracraft (1988: series IV, character 6); Cracraft and Mindell (1989: table 1, character 6); Chatterjee (1991: character 30); J. M. Clark et al. (1994); Elzanowski (1995: 38); Chiappe et al. (1996: appendix 1, character 98); Holtz (2000 [1998]: appendix I, character 106); J. A. Clarke and Chiappe (2001: character 56); Cracraft and Clarke (2001: appendix 2, character 3); Norell and Clarke (2001: appendix I, character 6), treated similarly by J. A. Clarke (2002: appendix I, character 6), J. A. Clarke and Norell (2002: appendix 2, character 6), and J. A. Clarke (2004: appendix 1, character 6); Maryanska et al. (2002: appendix 1, characters 71–72); Xu et al. (2002b); Zhou and Zhang (2002: appendix III, character 6); G. Mayr and Clarke (2003: appendix A, character 42); Ji et al. (2005: supplement, part I, character 6).

Articulationes Mandibulae et Ossis Quadrati

Note.—Morphological aspects of the mandibula and other ossa involved in the suspensorium mandibulae form a substantial complexus of osteological, arthrological, and myological structures. Although efforts to avoid redundancy of characterizations were taken (e.g., coding features of os quadratum or os articulare), some failures of independence were essentially unavoidable.

0709. Syndesmosis (articulatio) mandibulooccipitalis, status:
a. absent; **b.** present.
Note.—See: Bühler (1981).

0710. Articulatio quadratomandibularis, incorporation of "locking" mechanism by means of an involucral margo medialis of cotyla medialis mandibulae, status:
a. absent; **b.** present.
Note.—This articulatio may reflect several quadratomandibular characters. See: Van Gennip (1986) regarding comparatively typical articulatio quadratomandibularis of Columbidae.

Zonae Flexoriae Ossium Mandibularis

0711. Zona flexoria intramandibularis rostralis, effected by variably distinct, localized thinning and flattening (loss of curvature) of rami mandibulae immediately proximal to symphysis mandibulae, status:
a. absent, flexibility variable but generalized throughout ramus;
b. present, localized.
Note.—Rallidae (here included in state "a") are variable, perhaps best to treat as polymorphic. See: Livezey (1997a: appendix 1, character 27; *corrigenda*, Livezey 1998a); G. Mayr (2002a: appendix 1, character 13), with respect to Caprimulgiformes; G. Mayr (2005b: appendix A, character 11).

0712. Articulatio synovialis intramandibularis caudalis, status:
a. present; **b.** absent.
Note.—Zusi and Warheit (1992: fig. 2) diagram articulationes intramandibulares of Pelecaniformes and allies. A nonhomologous articulatio synovialis involving different bones present in Hesperornithiformes and Ichthyornithiformes. See: Sereno and Novas (1992: appendix, character 18); Sereno et al. (1993: legend for fig. 3a); Currie (1995: appendix, character 27); Holtz (2000 [1998]: appendix I, character 111), regarding "intramandibular joint."

0713. Syndesmosis intramandibularis caudalis, status:
a. absent; **b.** present.
Note.—See: G. Mayr et al. (2003: appendix 1, character 21).

Ossa Accessoria Cranii

Note.—One variably ossified (bilaterally paired) element, os siphonium, is probably uniformly possessed by Neornithes but seldom preserved or recovered, precluding characterization.

Os Nuchale

0714. Os (corpus) nuchale, status et typus (**ordered**):
a. absent;
b. present, aponeurotic, derived from junctura caudalis mm. adductores mandibulae;
c. present, osseus.
Note.—Infrequently referred to as "stylus occipitalis" or "styliform process." See: Owre (1967); Cracraft (1985: character 18); Siegel-Causey (1997: table I, character 18); G. Mayr (2004b: appendix 1, character 22); Bourdon et al. (2005: appendix 1, character 17).

Ossa Sclerae

Note.—In Aves, as well as Reptilia generally, the ossa sclerae generally are joined by suturae to form an anulus (annulus) ossicularis sclerae. Most of the suturae involve the edge of one ossiculum laying upon that of an adjacent ossiculum, forming a sutura squamosa; a minority involve a "sigmoid" junctura in which each os is partly lateral and partly medial to the other, forming a comparatively simple sutura serrata. Synchondroses among ossiculae are permanent and inflexible, rendering the anulus functionally rigid. Although variation in numbers of ossiculae and (rarely) typus occurs within taxa and to a limited extent within individuals (i.e., bilateral asymmetry, notably in Strigiformes and Piciformes), modalities are strongly established. See: Giebel (1857); Dabelow (1926); Edinger (1929); Lemmrich (1931); Curtis and Miller (1938); Coulombre et al. (1962); Coulombre and Coulombre (1973); de Queiroz and Good (1988); and Warheit et al. (1989). A more-inclusive survey was performed on *Passer* by Slonaker (1918), with an ontogenetic supplement (Slonaker 1921). A recent analysis by Livezey (1998b: fig. 14) included general typus (character 92), pattern (characters 93–96), and conicality of anulus (character 97). Known for some nonavian theropods, including dromaesaurids (Ji et al. 2001).

0715. Anulus ossicularis sclerae, *sensu* Lemmrich (1931), typus *sensu* numerus ossicularae unilateralium modalis per anulus (**ordered**):

a. typus "B," including only *one* lateral and *one* medial ossicula per anulus, and defining a single, variably extensive, intervening series of imbricated ossiculae;

b. typus "A," including *two* lateral and *two* medial ossiculae per anulus, and defining variably extensive, intervening series of imbricated ossiculae;

c. typus "C," including *three* lateral and *three* medial ossiculae per anulus, and defining variably extensive, intervening series of imbricated ossiculae.

Note.—Basal polarity for Neornithes inferred to be typus "B." See: Lemmrich (1931); Curtis and Miller (1938); de Queiroz and Good (1988); and Livezey (1998b: appendix A, character 92). Note that Lemmrich (1931) defined only typae "A" and "B," with typus "C" being defined here to accommodate the autapomorphic "triple" configuration of the Gaviidae (Curtis and Miller 1938).

0716. Anulus ossicularis sclerae, ossiculae, numerus modalis per anulus (**ordered**):

a. 10–11; **b.** 12–13; **c.** 14–15;
d. 16–17; **e.** 18–19.

Note.—Basal polarity for Neornithes typus "C." See: Lemmrich (1931); de Queiroz and Good (1988); Warheit et al. (1989); Livezey (1998b: appendix A, characters 93–96; fig. 14); G. Mayr (2004b: appendix 1, character 21). Heilmann (1926) reported 14 ossiculae for *Archaeopteryx*, whereas Wellnhofer (1974) tallied "approximately 12" and Elzanowski (2002) "11–12" in Münich specimen.

0717. Anulus ossicularis sclerae, comparative lateromedial depth in planum transversus (**unordered**):

a. essentially laminar, inner rima lateral to outer rima;

b. distinctly conical, often with margo (internus) lateralis of anulus markedly angled craniad;

c. subcircular and narrow.

Note.—See: Lemmrich (1931); Strauch (1985: character 7); Livezey (1998b: appendix A, character 97). Reflects the shape of bulbus oculi.

Os Nervi Optici

0718. Os nervi optici, status et forma modalis (**unordered**):

a. absent, homologous structure remaining a cartilago;

b. present, typically crescentiform (rarely anulate), without enclosed fenestra;

c. present, typically crescentiform (rarely semicircular), with enclosed fenestra laterale accessoria (**new term**).

Note.—See: Tiemeier (1950, 1953). Represents ossifications in the sclera, posterior to the equator and distinct from the anulus ossicularis sclerae, having formed in union around the nervus opticus. Preserved especially well in picid *Colaptes auritus* (BMNH 1977.81.25).

Os Supra-Surangulodentale (Supra-Tomiale)

0719. Os supra-surangulodentale (**new term**), status:

a. absent; **b.** present.

Os Suprajugale

0720. Os suprajugale, status:

a. absent; **b.** present.

Note.—Markedly developed in Sulidae, barely discernable in fully mature (synostotic) specimens of some Pelecaniformes; element typically ventral or processus orbitalis ossis lacrimale to fenestra antorbitalis, and distinct from tuberculum lacrimalis jugale, often synostotic rostrally with os maxillare.

Ossa Supraorbitalia

0721. Ossa supraorbitalia, status et numerus per latus (**unordered**):

a. absent;

b. present, typically single ossiculus attached by weak sutura or ligamentum to margo caudalis processi supraorbitalis ossis lacrimale;

c. present, typically several ossa per latus attached by weak suturae to form rima supraorbitalia.

Note.—See: Beddard (1898a: 137); Jollie (1977); Livezey (1998b: appendix A, character 90).

Os Lacrimopalatinum

0722. Os lacrimopalatinum, status et forma (**unordered**):
a. absent; **b.** present, sublinear;
c. present, angular.
Note.—Element in *Pelecanoides* vestigial, a small ossicula adherent to facies dorsolateralis palatini by ligamentum, suggestive that complete spiculate element represents apomorphic ligamentum palatinolacrimale ossificans (**emended term**). Os varies in status among Sphenisciformes.

Ossa Suturarum

0723. Ossa suturarum, status:
a. absent; **b.** present.
Note.—See: Baumel and Witmer (1993: annotation 78). Possibility exists that these ossa supernumeraria may occur in other avian groups but remain undetected in the absence of ontogenetic series.

Os Uncinatum

0724. Os (uncinatum) jugo-lacrimale, status:
a. absent; **b.** present.
Note.—See: Burton (1970); Livezey (1998b: appendix A, character 91). Elzanowski (pers. comm.) reported presence in three additional modern families: Laridae (probably a sesamoideum), Alcidae, and Accipitridae.

Os Jugo-Ectethmoidale

0725. Os (uncinatum) jugo-ectethmoidale, status:
a. absent; **b.** present.
Note.—See: Cracraft (1968a).

Os Ectopterygoideum

0726. Os ectopterygoideum, status:
a. present; **b.** absent.
Note.—Small element oriented laterad toward os jugale, considered homologous with os uncinatum of Aves by Elzanowski. See: Gauthier (1986: 13); Witmer and Martin (1987: character 6); Chatterjee (1991: character 20); Chiappe and Calvo (1994: appendix I, character 8); Chatterjee (1995: character 5); Chiappe (1995b: character 8); Elzanowski (1995: character N8); Sanz et al. (1995, 1997: character 8); Chiappe (1996b: character 8); Chiappe et al. (1996: appendix 1, character 8); Elzanowski and Wellnhofer (1996); Chiappe (2001a: appendix 1, character 11); Norell and Clarke (2001: appendix I, character 13), treated similarly by J. A. Clarke (2002: appendix I, character 13), J. A. Clarke and Norell (2002: appendix 2, character 13), and J. A. Clarke (2004: appendix 1, character 13); Chiappe (2002: appendix 20.2, character 11); Xu et al. (2002b); Zhou and Zhang (2002: appendix III, character 13); Ji et al. (2005: supplement, part I, character 13).

0727. Os ectopterygoideum, recessus (pneumaticus) dorsalis (**new term**), status:
a. absent; **b.** present.
Note.—See: Norell et al. (2001: appendix 1, character 63); J. M. Clark et al. (2002a: appendix 2.2, character 62); Xu (2002: suite II, character 244); Xu et al. (2002a: supplement, character 189); Currie et al. (2003: appendix, character 9); Hwang et al. (2004: supplement, character 61); Xu and Norell (2004: supplement, character 61).

0728. Os ectopterygoideum, recessus (pneumaticus) ventralis (**new term**) et ostium recessi, status, forma et situs (**unordered**):
a. absent, both recessus et ostium;
b. present, recessus broad and ventral;
c. present, recessus broad and ventral, element expanded with deep sulcus in facies medialis;
d. present, recessus expansive, penetrated through foramen in facies medialis;
x. noncomparable (Aves).
Note.—See: Barsbold (1983); Gauthier (1986: text character 54); Holtz (1994a: appendix 1, character 88); Russell and Dong (1994b [1993b]: list A, character 2); Sereno et al. (1994: footnote 12); Elzanowski (1995: 40) and Elzanowski and Wellnhofer (1996: 89) attributed recessus to "hooked jugal process" of os ectopterygoideum; Sereno et al. (1996: footnote 45, character 23); Sues (1997: appendix 1, character 7); J. D. Harris (1998: appendix 2, characters 34–35), pertaining to penetration into processus jugalis; Makovicky and Sues (1998: appendix 1, character 10); Sereno et al. (1998: footnote 22, character 57), including forma; Xu et al. (1999a: character 13, modified), with respect to "expansion with deep ventral pocket"; Azuma and Currie (2000: appendix 1, character 39); Currie and Carpenter (2000: appendix 1, character 36); Holtz (2000 [1998]: appendix I, character 81); Norell et al. (2001: appendix 1, character 62); J. M. Clark et al. (2002a: appendix 2.2, character 61); Maryanska et al. (2002: appendix 1, character 61); Xu (2002: suite II, character 181); Xu et al. (2002a: supplement, character 46); Xu et al. (2002b); Currie et al. (2003: appendix, character 10); Ji et al. (2003b); Rauhut (2003: character 67); Hwang et al. (2004: supplement, character 60); Xu and Norell (2004: supplement, character 60).

0729. Os ectopterygoideum, situs caudolateralis relative to os palatinum:
a. caudal; **b.** lateral;
x. noncomparable (Neornithes).
Note.—See: Sues (1997: appendix 1, character 20); Xu et al. (1999a: character 10, modified); Rauhut (2003: character 66).

0730. Os ectopterygoideum, situs lateroventrorostrodorsalis relative to os pterygoideum:
a. lateral or ventral; **b.** rostral or dorsal;
x. noncomparable, os ectopterygoideum absent (Neornithes).
Note.—See: Sereno and Novas (1992: appendix, character 12); Sereno et al. (1993: legend for fig. 3a); Maryanska et al. (2002: appendix 1, character 59).

0731. Ossa pterygoideum et ectopterygoideum, relative structural contributions *per se* to palatum osseum, pars caudalis (**ordered**):
a. major component;
b. principal component;
c. significant, but minor, component;
d. minor component, if included.
Note.—See: Witmer and Martin (1987); Currie (1995: appendix, character 16); Xu et al. (1999b: character 94); Xu et al. (2000: supplement, character 74). With few exceptions (e.g., McDowell 1978; Elzanowski 1999a–b), os ectopterygoideum has not been discerned in Neornithes.

Ossa Laryngeales, Tracheales, et Syringeales

Note.—These elements manifest significant variation in ossification, resulting in serial homologues being cartilagines or ossa. Originally considered from phylofunctional perspective for birds by Latham (1798) and Yarrell (1833). See Brown and Ward (1990).

Larynx

Note.—Elements of the larynx are delicate, rarely preserved, and best studied during dissection. Moreover, the skeleton of the larynx is typically listed under systema respiratorium, whereas these typically are examined during myological study. Included elements manifest potentially informative variation, but few if any have received attention adequate for analysis here. See: Watson (1883); White (1975), Bock (1978); Zweers et al. (1981); Zweers and Berkhoudt (1987); Hesse (1990: fig 12); Livezey (1998b: appendix A, character 99).

Trachea

Note.—See: King (1989); McLelland (1989), regarding larynx and trachea.

0732. Cartilagines (ossa aut anulae osseae) tracheales; forma generalis:
a. shallow, height significantly less than one-fourth of the diameter of single anulus;
b. deep, height significantly greater than one-fourth of the diameter of single anulus.
Note.—See: Archey (1941: fig. 13); (Livezey (1998b: appendix A, character 100).

0733. Cartilagines tracheales, septum trachealis dorsalis (**new term**), status et forma (**ordered**):
a. absent; **b.** present, incomplete;
c. present, complete, dividing trachea into divisiones tracheales dextrus et sinistris.
Note.—See: Watson (1883); Beddard (1898a); Beddard (1902a–c); Zeek (1951); Stephan (1979); McLelland (1989); King (1993: annotation 36). A jugum trachealis dorsalis (**new term**), resembling in some respects a precursor or vestigium of the septum, occurs in *Casuarius* (Forbes 1881a).

0734. Bulbus trachealis, status:
a. absent; **b.** present.
Note.—Variation within families and tribes frequent among Anseriformes. See: Livezey (1995b: appendix 1, character 21); Livezey (1996c: tracheal character 3). A structurally similar, but positionally distinct feature—bulbus tracheosyringealis—distinguishes some Anatidae (Livezey 1996a: appendix 1, character 79).

Syrinx

Note.—See: Cannell (1986) concerning ordinal evolutionary patterns of syringeal "complexity."

0735. Syrinx, status definitivum:
a. absent or cartilaginous;
b. present or osseus.
Note.—See: Köditz (1925); Warner (1972a–b); King (1989).

0736. Syrinx, tympanum, status definitivum:
a. present; **b.** absent.
Note.—See: Beddard (1903a–b), regarding Falconiformes; Oliver (1949: fig. 26); King (1989); Griffiths (1994a–b: appendix II, character 1 [1]); Livezey (1996a: appendix 1, character 80).

0737. Syrinx, bulla syringealis, status masculinus definitivum:
a. absent; **b.** present.
Note.—See: Livezey (1986: appendix 1, character 6), Raikow (1987: table 1; character 28), Livezey (1991: appendix 1, characters 129–149), Livezey (1995a: appendix 1, characters 14–15), Livezey (1995b: appendix 1, characters 21–28), Livezey (1995c: appendix II, character 40), Livezey (1996a: appendix 1, characters 81–84), Livezey (1996b: ap-

pendix 1, characters 40–43), Livezey (1996c: tracheal characters 1–6), Livezey (1997b: appendix 1, characters 12–15); Griffiths (1994a–b); Ames (1971, 1975), W. E. Lanyon (1984, 1986, 1988a–b), and Prum (1990, 1992).

0738. Syrinx, cartilagines syringeales, cartilagines tracheosyringeales et/aut broncheosyringeales, typus definitivum (**unordered**):

a. typus bronchialis—syrinx includes only cartilagines bronchiales, in which syringeal refinements occur bilaterally within the paired bronchi;

b. typus tracheobronchialis—syrinx includes both cartilagines tracheosyringeales et bronchosyringeales;

c. typus trachealis—syrinx includes only cartilagines tracheales;

Note.—Essentially trichotomous scheme for composition of syrinx originated by Huxley (1877) and refined by Gadow (1896). Cranial to syrinx, tracheal elements limited to cartilagines tracheales, and caudal to bifurcation of the trachea into bronchi the elements are cartilagines bronchiales; elements directly incorporated into bifurcation are termed cartilagines tracheobronchiales. See: Garrod (1879b); Forbes (1881a), regarding ratites; Beddard (1886d, 1888a), regarding Caprimulgiformes and *Balaeniceps*; J. Steinbacher (1937), regarding Galbulidae and Bucconidae; Oliver (1949: fig. 26); A. H. Miller (1965); Amadon (1970); Ames (1971, 1975); King (1989); S. M. Lanyon and Lanyon (1989); King (1993: annotation 37); Griffiths (1994a–b); Dyke and van Tuinen (2004: appendix 1, characters 109–110), regarding "fusion of A elements" among Falconiformes.

0739. Syrinx, cartilagines syringeales, pessulus, status:

a. absent or incomplete;

b. present and complete.

Note.—The pessulus is considered herein to be the median partition (cartilago aut os) at the division of the trachea into two bronchi (King 1993: annotation 43), independent of differentiation a syrinx (King 1989). See: Owen (1842); Garrod (1879a); Ames (1971, 1975), including report that Alaudidae lack a pessulus; King (1989), regarding absence of pessulus.

0740. Bronchi secundarii, cartilagines bronchiales, bronchi immediately caudal to syrinx, facies lateralis, forma:

a. essentially sublinear;

b. distinctly convex, defining distinct angulus lateralis and aspect (dorsoventral perspectives) of bilateral laminae angulares approximately perpendicular to trachea.

Note.—See: Wunderlich (1886 [1884]); Beddard (1898a).

Apparatus Hyobranchialis

Note.—Skeleton lingualis avium derives principally from elements of both the arcus hyoideus—Copulae I et II of H. J. Müller (1963)—et arcus branchialis (Goodrich 1958; H. J. Müller 1963; McLelland 1968). Important studies of this apparatus in birds include: Mivart (1895a); Beddard (1898a); Gröbbels (1922); Weymouth et al. (1964); Zweers (1974, 1982); Homberger (1986); Homberger and Meyers (1989); Tomlinson (2000). Comparative analysis is complicated by protracted and variable degrees of ossification of constituent elements in many taxa. Consequently, in the majority of hyobranchial characters we consider only osseous elements (ossa *sensu stricto*). In so doing, strictly cartilaginous elements (e.g., cartilagines post-epibranchiales) are not treated here, as thorough evaluations would require cleared-and-stained specimens of all exemplary taxa. Nomenclature largely follows Butendieck and Wissdorf (1982).

Apparatus hyobranchialis generalis

0741. Apparatus hyobranchialis generalis, entoglossum caudad to epibranchiales, forma in which ossae extremely thin, genuinely threadlike in aspect, status:

a. absent, elements variably thin but not threadlike;

b. present, elements extremely fine and typically flexible.

Note.—Although principally a feature of the cornu branchiale, this character is listed as an aspect of the apparatus because of its inherently comparative nature with more-rostral elements.

Os Paraglossum (Entoglossum)

0742. Ossiculae preparaglossae (**new term**), status:

a. absent; **b.** present.

Note.—Possibly homologous with partially ossified cartilagines pre-paraglossae.

0743. Os aut cartilago paraglossum (entoglossum), status:

a. absent entirely; **b.** present.

Note.—See: Burton (1984: figs. 25 and 26); Chu (1998: appendix 1, character 61); Livezey (1998b: appendix A, character 98). For ratites, consult: Mitchell (1894: fig. 7); Beddard (1898a); D. W. Thompson (1899); S. L. Olson and Feduccia (1980b: 60); Burton (1984: figs. 25 and 26); Homberger (1986: fig. 1). Bock and Bühler (1988) speculated conditions of poorly known, subfossil Aepyornithidae and Dinornithiformes.

0744. Os paraglossum (entoglossum), corpus, enclosed (i.e., circumlimited) perforatum—fovea aut foramen medialis entoglossae (**new term**)—status et forma (**unordered**):
a. absent; **b.** present, fovea;
c. present, foramen;
x. noncomparable where *ossa* entoglossae absent (see character status).
Note.—See: Mitchell (1894: fig. 7); Burton (1974a: fig. 28); Burton (1984: figs. 25 and 26); Livezey (1997a: appendix 1, character 55; *corrigenda*, Livezey 1998a).

Os Basihyale (Basibranchiale)

Note.—See: Bock and Morony (1978b) regarding purportedly neomorphic ossa preglossae in *Passer*.

0745. Os basihyale (basibranchiale) rostrale, length relative to that of os ceratobranchiale:
a. distinctly less; **b.** subequal.
Note.—See: Burton (1984: figs. 25 and 26).

0746. Os basihyale (basibranchiale) rostrale, forma marginalis (dorsal perspective) rhomboid with os urohyale joined at vertex caudalis and two margines caudales slightly concave, status:
a. absent; **b.** present.
Note.—A diversity or continuum of shape comprise state "a," including triangular, subrectangular, and narrow-rodular.

0747. Os basihyale (basibranchiale) rostrale, forma corporis strongly bilaterally compressed, markedly deeper than wide, status:
a. absent; **b.** present.

0748. Os basihyale (basibranchiale) rostrale, forma in which margines laterales are distinctly rounded throughout their lengths, and facies dorsalis is characterized by torus-shaped concavitas, status:
a. absent; **b.** present.

0749. Os basihyale (basibranchiale) rostrale, forma generalis (dorsal perspective) dorsoventrally compressed and triangular, facies dorsalis concave, and possessing one or more foramina pneumatica, status:
a. absent; **b.** present.
Note.—With possible exception of Anhimidae, the Pelecanidae possess most pneumatic os basibranchiale among Neornithes.

0750. Os basihyale (basibranchiale) rostrale, facies dorsalis, crista (dorsalis) dorsomedialis (**new term**), status:
a. absent; **b.** present.
Note.—Crista dorsalis herein restricted to conformations in which elongate fossae bilaterally define crista medialis on facies dorsalis, resulting in cruciate element in planum transversus. See: Butendieck and Wissdorf (1982), regarding "crista dorsalis"; Homberger and Meyers (1989), regarding "[crista] m. stylohyoideus"; Hughes (2000: appendix 2, character 55), under "os basibranchiale rostrale."

0751. Os basihyale (basibranchiale) rostrale, facies ventralis, crista (ventromedialis) ventralis (**new term**), status:
a. absent; **b.** present.
Note.—Crista ventromedialis (**new term**) herein restricted to conformations in which elongate fossae bilaterally define crista medialis on facies ventralis, resulting in cruciate element in planum transversus.

0752. Os basihyale (basibranchiale) rostrale, crista dorsalis, terminus rostralis, recessus dorsale basihyalis (**new term**), status:
a. absent;
b. present, moderately elongate, terminus rostralis occluded.
Note.—Autapomorphy of Phoenicopteridae of unknown function.

0753. Os basihyale (basibranchiale) rostrale, facies articularis rostralis, forma:
a. unelaborated, variably distinct but poorly differentiated from corpus basibranchialis;
b. strongly differentiated, dorsoventrally elongate, ventrorostrally angled, sharply bifacetate.
Note.—Ardeidae and Scopidae partially resemble apomorphic state, but are undistinguished in dorsoventral elongation.

0754. Os basihyale (basibranchiale) rostrale, facies articularis caudalis, situs dorsoventralis relative to extremitates rostrales ceratobranchiales:
a. coplanar or slightly ventral;
b. distinctly dorsal, junctura basibranchio-urobranchiale (**new term**) curved, dorsally convex.

0755. Os basihyale (basibranchiale) rostrale, processus et arcus parahyalis, status (**unordered**):
a. absent;
b. present, as bilateral, variably elongate, rostrally oriented processes;
c. present, as bilateral lamina in which dorsal elevation of pair meet mediad to compose an arcus parahyalis.
Note.—See: Beddard (1898a: figs. 131–133); Homberger (1986); Baumel and Witmer (1993: annotation 81).

0756. Os basihyale (basibranchiale) rostrale, crista lateralis basihyalis, status et forma (**ordered**):
a. absent;
b. present, primarily coplanar with corpus or lateral;
c. present, moderately dorsolateral;
d. present, strongly laterodorsal.
Note.—Beddard (1898a: figs. 131–133). Crista lateralis basihyalis derived from Homberger (1986), and here limited to laminae extending laterad to junctura basihyalo-ceratohyalis.

Os Urohyale (Basibranchiale Caudale)

0757. Os urohyale (basibranchiale caudale), status:
a. present;
b. absent or indeterminate angularity, accentuated by bilateral juxtaposition of extremitates rostrales ceratobranchiales medially.
Note.—Absence of ossa urohyales in Rheidae after Tomlinson (2000).

0758. Os urohyale (basibranchiale caudale), junctura basihylo-urohyalis (**new term**), typus:
a. syndesmosis, limitus ossium discernable;
b. synostosis, limitus ossium (e.g., sutura) indiscernable;
x. noncomparable where os urohyale absent (see character status).

0759. Os urohyale (basibranchiale caudale), forma as angular, extremely abbreviate tuberositas well separated bilaterally from ossa ceratobranchiales, status:
a. absent, element typically elongate, proximate to ossa ceratobranchiales;
b. present.

0760. Os urohyale (basibranchiale caudale) relative to os (cartilago) basihyale (basibranchiale rostrale), forma lateromedialis:
a. width of rostral segment distinctly wider than caudal segment;
b. widths approximately uniform;
x. noncomparable where element cartilaginous or rudimentary (see character status).
Note.—See: Burton (1984: figs. 25 and 26).

0761. Os urohyale (basibranchiale caudale), facies ventralis, nodulus (sesamoideum ligamenti noduloceratobranchiale), status:
a. absent; **b.** present.
Note.—See: Beddard (1898a: figs. 131–133); Butendieck and Wissdorf (1982: 77); Homberger (1986).

Cornu branchiale, os ceratobranchiale

0762. Cornu branchiale, os ceratobranchiale, forma:
a. essentially columnar;
b. distinctly laminar, dorsally concave.

Cornu branchiale, os (cartilago) epibranchiale

0763. Cornu branchiale, os epibranchiale, length:
a. typical, broadly comparable in length with os (cartilago) ceratobranchiale;
b. elongate, distinctly longer than os (cartilago) ceratobranchiale.
Note.—See: Burton (1984: figs. 25 and 26).

0764. Cornu branchiale, os epibranchiale, forma *sensu* curvature *in situ*:
a. essentially linear or subtly curved;
b. distinctly dorsomedially curved.
Note.—See: Burton (1984: figs. 25 and 26).

0765. Cornu branchiale, os (cartilago) epibranchiale, status ossis:
a. present, ossa in adults;
b. absent, cartilago only.
Note.—See: Tomlinson (2000).

Columna Vertebralis

Note.—An articulatio atlanto-occipitalis, mediated by a fibrocartilago atlantis and stabilized by a ligamentum apicis dentis (Goebloed 1958), is universal to Avialae, differing slightly as the form of the most-cranial vertebra varies (Weisgram and Zweers 1987). In an attempt to preempt nomenclatural confusion, this section is preceded by several comments concerning traditional but informal terminology and ontogenetic insights regarding homologies of the vertebrae and the columna vertebralis among Archosauria. Restriction of arguments of homology to the Archosauria is adequate for reconstructions among avialians, and numerous evolutionary derivations among Reptilia—e.g., arcus *vs.* corpus vertebrae, and respective articulationes (*i*) intervertebrales (inter-zygophysiales *vs.* inter-corporales) and intravertebrales (pleurocentra *vs.* intercentra), and (*ii*) vertebro-costales (costo-arcuales *vs.* costo-transversaria)—and their invariant avian homologues are rendered topically obsolete by apomorphy (Romer 1956; Romanoff 1960: fig. 350; Hammouda 1980). Aspects of the columna vertebralis avium were considered by Verheyen (1960g) and detailed by R. Tucker (1964a–b).

Among recent phylogenetic works treating Mesozoic taxa, the unpublished thesis by Makovicky (1995), related collaborative publication by Makovicky and Sues (1998), and recent compilations by Holtz (2000 [1998]) and Rauhut (2003) include the majority of analytical assessments of vertebral morphology informative for Theropoda. Information on vertebral pneumaticity in Sauropoda is provided by Wedel (2003). An important, well-illustrated work on the columna vertebralis of an anatid (Landolt and Zweers 1985) serves as a modern atlas to the nomenclature given by Baumel and Witmer (1993), and also provides a tabular synonymy of vertebral nomenclature relating ICAAN terminology with those adopted by Boas (1929), Zusi and Storer (1969), Baumel (1979a–b), and Zusi and Bentz (1984).

Columna vertebralis comprises numerous, variably nested cases of serial homology, which often combine problems of coding with important emergent patterns critical to an understanding of the component elements. For example, the evolutionary trend for the reduction in size and articulationes liberae of costae cervicales is important, and combines a tendency for cranial elements (e.g., atlas et axis) to undergo reduction of associated costae and a change from articulationes to synostoses costales before caudal vertebrae cervicales, with a large-scale evolutionary trend among Aves toward a reduction in size and increased replacement of articulationes with synostoses (e.g., ratites *vs.* passeriforms). In this specific serial character complex, most changes are treated as separate characters and (to an essential extent) considered separately by segments of the columna vertebralis showing fundamental structural or functional differences (e.g., axis, atlas, sectiones cervicales communis I–III, etc.); taken together, these were intended to summarize in detail a series of variably related trends across a serial set of structures (e.g., changes in juncturae vertebracostales, processes transversariae, et tuberculum costae). Among the most problematic character complexes of the columna vertebralis, both with respect to primary assessments and serial homology, is skeletal pneumaticity; this topic has been examined in Dinosauria by several recent works (Britt 1993; Witmer 1997; Wedel 2003), as well as in Anseriformes (O'Connor 2004).

The term "intercentrum" was applied to basal Reptilia for a considerable period (Romer 1956), and the term appeared in discussions of descendant lineages (e.g., modern Archosauria, Aves) in 19th-century works (e.g., Mivart 1874, 1878; Beddard 1897a, 1898a) and persists in a minority of recent studies (e.g., Ostrom 1976a; Gauthier 1986; Holtz 2000 [1998]). True intercentra are lacking in Archosauria (Benton 1990a)—as free or synostotic with adjacent vertebrae—except in the highly specialized axis and atlas or as "chevron bones" in some vertebrae caudales, in which cases these are termed **processes haemales**. Some authorities refer to "chevron bones" as "fused intercentra." In most other parts of the columna vertebralis, the intercentrum is replaced by the "centrum" in Aves and many allied archosaurs; the definitive "centrum" is termed the **corpus vertebrae**.

The prevalence of traditional anatomical nomenclature (Boas 1929) as applied to the columna vertebralis makes a synonymy advisable (Komárek 1970; Zweers et al. 1987; Baumel and Witmer 1993), illustrations of many being presented by Ostrom (1969). In the following list, the second term or set of terms (set in boldface) are those recommended by the *Nomina* (Baumel and Witmer 1993) and used herein, with reference to Landolt and Zweers (1985) for detailed illustrations:

- "catapophysis"—**processus caroticus**;
- "centrum"—**corpus vertebrae**;
- "chevron bone," possibly "fused intercentrum" or "hypocentrum"—**processus ventralis chevroniformis**;
- "diapophysis"—**processus transversus, including facies articulares costotransversaria**;
- "foramen costotransversarium"—**foramen transversarium**;
- "hypapophysis"—**processus ventralis corporis**;
- "hyperapophysis" or "epipophysis"—**torus dorsalis**;
- "incisura arcualis"—**lacuna interzygapophysialis**;
- "lamina ventralis"—**ansa costotransversaria**;
- "neurapophysis"—**processus (crista) spinosus (dorsalis)**;
- "odontoid process" or "processus odontoideus" of axis—**dens axis**;
- "parapophysis"—**eminentia costolateralis** (for capitulum costae on corpus vertebrae cervicales et thoracicae);
- "pleurapophysis"—**processus costalis**;
- "prezygapophysis" or "hypantra"—**zygapophysis cranialis**;
- "postzygapophysis" or "hyposphene"—**zygapophysis caudalis**;
- "processus inferolateralis"—**processus postlateralis**;
- "subvertebral canal"—**canalis caroticus cervicalis**;
- "ventral semi-ring"—**fossa condyloidea**.

Also of importance are the terms used to describe the forms of facies articulares or surfaces of contact between corpora of vertebrae (Romer 1956: fig. 117): (a) ***amphicoelous***—a cylindrical homologue of notochordal elements; (b) ***platycoelous***—simple cylinders with slight hollowing of ends; (c) ***amphiplatyan***—cylindrical, fully ossified elements with both facies articulares corporales flat; (d) ***procoelous***—cylindrical, cranial ends concave and caudal ends convex; (e) ***opisthocoelous***—cylinders cranially convex and caudally concave; and (f) ***heterocoelous***—in which elements have counter-sellariform facies articulares cranialis et caudalis that constrain rotation of vertebrae about axis majoris corporis.

In addition, we formalized the functional subsegments of the columna vertebralis cervici of Boas (1929)—subsequently employed by Zusi (1962) and Zusi and Storer (1969)—by reference to vertebrae cervicales speciales (atlas et axis) and vertebrae cervicales communis (latter subdivided into sectiones I, II, et III). Classical studies provided some information (Mivart 1874, 1878), but were extremely limited in taxonomic diversity. It was necessary to propose new formal names for a number of characters, unfortunately, because a recent nomenclature for lamina vertebrae cervicales of Sauropoda (J. A. Wilson 1999) was of little assistance in large part because of the highly specialized columnae vertebrales of this group.

See: Gegenbaur (1861); Boas (1894, 1929, 1934); Beddard (1897a); W. K. Parker (1888b); Piiper (1928).

0766. Columna vertebralis, length relative to that of skull:

a. less than twice as long as skull;

b. equal to or more than twice as long as skull.

Note.—See: Pérez-Moreno et al. (1994: legend for fig. 3, character 12); Holtz (2000 [1998]: appendix I, character 136).

Vertebrae Cervicales

0767. Vertebrae cervicales communis et thoracicae, serial *Gestalt* of arcus vertebrae, lamina dorsalis arcus (especially areae ligamentorum elastici cranialis et caudalis), et zygapophysis caudalis, crista transverso-obliqua:

a. areae ligamentorum elastici cranialis et caudalis distinct and concave throughout series (least prominent in vertebrae cervicales, sectio II), attaining maximal dorsal prominence and biconcavity of areae in vertebrae cervicales, sectio III, wherein the cristae transverso-obliquae rise precipitously, meeting medially to form a triangular, distinctly bilaminate enclosure;

b. areae ligamentorum elastici cranialis et caudalis indistinct and at most weakly concave throughout series, often obsolete in vertebrae cervicales, section II.

Note.—See: G. Mayr and Ericson (2004: appendix I, character 32), regarding status of crista transverso-obliqua in sectio III of vertebrae cervicales; Tsuihiji (2004), regarding system of ligamenta of vertebrae cervicales in Sauropoda.

Vertebrae cervicales speciales

Note.—For purposes of brevity, three enantiornithine taxa (*Iberomesornis*, *Concornis*, *Eoalulavis*) lacking both axis and atlas implicitly may be included among those taxa for which characters of these elements were of undetermined state, unless otherwise indicated explicitly.

0768. Proatlas, arcus proatlantis (**new term**), status:

a. present; **b.** absent.

Note.—See: Sereno and Novas (1994 [1993]); Madsen et al. (1995); Brochu (2003). Retention of these comparatively minute elements difficult to establish, including possible variation in ossification, rendering uncertain node at which synapomorphic loss occurred.

0769. Atlas, corpus atlantis, depressiones aut recessus pneumaticus, status et typus (**ordered**):

a. absent;

b. present, as jugum or shallow recessus in homologous *situs*;

c. present, as depressio.

Note.—This character negates statement by Baumel and Witmer (1993: 89) that the avian atlas is apneumatic.

0770. Atlas, corpus atlantis, fossa condyloidea, relative size:

a. small (width of vertebra at least three times the height of fossa), incisura large;

b. large (width of vertebra no more than 2.5 times as great as height of fossa), incisura small.

Note.—See: Gauthier (1986); Holtz (2000 [1998]: appendix I, character 137), in reference to occipital fossa and odontoid notch of "first intercentrum."

0771. Atlas, corpus atlantis, fossa condyloidea, incisura aut foramen fossae (including much of facies articularis dentalis aut axialis), status et typus (**ordered**):

a. present, rima dorsalis incomplete, variably broad incisura fossae marked by variably prominent, paired, tuberositas ligamenti transversi;

b. present, rima dorsalis essentially complete, very narrow, shallow incisura fossae marked by comparatively minute, paired, tuberositas ligamenti transversi;

c. absent, rima dorsalis entire, tuberositas ligamenti transversi abutting and forming continuous rima, whereas enclosed corpus perforate, forming foramen fossae;

d. absent, rima dorsalis entire, rima dorsalis and lamina of fossa essentially complete, lacking foramen fossae.

Note.—Fragile, showing considerable variation, and in life the articulatio atlantico-occipitalis is covered by intervening fibrocartilago atlantis.

See: Berger (1960: table 4, character 5), contrasting Cuculidae with Musophagidae; Raikow (1982: character 2), regarding typical possession of foramen fossae of corpus atlantis in Passeriformes; Chu (1998: appendix 1, character 65), regarding feature in modern larids; Hughes (2000: appendix 2, character 126), regarding modern cuculiforms; G. Mayr (2003b: appendix I, character 7); G. Mayr et al. (2003: appendix 1, character 23); G. Mayr and Ericson (2004: appendix I, character 23).

0772. Atlas, corpus atlantis, processus ventralis corporis, status et forma modalis (**unordered**):

a. present, variably prominent, represented as shallow shelf, bifurcate or tripartite flange, or single medial processus;

b. present, represented by prominent, caudally extensive (craniocaudal depth significantly exceeding that of arcus atlantis), dorsoventrally compressed, bilaterally convex, typically carinate lamina;

c. absent.

Note.—See: G. Mayr and Clarke (2003: appendix A, character 46); Dyke and van Tuinen (2004: appendix 1, character 28); G. Mayr (2004a: appendix 1, character 26); Ji et al. (2005: supplement, part I, character 202), in part.

0773. Atlas, arcus atlantis et corpus atlantis, synchondrosis, status:

a. absent, atlas tripartite, comprising basal corpus (centrum) ventrally and bilateral "neural arches";

b. present, atlas an uninterrupted ring, bilateral synchondrosis between arcus and corpus.

Note.—Ontogenetic study reveals that corpus atlantis conceals caudal deficiency in which intercentrum and (pleuro)centrum atlantis are co-opted by the adjacent axis, the transferred elements forming much of the dens or "odontoid process" of the axis (Gilmore 1907; Romer 1956); sutura delimiting the primordial centrum atlantis from that of axis is discernable in some archosaurs (e.g., *Caiman*). Chiappe (1992) inferred that retention of "unfused atlantal hemiarches" is primitive for birds, although Chiappe and Walker (2002: 247) concluded that the asynostotic condition of the atlas of the hatchling from Catalan (Sanz et al. 1997) reflected immaturity. Nevertheless, despite rarity of preservation of the atlas, it remains that the latter Euenantiornithine, *Archaeopteryx* (Wellnhofer 1974), and *Shuvuuia* (Chiappe et al. 2002) retained an asynostotic atlas. The condition for *Confuciusornis* is not clear, having been described only as "ring-shaped" by Chiappe et al. (1999: 25). Evidence available for *Ichthyornis* precluded a determination by J. A. Clarke (2004: 85), but Marsh (1880: plate XXVII) depicted it as synchondrotic, contrary to Chiappe (2002: appendix). Photographs of *Avimimus* (Vickers-Rich et al. 2002) are inconclusive. Intraspecific variation in some Neornithes (e.g., *Casuarius*, Anatidae) suggests that protracted skeletal development can result in variation in final closure of sutura interarcualis atlantis (Brochu 2003).

See: Chiappe et al. (1999); Chiappe (2001a: appendix 1, character 29); Chiappe (2002: appendix 20.2, character 29), with respect to "atlantal hemiarches"; Chiappe and Lacasa-Ruiz (2002), regarding *Noguerornis*; Chiappe and Walker (2002); J. A. Clarke (2004).

0774. Atlas et axis, arcus atlantis et arcus axis, respectively, ansa costotransversaria, modally delimiting foramina transversaria, status (**ordered**):

a. present and complete in **both atlas and axis**, continued caudally in other vertebrae cervicales;

b. absent in atlas, present and complete in **axis and other vertebrae** cervicales;

c. absent in atlas (arcus atlantis rarely vestigial) et axis, but present in **other vertebrae** cervicales;

d. present and complete in **atlas and other vertebrae** cervicales, absent in axis;

x. noncomparable (Dromornithidae).

Note.—Processus caudolateralis, listed in Butendieck (1980), Butendieck and Wissdorf (1981), and Butendieck et al. (1981), but not Baumel and Witmer (1993), is perhaps limited to atlas and probably homologous to ventral vestigium of the ansa costotransversaria or that of the capitulum costalis atlanticus. Depth of the incisura arcus caudalis atlantis is a parallel reflection of the adjacent "processus caudolateralis." A "complete" foramen transversarium reflects the presence of an ossified ansa costotransversaria in adults; together the foramina transversaria of the column vertebralis compose the canalis vertebrarterialis (bilaterally paired), a homology confirmed by common passages of arteriae vertebrales ascendens et descendens, "paravertebral autonomic nerve trunk," as well as position. Ossification of the ansae vertebrales occurs relatively late in ontogeny (T. J. Parker 1892; Piiper 1928; Romanoff 1960), timing consistent with variation evident both inter- and intraspecifically.

In Dromornithidae, adults possess single ostium cranialis of foramen transversaria atlantis continued caudally to the paired foramina transversaria axiales by two, bilateral, obliquely (caudoventrally) oriented ostia caudales for foramen transversarium atlantis (coded as separate state).

Dromornithidae unique and treated as not comparable; atlas possesses foramina obliquely entering foramen vertebrale giving appearance of single, common, dorsal foramen cranially, but at margo caudalis atlantis bilateral foramina distinct and respectively serve two bilateral foramina of axis.

See: Molnar et al. (1990: fig. 6.16); Chu (1998: appendix 1, character 66); G. Mayr and Clarke (2003: appendix A, character 47); Dyke and van Tuinen (2004: appendix 1, character 29); G. Mayr (2004a: appendix 1, character 27); G. Mayr and Ericson (2004: appendix I, character 24).

0775. Atlas, arcus atlantis, lamina lateralis, lacuna subarcualis (**new term**), status:

a. present, a prominent depressio on facies lateralis ventral to ansa transversarium;

b. absent.

0776. Atlas, arcus atlantis, zygapophysis caudalis, comparatively extreme caudal extension with facies articularis possessing significant dorsal prominence, acting to restrict ventral flexion of atlas relative to axis, status:

a. absent or obsolete;

b. present, variably extensive, laterodorsally positioned.

0777. Atlas, arcus atlantis (lateral perspective), processus spinosus, status (**unordered**):

a. present, true processus not triangular in shape;

b. present, true triangular processus;

c. absent, including those possessing "lamina dorsalis" or rounded jugum or subellipsoid eminentia.

Note.—See: Currie and Zhao (1994a [1993a]); J. D. Harris (1998: appendix 2, character 49); Azuma and Currie (2000: appendix 1, character 9); Currie and Carpenter (2000: appendix 1, character 43). Prominent and complex in some Sauropoda, e.g., *Stegosaurus*.

0778. Axis, corpus axis, processus odontoideus axis, "intercentrum," angulus with respect to axis craniocaudalis corpus et facies ventralis corporis:

a. subparallel; **b.** angled dorsally;

x. noncomparable by absence of intercentra (Neornithes).

Note.—Axis is synonymous with "epistropheus" of classical literature. See: Gauthier (1986: 14, unindexed synapomorphy of Aves); J. D. Harris (1998: appendix 2, character 50); Currie and Carpenter (2000: appendix 1, character 44).

0779. Axis, corpus axis, facies articularis atlantica, forma:

a. broad, crescentic or subellipsoidal fossa;

b. slightly convex.

Note.—See: Holtz (2000 [1998]: appendix I, character 138), in reference to "second intercentrum cranial articulation with first intercentrum."

0780. Axis, corpus axis, facies articularis atlantica, foramen pneumaticum, status (**unordered**):

a. absent;

b. present, but indicated only by depressio et foramina et/aut pori;

c. present, conspicuous.

Note.—Whether the variably "reduced" state of Sulidae represents a rudimentum or vestigium is uncertain. The conformational details of articulatio atlantoaxialis are difficult to reconstruct from traditional osteological specimens in that several ligamenta—ligamenta transversum atlantis, medianum atlantoaxiale, et collaterale atlantoaxilae—and the capsula cartilaginis articulationis typically are not preserved.

0781. Axis, corpus axis, facies lateralis corporis, eminentia costolateralis, status (**ordered**):

a. present, prominent;

b. vestigial; **c.** absent.

Note.—See: Gauthier (1986); Holtz (1994a: appendix 1, character 9); Holtz (2000 [1998]: appendix I, character 142), regarding reduction of the "axial parapophysis" among Theropoda, upon which the provisional binary states of "prominent" and "reduced" were based.

0782. Axis, *corpus* axis, recessus lateralis pneumaticus axis (**new term**), status:

a. present; **b.** absent.

Note.—As with most characters of pneumaticity, variation may be observed in series of conspecifics. See: Gauthier (1986); Holtz (1994a: appendix 1, character 11); Holtz (1994a: appendix 1, characters 4 and 90); Makovicky and Sues (1998: appendix 1, character 36), concerning "pneumatic openings" in vertebrae cervicales in general; Holtz (2000 [1998]: appendix I, character 145), regarding loss of "pleurocoel" of axis specifically; Holtz (2000 [1998]: appendix I, character 148), regarding presence and numbers of postaxial cervical pleurocoels; Xu et al. (2002a: supplement, character 79); G. Mayr and Clarke (2003: appendix A, character 48); Rauhut (2003: character 91); Dyke and van Tuinen (2004: appendix 1, character 30).

0783. Axis, corpus axis, processus ventralis corporis, status (**unordered**):

a. present, represented by variably thick, rounded or subangular crista;

b. present, represented by a ventrally elongated, caudally deflected, rounded spina;

c. present, represented by a ventrally elongated, bilaterally compressed, craniocaudally restricted lamina;

d. obsolete;

e. "absent."

Note.—See: Currie and Zhao (1994a [1993a]); J. D. Harris (1998: appendix 2, character 51); Livezey (1998b: appendix A, character 105); Makovicky and Sues (1998: appendix 1, character 37); Azuma and Currie (2000: appendix 1, character 10); Currie and Carpenter (2000: appendix 1, character 45); Holtz (2000 [1998]: appendix I, character 146); Chiappe (2002: fig. 13.7); J. A. Clarke (2004).

0784. Axis, arcus axis, lamina dorsalis arcus, distinct bilateral aliform aspect ("spine tables"), status:

a. absent; **b.** present.

Note.—A minority of workers extend the term "spine tables" to elaborations of this kind in the axis, whereas most restrict "spine tables" to vertebrae other than vertebrae cervicales speciales. See: Gauthier (1986: text character 39); Holtz (1994a: appendix 1, character 112); Holtz (2000 [1998]: appendix I, character 139); Zhou and Zhang (2003: fig. 24C).

0785. Axis, arcus axis, processus transversus axis (**new term**), status:

a. present; **b.** absent.

Note.—See: Gauthier (1986); Rowe (1989); Holtz (1994a: appendix 1, character 10); Holtz (2000 [1998]: appendix I, character 143), regarding primitive presence of the "axial diapophysis" among Theropoda; Chiappe (2002: fig. 13.7F).

0786. Axis, arcus axis, ansa costotransversaria, foramen transversarium, status:
a. present; **b.** absent.
Note.—See: Livezey (1998b: appendix A, character 104); G. Mayr and Clarke (2003: appendix A, character 49); G. Mayr et al. (2003: appendix 1, character 24); Dyke and van Tuinen (2004: appendix 1, character 31).

0787. Axis, arcus axis, processus costalis axis, status:
a. present, typically vestigial, i.e., represented only by caput;
b. absent.
Note.—See: Chiappe (2002: fig. 13.7F); G. Mayr and Clarke (2003: appendix A, character 50); Dyke and van Tuinen (2004: appendix 1, character 32); G. Mayr (2004a: appendix 1, character 28).

0788. Axis, arcus axis, lamina dorsalis arcus, processus spinosus, status:
a. present, variably conformed, but not markedly elongate relative to zygapophyses caudales;
b. absent or obsolete.
Note.—See: Chiappe (2002: fig. 13.7F); J. A. Clarke (2004: fig. 33A).

0789. Axis, arcus axis, lamina dorsalis arcus, processus spinosus, forma:
a. craniocaudally elongate, bilaterally compressed lamina;
b. processus (if evident) craniocaudally reduced, rodular, spinous;
x. noncomparable (Dromornithidae).
Note.—See: Gauthier (1986: Tetanurae, character 39); Molnar et al. (1990); Sereno et al. (1996: footnote 45, character 7); J. D. Harris (1998: appendix 2, character 53); Makovicky and Sues (1998: appendix 1, character 31); Currie and Carpenter (2000: appendix 1, character 47); Holtz (2000 [1998]: appendix I, character 140); Norell et al. (2001: appendix 1, character 96); J. M. Clark et al. (2002a: appendix 2.2, character 97); Xu (2002: suite II, character 128); Xu et al. (2002a: supplement, character 73); Rauhut (2003: character 93); Hwang et al. (2004: supplement, character 94); Xu and Norell (2004: supplement, character 94); Ji et al. (2005: supplement, part I, character 202).

0790. Axis, arcus axis, lamina dorsalis arcus, processus spinosus, margo craniodorsalis (lateral perspective), forma:
a. concave; **b.** linear or convex.
Note.—See: J. D. Harris (1998: appendix 2, character 54); Makovicky and Sues (1998: appendix 1, character 32); Holtz (2000 [1998]: appendix I, character 141).

0791. Axis, *arcus* axis, facies lateralis, foramen pneumaticum, status:
a. present; **b.** absent.
Note.—Distinct, at least in part, from characterization of recessus lateralis pneumaticus axis. See: Livezey (1998b: appendix A, character 107), ascertaining whether arcus et/aut corpus was distinguished.

0792. Axis, arcus axis, processus spinosus et zygapophysis caudalis, dorsal elevation on a common pedicel, status:
a. absent; **b.** present.

0793. Axis, arcus axis, zygapophysis caudalis, torus dorsalis ("axial epipophyses"), caudal prominence relative to margo caudalis of zygapophysis caudalis, status et forma (**ordered**):
a. absent;
b. present, small jugum, not extending caudad to zygapophysis caudalis;
c. present, great, extending caudad to zygapophysis caudalis.
Note.—See: Ostrom (1976a); Gauthier (1986: text character 69, modified); Novas (1994 [1993]: appendix, character 28), regarding lateral departure from midline; Russell and Dong (1994b [1993b]: list B, character 2); Chatterjee (1995: character 6, part); J. D. Harris (1998: appendix 2, character 52); Makovicky and Sues (1998: appendix 1, character 30); Currie and Carpenter (2000: appendix 1, character 46); Holtz (2000 [1998]: appendix I, character 144); Norell et al. (2000: appendix 1, character 26); Norell et al. (2001: appendix 1, character 95); J. M. Clark et al. (2002a: appendix 2.2, character 96); Xu (2002: suite II, character 127); Xu et al. (2002a: supplement, character 72); Rauhut (2003: character 92). Note that in some Sauropoda (e.g., *Stegosaurus*), the zygapophyses caudalis extend caudad to articulate with *two* vertebrae cervicales; Hwang et al. (2004: supplement, character 93); Xu and Norell (2004: supplement, character 93).

0794. Axis, arcus axis, zygapophysis caudalis, facies ventralis aut medialis, foramina pneumatica, status:
a. absent; **b.** present.

0795. Axis, arcus axis, arcus interzygopophysialis axis (**new term**), status:
a. absent; **b.** present.
Note.—See: G. Mayr and Clarke (2003: appendix A, character 51), limited to axis; Dyke and van Tuinen (2004: appendix 1, character 33).

0796. Axis, arcus axis, zygapophysis cranialis, status:
a. distinct;
b. obsolete, facies articularis atlantica structurally indistinguishable.
Note.—Significant intraspecific variation in some taxa. See: Livezey (1998b: appendix A, character 106).

0797. Axis, arcus axis, zygapophyses craniales, facies articularis, lateromedial position relative to that of respective zygopophyses caudales:

a. subequal; **b.** distinctly medial.

Note.—See: Benton (1990a: 20).

*Vertebrae cervicales communis (**new term**)*

0798. Vertebrae cervicales cunctes (speciales et communis), numerus modalis (**ordered**):

a. nine or fewer; **b.** ten to 12;
c. 13 or 14; **d.** 15 or 16;
e. 17 or more.

Note.—See: Mivart (1874, 1878); S. L. Olson and Feduccia (1980b: table 1, character 40); Thulborn (1984: 126–127, character 6); Poplin and Mourer-Chauviré (1985); Gauthier (1986: 13); Livezey (1986: appendix 1, character 21); Livezey (1989: table 1, character 21); Worthy (1989), for tally of presacral vertebrae in *Dinornis*; Holdaway (1991: appendix 5.1, character 272); Andors (1992); Livezey (1996a: appendix 1, character 16); Livezey (1996b: appendix 1, character 8); Livezey (1996c: character 1); Livezey (1998b: appendix A, character 103); J. A. Wilson and Sereno (1998: appendix, character 37), regarding Sauropoda; Hughes (2000: appendix 2, character 128); Zhou et al. (2000); Currie and Chen (2001: 1711), in reference to *Sinosauropteryx*; Ji et al. (2001), regarding approximately ten vertebrae cervicales in unnamed dromaeosaurid NGMC 91-A; Norell et al. (2001: appendix 1, character 94); J. M. Clark et al. (2002a: appendix 2.2, character 95); Maryanska et al. (2002: appendix 1, character 98); Xu (2002: suite II, character 126); Xu et al. (2002a: supplement, character 71); G. Mayr et al. (2003: appendix 1, character 26); Zhou and Zhang (2003); Hwang et al. (2004: supplement, character 92); G. Mayr (2004a: appendix 1, character 31), by number of "presacral vertebrae"; G. Mayr (2004d: appendix I, character 8), by number of "presacral vertebrae"; Xu and Norell (2004: supplement, character 92); G. Mayr (2005a: appendix 1, characters 8 and 12); G. Mayr (2005b: appendix A, character 12).

0799. Vertebrae cervicales speciales et communis, sectio I (together with a caudal element transitional to section II), numerus modalis (**ordered**):

a. three to four; **b.** five to six;
c. seven to eight; **d.** nine to ten.

Note.—Sequential pairs of primary tallies were combined to define states to reduce disproportionate influence of multistate characterizations. *Aepyornis* possessed approximately 13 vertebrae in sectiones II et III.

0800. Vertebrae cervicales communis (especially cranial elements), gross conformation of corpus vertebrae, facies articularis, forma *sensu* height relative to width within elements (**unordered**):

a. height and width subequal;

b. significantly wider than high;

c. wider than high and higher laterad than mediad, facies articularis reniform.

Note.—See: Gauthier (1986: text character 57); Holtz (1994a: appendix 1, character 82); Russell and Dong (1994a [1993a]: table 2, character 23); Russell and Dong (1994b [1993b]: list A, character 5); Makovicky (1995); Sereno et al. (1996); Sues (1997: appendix 1, character 22); J. D. Harris (1998: appendix 2, characters 56–57); Makovicky and Sues (1998: appendix 1, character 34); Xu et al. (1999a: character 33); Azuma and Currie (2000: appendix 1, character 26); Currie and Carpenter (2000: appendix 1, characters 49–50); De Klerk et al. (2000: 330, character 1); Holtz (2000 [1998]: appendix I, character 157); Norell et al. (2001: appendix 1, character 100); J. M. Clark et al. (2002a: appendix 2.2, character 101); Maryanska et al. (2002: appendix 1, character 100); Xu (2002: suite II, character 132); Xu et al. (2002a: supplement, character 77); Rauhut (2003: character 101); Hwang et al. (2004: supplement, character 98); Xu and Norell (2004: supplement, character 98).

0801. Vertebrae cervicales communis (sectio I), corpus vertebrae, length relative to diameter of facies articularis cranialis within elements (**ordered**):

a. former greater than four times latter;

b. former approximately twice latter;

c. former less than two times latter.

Note.—See: De Klerk et al. (2000: 330, character 2); Holtz (2000 [1998]: appendix I, character 160, revised); Murray and Vickers-Rich (2004: table 9, character 4).

0802. Vertebrae cervicales communis (especially sectio I, typically applicable throughout most or all vertebrae cervicales), corpus vertebrae, facies articularis cranialis et caudalis, typus (**ordered**):

a. "amphiplatyan"—both facies cranialis et caudalis sublaminar, amphicoelous and dorsoventrally compressed or weakly amphicoelous;

b. weak "opisthocoely"—facies cranialis heterocoelous, facies caudalis amphicoelous;

c. "bi-heterocoely"—both facies cranialis et caudalis heterocoelous, opposing facies mirrored examples of heterocoely.

Note.—Terms describe amphicoelous ("biconcave"), "bi-amphiplatous" (biplanar), "platycoelous" (both facies shallowly concave), and heterocoelous ("saddle-shaped," typically opposite in conformation on facies cranialis et caudalis). Ultimately optimal to subpartition state "b" into two ordered substates—(*i*) moderately developed, restricted to cranial elements, and (*ii*) well developed, extending into caudal elements.

See: Gauthier (1986: 13–14, unindexed synapomorphies of Ornithurae and Aves, respectively); Chiappe and Calvo (1994: appendix I, character 19); Russell and Dong (1994a [1993a]: table 2, character 24); Chatterjee (1995: character 6, part); Chiappe (1995a: legend for fig. 1); Chiappe (1995b: character 19); Sanz et al. (1995, 1997: character 18); Chiappe (1996b: character 17); Chiappe et al. (1996: appendix 1, character 17); Novas (1996: appendix, character A1), in which heterocoely evidently was equated with either "amphiplaty" or "opisthocoely"; Chiappe et al. (1998: character 14); Forster et al. (1998: supplement, character 27); J. D. Harris (1998: appendix 2, character 55); Ji et al. (1998: supplement, character 14); Chatterjee (1999: appendix II, character 33), concerning "anterior cervical vertebrae"; Azuma and Currie (2000: appendix 1, character 28); Currie and Carpenter (2000: appendix 1, character 49); Holtz (2000 [1998]: appendix I, character 147); Chiappe (2001a: appendix 1, character 31); Currie and Chen (2001); Ji et al. (2001), regarding unnamed dromaeosaurid NGMC 91-A; Norell and Clarke (2001: appendix I, character 52), treated similarly by J. A. Clarke (2002: appendix I, character 52), J. A. Clarke and Norell (2002: appendix 2, character 52), and J. A. Clarke (2004: appendix 1, character 52); Chiappe (2002: appendix 20.2, character 31); Zhou and Zhang (2002: appendix III, character 52); Ji et al. (2005: supplement, part I, character 52).

0803. Vertebrae cervicales communis, corpus vertebrae, facies articularis cranialis, ventrocaudal inclination relative to axis majoris of columna vertebralis, status:

a. inclination absent or only slight;
b. inclination strong.

Note.—See: Maryanska et al. (2002: appendix 1, character 101).

0804. Vertebrae cervicales communis (sectio I), corpus vertebrae, facies articularis caudalis, forma craniocaudalis relative to margo caudalis, arcus vertebrae, lamina dorsalis arcus:

a. former does not extend caudad to latter;
b. former extends caudad to latter.

Note.—See: Makovicky and Sues (1998: appendix 1, character 33); Holtz (2000 [1998]: appendix I, character 158); Norell et al. (2001: appendix 1, character 98); J. M. Clark et al. (2002a: appendix 2.2, character 99); Maryanska et al. (2002: appendix 1, character 102); Xu (2002: suite II, character 130); Hwang et al. (2004: supplement, character 96); Xu and Norell (2004: supplement, character 96).

0805. Vertebrae cervicales communis, sectio I, corpus vertebrae, facies ventralis corporis, crista (processus) ventralis corporis, status:

a. present, often a low jugum with a cranial spina;
b. absent.

Note.—"Hypapophysis" can be present in all or only some elements of sectio I, and may rarely extend to the cranialmost element of sectio II (e.g., *Oceanites*, Strigidae, Trogonidae, and *Momotus*).

See: Gauthier (1986); Makovicky (1995); J. D. Harris (1998: appendix 2, character 63); Makovicky and Sues (1998: appendix 1, character 42); Chiappe et al. (1999); Holtz (2000 [1998]: appendix I, character 166, modified); Rauhut (2003: character 97); J. A. Clarke (2004).

0806. Vertebrae cervicales communis (sectio I), arcus vertebrae, lamina dorsalis, arcus interzygopophysialis lateralis (**new term**), status:

a. absent on all elements; **b.** present.

Note.—In reference to arcus passing bilaterally and parallel to axis majoris corporis vertebrae. Significant interspecific variation occurs in the number of elements possessing an arcus and in the robustness of the arcus. Structure termed the *Seitenkante* by Boas (1929). See: G. Mayr and Clarke (2003: appendix A, character 52) and G. Mayr (2004a: appendix 1, character 29), in reference to arcus in vertebra cervicalis tertius, arcus described as bridging between processus transversus and processus articularis caudalis; Dyke and van Tuinen (2004: appendix 1, character 34); G. Mayr (2004b: appendix 1, character 24).

0807. Vertebrae cervicales communis, sectio I, corpus vertebrae, facies lateralis corporis, processus costalis, forma (**ordered**):

a. well developed; **b.** vestigial;
c. absent.

Note.—See: Payne and Risley (1976: character 16), regarding "posteriormost [postaxial cervical vertebrae] with no facets for bicipital rib" in Ardeidae; Azuma and Currie (2000: appendix 1, character 23), regarding "anteroventral process at base of anterior rib shafts" in Mesozoic taxa; Livezey (1998b: appendix A, character 108), sectio I of Zusi and Storer (1969); Maryanska et al. (2002: appendix 1, character 106), relating lengths of "cervical ribs" to those of respective "centra"; Ji et al. (2005: supplement, part I, character 202), relating widths of costae with those of respective vertebrae cervicales.

0808. Vertebrae cervicales communis (especially sectio I), arcus vertebrae, zygapophyses craniales, jugum laterodorsalis (**new term**), status:

a. absent; **b.** present.

Note.—This feature resembles a ligamentum ossificans, and passes from facies laterodorsalis of arcus transversarium to facies lateralis of basis for processus dorsalis; further distinguished by inclusion of foramen at lateroventral basis of jugum and lateromedially elongate, ellipsoidal foramen delimited by the jugum.

0809. Vertebrae cervicales communis (sectiones I–II), arcus vertebrae, lamina dorsalis arcus, processus spinosus, status et forma (**ordered**):

a. prominent throughout sectiones I and II, typically laminar and often extending caudally to margo dorsalis of arcus vertebrae;

b. prominent through sectio I and (perhaps) cranialmost elements of sectio II, but obsolete in middle and caudal elements of sectio II;

c. significantly reduced in prominence or obsolete in caudal elements of sectio I and throughout most or all of sectio II;

d. obsolete or absent through vertebrae cervicales.

Note.—See: Sanz and Bonaparte (1992: character 1), reporting poorly developed processes spinoses of the vertebrae cervicales in *Iberomesorni*s; Russell and Dong (1994a [1993a]: table 2, character 21); Russell and Dong (1994b [1993b]: troödontid character 12); Novas (1997: appendix, character 19); Novas and Puerta (1997), see identical characters in Novas (1997); Maryanska et al. (2002: appendix 1, character 103).

0810. Vertebrae cervicales communis (sectio I), arcus vertebrae, zygapophysis cranialis, transverse interzygapophysial distance relative to width of foramen vertebrale, forma:

a. former wider than latter;

b. former wider than and situated lateral to latter.

Note.—See: Makovicky (1995); Rauhut (2003: character 99).

0811. Vertebrae cervicales communis (especially sectiones I–II), arcus vertebrae, zygapophyses craniales, facies articularis, forma superficialis:

a. straight;

b. craniocaudally convex, flexed ventrad cranially.

Note.—See: Gauthier (1986); Holtz (1994a: appendix 1, character 78); Russell and Dong (1994b [1993b]: list A, character 4); Makovicky (1995); J. D. Harris (1998: appendix 2, character 60); Azuma and Currie (2000: appendix 1, character 27); Currie and Carpenter (2000: appendix 1, character 51); De Klerk et al. (2000: 330, character 4); Holtz (2000 [1998]: appendix I, character 153); Rauhut (2003: character 100).

0812. Vertebrae cervicales communis (sectio I), arcus vertebrae, zygapophysis caudalis, torus dorsalis (“epipophysis”), status et forma *sensu* caudal prominence relative to margo caudalis of zygapophysis caudalis (**ordered**):

a. absent or rudimentary;

b. present, moderately developed;

c. present, prominently developed, extending caudodorsad to zygapophysis caudalis.

Note.—See: Gauthier (1986); Rauhut (2003: character 102).

0813. Vertebrae cervicales communis, arcus vertebrae, zygapophysis caudalis, craniocaudal elongation (dorsal perspective) relative to facies articularis caudalis corpus, status:

a. elongate; **b.** truncate;

x. noncomparable by analogous hyperdevelopment of spinus dorsalis instead of elongation of torus dorsalis (*Carnotaurus*).

Note.—Elongation here shows significant relationship with body size (P. Currie, pers. comm). See: Holtz (1994a: appendix 1, character 85), regarding elongation of “anterior cervical zygapophyses”; Sanz et al. (1997: footnote 29, character *vi*), concerning elongation and distribution of such in vertebrae cervicales; Holtz (2000 [1998]: appendix I, character 152), regarding “cervical epipophyses” of Mesozoic taxa. See related aspects of torus dorsalis (“epipophysis”) encoded by: Azuma and Currie (2000: appendix 1, character 22); Holtz (2000 [1998]: appendix I, characters 149–152); G. Mayr and Clarke (2003: appendix A, character 54).

0814. Vertebrae cervicales communis (sectio I) et vertebrae thoracicae (cranial elements), arcus vertebrae, craniocaudal increase in dorsal prominence of zygapophysis caudalis and lateral orientation of corresponding facies articularis, ultimately apparently forming a spinus dorsalis with facies zygopophysialis on facies caudolateralis of spinus in caudalmost elements, status:

a. absent; **b.** present.

0815. Vertebrae cervicales communis, arcus vertebrae, zygapophysis caudalis, torus dorsalis relative to processus spinosus, forma dorsoventralis et dorsocaudalis:

a. shorter and caudolaterad;

b. taller and dorsolaterad.

Note.—See: Novas (1994 [1993]: appendix, character 34); Chiappe et al. (1999); Azuma and Currie (2000: appendix 1, character 22); Holtz (2000 [1998]: appendix I, characters 149–152); Maryanska et al. (2002: appendix 1, character 104); Xu et al. (2002a: supplement, character 75), pertaining to caudal extents of “anterior cervical centra” relative to those of “posterior extent of neural arch”; J. A. Clarke (2004).

0816. Vertebrae cervicales communis, caudalmost elements of sectio I and (especially) cranialmost elements of sectio II, arcus vertebrae, zygapophysis caudalis, torus dorsalis, forma:

a. indistinct boss or area tuberculata;

b. variably prominent tuberculum or alula.

Note.—Torus dorsalis typically located on crista transverso-obliqua, and is ancorae insertiorum mm. ascendentes. See: Ostrom (1976a); Sereno and Novas (1992: appendix, character 19), limited to “postaxial epipophyses”; Sereno et al. (1993: legend for fig. 3a); Novas (1994 [1993]: appendix, characters 9 and 34), regarding "postaxial epipophyses"; Russell and Dong (1994a [1993a]: table 2, character 22); Novas (1996: appendix, character A2); Novas (1997: appendix, character 20); Novas and Puerta (1997), see identical characters in Novas (1997); Azuma and Currie (2000: appendix 1, character 24), regarding "epipophyseal shape"; Holtz (2000 [1998]: appendix I, character 149), regarding "cervical epipophyses."

0817. Vertebrae cervicales communis (sectiones I et II), arcus vertebrae, zygapophysis caudalis, torus dorsalis, proximodistal position relative to that of respective facies articularis zygapophysialis caudalis:

a. distal; **b.** proximal or equally caudal.

Note.—See: Makovicky and Sues (1998: appendix 1, character 41); Holtz (2000 [1998]: appendix I, character 151), in reference to proximodistal position of "epipophyses" on "postzygapophyses" of cervical vertebrae; Chiappe (2001a: appendix 1, character 33); Norell et al. (2001: appendix 1, character 97); Chiappe (2002: appendix 20.2, character 33); J. M. Clark et al. (2002a: appendix 2.2, character 98); Xu (2002: suite I, character 78; suite II, character 129); Xu et al. (2002a: supplement, character 74); Hwang et al. (2004: supplement, character 95); Xu and Norell (2004: supplement, character 95).

0818. Vertebrae cervicales communis (sectiones I et II), corpus vertebrae, lamina dorsalis arcus, processus spinosus (arcus), dorsoventral and craniocaudal (axial) elongation (lateral perspective), forma:

a. dorsoventrally elongated and craniocaudally abbreviated;

b. dorsoventrally short and craniocaudally elongated;

x. noncomparable by obsolescence of processus (Dromornithidae).

Note.—See: Sanz and Bonaparte (1992); Novas (1996: appendix, character 18); Sues (1997: appendix 1, character 21); Forster et al. (1998: supplement, character 39); Makovicky and Sues (1998: appendix 1, character 39); Chatterjee (1999: appendix II, character 35); Xu et al. (1999a: character 31); Xu et al. (1999b: character 33); Holtz (2000 [1998]: appendix I, character 154); G. Mayr (2004a: appendix 1, character 30), specifying fourth through seventh vertebrae cervicales, and including ridgelike processus spinosus.

0819. Vertebrae cervicales communis (sectio II), corpus vertebrae, forma *sensu* relative breadth:

a. less than 20% broader than tall;

b. greater than 20% broader than tall.

Note.—See: Holtz (2000 [1998]: appendix I, character 161); apparently related character by Holtz (2000 [1998]: appendix I, character 159), the latter considered uninformative and excluded from analysis; G. Mayr and Ericson (2004: appendix I, character 28).

0820. Vertebrae cervicales communis (sectio II), corpus vertebrae, facies lateralis corporis, processus costalis, status (**ordered**):

a. present throughout sectio II;

b. present in cranial elements but absent in caudal elements of sectio II;

c. absent throughout sectio II.

Note.—See: Payne and Risley (1976: character 16), regarding "posteriormost [postaxial cervical vertebrae] with no facets for bicipital rib" in Ardeidae; also consider relative size of cranial part of processus costalis in nonavian theropods. The interpretation of the processes costales of vertebrae cervicales as vestigia costales is comparatively well documented (Sonies 1907; Hommes 1924; Komárek 1970); accordingly, see under "costae cervicales" regarding presence of true articulating ribs in association with vertebrae cervicales. Maryanska et al. (2002: appendix 1, character 106), related lengths of "cervical ribs" to those of respective "centra"; G. Mayr and Ericson (2004: appendix I, character 29).

0821. Vertebrae cervicales communis (sectio III), corpus vertebrae, facies lateralis corporis, processus costalis, status (**ordered**):

a. well developed, articulatio costovertebralis present;

b. vestigial, synostosis costovertebralis present;

c. absent, even vestigia (processes costales) lacking.

Note.—These synostotic vestigia or rudimentia of costae (Sonies 1907; Hommes 1924; Komárek 1970) typically grade into costae incompletae in articulatio *sensu stricto* with caudalmost vertebrae cervicales in most Aves (see under "costae incompletae"). With respect to nonavian theropods, see: Gauthier (1986: text character 55); Sanz and Bonaparte (1992: character 3); Russell and Dong (1994a [1993a]: table 2, character 25, part); Russell and Dong (1994b [1993b]: list A, character 3); Chiappe et al. (1996: appendix 1, character 73), regarding "cervical ribs fused to centra in adults"; Holtz (2000 [1998]: appendix I, character 165), regarding "cervical ribs" being "unfused to centra" *vs*. "fused to centra"; Maryanska et al. (2002: appendix 1, characters 105–106).

0822. Vertebrae cervicales communis, sectio II, corpus vertebrae, facies ventralis corporis, processus caroticus et/aut canalis caroticus cervicalis, status et forma (**ordered**):

a. absent;

b. present, variably prominent ventrad;

c. present, closely approach mediad or meet to form canalis caroticus cervicalis.

Note.—Situs insertii m. longus colli ventralis (Boas 1929; Zusi and Storer 1969; Landolt and Zweers 1985); this muscle may also insert on the processus costalis. Prominence of processus postlateralis is related in part to disappearance of processus costalis, and evidently is only present in subset of taxa lacking the latter. Where processus postlateralis present, homologous ancorae may extend to caudalmost elements of sectio I.

See: Beddard (1898a: 118); Chiappe et al. (1996: appendix 1, character 90), explicitly in reference to "carotid processes in intermediate cervicals"; Chiappe et al. (1998: character 15); Ji et al. (1998: supplement, character 15); Livezey (1998b: appendix A, character 109); Livezey (1998b: appendix A, character 112), for distribution of processus caroticus throughout cervical series, with emphasis on extension into series III; Makovicky and Sues (1998: appendix 1, character 40); Chatterjee (1999: appendix II, character 32), with respect to "carotid processes in intermediate cervicals"; Holtz (2000 [1998]: appendix I, character 162); Chiappe (2001a: appendix 1, character 32); Norell et al. (2001: appendix 1, character 99); Chiappe (2002: appendix 20.2, character 32); Xu et al. (2002a: supplement, character 76); J. M. Clark et al. (2002a: appendix 2.2, character 100); Xu (2002: suite II, character 131); G. Mayr (2003a: appendix I, character 21); Hwang et al. (2004: supplement, character 97); G. Mayr (2004b: appendix 1, character 25), pertaining to canalis in vertebrae cervicales 8–11; Xu and Norell (2004: supplement, character 97).

0823. Vertebrae cervicales communis, sectio II, corpus vertebrae, facies ventralis corporis, processus caroticus (if present), position relative to caput processus costalis:

a. directly medial to caput processus costalis;

b. cranial to caput processus costalis;

x. noncomparable, processus caroticus obsolete or absent (*Anhinga*).

0824. Vertebrae cervicales communis, sectio II, corpus vertebrae, facies ventralis corporis, sulcus caroticus cervicalis, status:

a. present; **b.** absent.

Note.—See: Novas (1996: appendix, character M2), regarding presence of sulcus caroticus in vertebrae cervicales generally.

0825. Vertebrae cervicales communis, sectio II, corpus vertebrae, marked elongation producing tubular aspect of elements and resulting in conspicuous heterogeneity of corpora of vertebrae cervicales and long, shallow concavitas laterales relative to the narrow lacunae interzygopophysiales, status:

a. absent; **b.** present.

Note.—See: Livezey (1998b: appendix A, character 111). Novas (1994 [1993]: appendix, character 48) described a similar dichotomy among basal Theropoda, the longest elements being either third through fifth or sixth through ninth in series.

0826. Vertebrae cervicales communis, sectio II, corpus et arcus vertebrae, ansa costotransversaria, processus costalis, lamina corporocostalis, status:

a. absent or poorly developed;

b. moderately or well developed.

Note.—In those taxa with well-developed lamina, the free spina costalis is correspondingly reduced.

0827. Vertebrae cervicales communis, sectio II, arcus vertebrae, lamina arcocostalis et foramina laterales arcus (**new term**), status (**unordered**):

a. absent;

b. present, incomplete, enclosing one or (uncommonly) two foramina—foramen(ina) laterale(s) arcus (**new term**)—and represented by a broad or narrow arcus;

c. present, complete or with one or more minute or irregular foramina, forming a continuous osseus lamina (lacking enclosed foramina) between ansa costotransversaria and arcus vertebrae.

Note.—See: Strauch (1978: character 33), reanalyzed by Björklund (1994: appendix) and Chu (1995); Chu (1998: appendix 1, character 64); Livezey (1998b: appendix A, character 110); G. Mayr and Clarke (2003: appendix A, character 53), pertaining to "osseous bridge from processus costalis to midsection of corpus vertebrae" of vertebrae cervicales VII–VIII; Dyke and van Tuinen (2004: appendix 1, character 35).

0828. Vertebrae cervicales communis (sectio II), arcus vertebrae, lamina arcocostalis, craniocaudal trend in which margo caudalis of lamina arcocostalis is reduced to narrow arcus septalis (**new term**), the latter passing from extremitas lateralis of margo caudalis of ansa arcotransversaria mediad to unite with corpus vertebralis, facies lateralis, effecting a transverse partitioning of margo costalis foraminis transversarium, status:

a. absent; **b.** present.

0829. Vertebrae cervicales communis, sectio II, arcus vertebrae, lamina arcocostalis, foramen transversarium caudalis (**new term**), delimited medially by corpus et arcus vertebrae, dorsolaterally by the lamina arcocostalis, and ventrally by the solum arcocostalis (**new term**) of variable craniocaudal breadth, status:

a. absent; **b.** present.

0830. Vertebrae cervicales communis, sectio II, arcus vertebrae, ansa costotransversaria, processus costalis, lamina supracostalis (**new term**), status:

a. absent or poorly developed;

b. moderately or well developed, and, in those taxa possessing both structures, fused with the ventral margin of the lamina arcocostalis.

Note.—In those taxa with well-developed lamina, the free spina costalis is correspondingly reduced. See: G. Mayr and Ericson (2004: appendix I, characters 25–27), in reference to "osseous bridge from processus transversus to midsection of corpus vertebrae."

0831. Vertebrae cervicales communis (sectio III), arcus vertebrae, lamina dorsalis arcus, processus spinosus, margo dorsalis, conformation as bilaterally paired lamina separated by narrow sulcus throughout length (i.e., neither caudally divergent nor having cranial, uniting tuberculum), status:
a. absent; **b.** present.

0832. Vertebrae cervicales communis (sectio III), arcus vertebrae, lamina dorsalis arcus, processus spinosus, margo dorsalis, bilaterally paired, osseus shelves having variable caudal extensions and undercut to varying degrees, "bi-alar" *Gestalten* not to be confused with structures derived from caudodorsally elevated zygapophyses caudales and associated torus dorsales, status:
a. absent; **b.** present.

Note.—Critical to the aspect of the feature is dorsal prominence of margo dorsalis of processus spinosus, which projects beyond the laminae laterales cranially, and the projection of the laminae beyond the former margo caudally. Possibly related to the insertiones of robust aponeuroses to processus spinosus. See: Makovicky and Sues (1998: appendix I, character 35); Holtz (2000 [1998]: appendix 1, character 155).

0833. Vertebrae cervicales communis (sectio II), arcus vertebrae, lamina dorsalis arcus (dorsal perspective), processus spinosus, craniocaudal elongation and position on arcus vertebrae, forma:
a. craniocaudally elongated;
b. craniocaudally truncated and centered on arcus vertebrae, resulting in cruciate ("X-shaped") aspect.

Note.—See: Norell et al. (2001: appendix 1, character 101); J. M. Clark et al. (2002a: appendix 2.2, character 102); Xu (2002: suite I, character 79; suite II, character 123); Xu et al. (2002a: supplement, character 78); Hwang et al. (2004: supplement, character 99); Xu and Norell (2004: supplement, character 99).

0834. Vertebrae cervicales communis, sectio III (vertebrae "cervicodorsales"), processus ventralis, dorsoventral dimension relative to that of associated corpus, facies articularis cranialis:
a. less than or equal to one-half;
b. greater than one-half.

Note.—See: Chiappe (2001a: appendix 1, character 34); Chiappe (2002: appendix 20.2, character 34).

0835. Vertebrae cervicales communis, sectio III (vertebrae "cervicodorsales") et cranialmost vertebrae thoracicae (dorsales), corpus vertebrae, facies articularis cranialis et caudalis, forma et typus:
a. amphiplatycoelous or platycoelous—both facies flat;
b. opisthocoelous—i.e., isomerously heterocoelous.

Note.—See: Gauthier (1986); Norell et al. (2001: appendix 1, character 103); J. M. Clark et al. (2002a: appendix 2.2, character 104); Xu (2002: suite II, character 135); Xu et al. (2002a: supplement, character 80); Rauhut (2003: character 95); Hwang et al. (2004: supplement, character 101); Xu and Norell (2004: supplement, character 101).

0836. Vertebrae cervicales communis, sectio III, corpus vertebrae, facies lateralis corporis, concavitas lateralis, recessus corporis caudolateralis (**new term**), status:
a. absent; **b.** present.

Note.—Site of foramen pneumaticum of some taxa, and where this is large (e.g., *Cochlearius*, *Sagittarius*, *Hemiprocne,* Apodidae, Alcedinidae, Meropidae) the aspect can be similar to the apneumatic recessus referred to here; e.g., *Puffinus* is similar in aspect, but "recessus" conspicuously pneumatic, and taxa *Pachyptila*, *Oceanites*, and *Pelecanoides* lack a true recessus and show only bilateral compression similar to the depressio ovalis of the vertebrae thoracicae (coded separately). See: Livezey (1998b: appendix A, character 113); Dyke et al. (2003: appendix 1, character 23).

0837. Vertebrae cervicales communis (sectio III), corpus vertebrae, facies lateralis corporis, eminentia costolateralis ("parapophyses"), craniocaudal position relative to arcus vertebrae, zygapophyses (processus articularis) craniales ("prezygapophyses"):
a. distinctly different;
b. approximately equal.

Note.—See: Chiappe et al. (1998: character 17); Ji et al. (1998: supplement, character 17), with respect to "cervico-dorsal vertebrae with parapophyses located at the same level as the prezygapophyses"; Chiappe (2001a: appendix 1, character 35); Chiappe (2002: appendix 20.2, character 35). All Theropoda have parapophyses, but these features differ in position, e.g., in *Sinosauropteryx* (Currie and Chen 2001: fig. 5a), *Mononykus* (Perle et al. 1994: fig. 5A), and Velociraptorinae (Norell and Makovicky 1999: fig. 20a).

0838. Vertebrae cervicales communis, sectio III (vertebrae "cervicodorsales"), processus (crista) ventralis corporis ("hypapophyses"), status:
a. absent or weakly developed;
b. present, well developed.

Note.—See: Gauthier (1986: text character 70); Sanz and Bonaparte (1992: character 4); Chiappe and Calvo (1994: appendix I, character 14); Russell and Dong (1994b [1993b]: list B, character 3); Chiappe (1995a: legend for fig. 1); Chiappe (1995b: character 14); Sanz et al. (1995, 1997: character 13); Chiappe (1996b: character 13); Chiappe et al. (1996: appendix 1, character 13); Novas (1996: appendix, character 67); Novas (1997: appendix, character 68);

Novas and Puerta (1997), see identical characters in Novas (1997); Sues (1997: appendix 1, character 24); Forster et al. (1998: supplement, character 28); Xu et al. (1999b: character 24); Currie and Carpenter (2000: appendix 1, character 54); Xu et al. (2000: supplement, character 16); Sereno (2001: table 1, character 13), regarding Alvarezsauridae; Maryanska et al. (2002: appendix 1, character 122). In paleontological literature, often referred to as hypapophyses of "cervicodorsal" vertebrae; treatment of this character as pertaining to the "anterior cervicals" by Chatterjee (1999: appendix II, character 32) considered *lapsus calami*.

0839. Vertebrae cervicales communis (sectio III) or vertebrae cervicothoracicae, corpus vertebrae, facies ventralis corporis, processus caroticus, status:

a. absent; **b.** present.

Note.—See: Norell et al. (2000: appendix 1, character 27).

0840. Vertebrae cervicales communis, corpus vertebrae, facies lateralis corporis, recessi laterales pneumatici *externum*, status et numerus modalis per latus (**unordered**):

a. absent; **b.** present, one;

c. present, two, arranged horizontally.

Note.—At this inclusive taxonomic scale, these recessi may not conform with *Gestalt* of traditionally recognized "pleurocoel." See: Ostrom (1976a); Gauthier (1986); Holtz (1994a: appendix 1, character 4), regarding gain of two pairs of "pleurocoel" in cervical vertebrae; Holtz (1994a: appendix 1, character 90); Makovicky (1995); Novas (1996: appendix, character M1); Sereno et al. (1996: footnote 45, characters 53–54); Sues (1997: appendix 1, character 23), with respect to presence of "two pneumatic openings" in "cervical vertebrae"; Chiappe et al. (1998: character 13); Forster et al. (1998: supplement, character 30), with respect to "pneumatic foramina piercing the centra of mid-anterior cervicals beyond the level of the parapophysis-diapophysis"; J. D. Harris (1998: appendix 2, character 61); Ji et al. (1998: supplement, character 13); Makovicky and Sues (1998: appendix 1, character 36), concerning "pneumatic openings" in vertebrae cervicales; J. A. Wilson and Sereno (1998: appendix, character 69), pertaining to shape and subdivision among Sauropoda; Currie and Carpenter (2000: appendix 1, character 52); Holtz (2000 [1998]: appendix I, character 148), regarding numbers of postaxial cervical pleurocoels; Chiappe (2001a: appendix 1, character 30); Norell et al. (2001: appendix 1, characters 102 and 107); Chiappe (2002: appendix 20.2, character 30); J. M. Clark et al. (2002a: appendix 2.2, characters 103 and 109); Maryanska et al. (2002: appendix 1, character 99); Xu (2002: suite I, characters 80–81; suite II, characters 134 and 139); Xu et al. (2002a: supplement, character 84); Rauhut (2003: characters 88–89); Hwang et al. (2004: characters 100 and 106); Xu and Norell (2004: supplement, characters 100 and 106).

0841. Vertebrae cervicales communis, corpus vertebrae, facies lateralis corporis, recessi laterales pneumatici, forma:

a. deep depressiones, large foramina;

b. small foramina aut pori.

Note.—See: Rauhut (2003: character 90).

0842. Vertebrae cervicales communis, corpus vertebrae, recesses pneumatici *internum*, status et typus (**ordered**):

a. absent; **b.** present, structure **camerate**;

c. present, structure **camellate**.

Note.—See: Britt (1993: 262–264); Azuma and Currie (2000: appendix 1, character 25), regarding pneumaticity (e.g., apneumatic, simple camerate, or complex camellate) "interior of centrum" of vertebrae cervicales; Rauhut (2003: character 96), pertaining to "interior pneumatic spaces in cervicals."

0843. Vertebrae cervicales communis (especially sectio III) et thoracicae (especially cranial elements), foramina pneumatica, status et forma exclusive of major recessi (**unordered**):

a. present as dorsolateral series in arcus vertebrae, typically located within foramen transversarium in vertebrae cervicales and at base of processus transversus in vertebrae thoracicae;

b. present as dorsal series in (*i*) arcus vertebrae and (*ii*) in lamina dorsalis arcus, foveae dorsales, and (*iii*) singly in area ligamentum elastici caudalis;

c. present both as (*i*) dorsolateral series in arcus vertebrae and (*ii*) ventrolateral series of facies lateralis in corpus vertebrae, indicative of extreme pneumaticity of columna vertebralis;

d. absent in all vertebrae cervicale et thoracicae.

Note.—Foveae dorsales (state "b") after term of Boas (1929) for paired depressiones at basis cristae dorsalis. *Aepyornis* has appearance of duplex conformation of dorsal of two "lateral" recessi pneumatica giving rise to dorsal recessi. See character for "recessus corporis caudolateralis," which in Charadriiformes appears to be (evidently) apneumatic homologue of large, relatively caudal foramina pneumatica in the *corpus* vertebrae, facies lateralis (most notably in vertebrae thoracicae, coded below) of some taxa. Dorsal foramina pneumatica are infrequent in some vertebrae of several taxa typified by dorsolateral and ventrolateral foramina (e.g., *Rhea*, *Chauna*). The area ligamentum elastici marks the situs of attachment of ligamenta elastici interlaminares that connect adjacent vertebrae, ligamenta especially well developed in vertebrae cervicales communis (sectio III) et thoracicae (Boas 1929). Additional ligamenta support the articulationes intervertebralia, including (Landolt and Zweers

1985; Zweers et al. 1987): ligamenta elastici interspinales (between adjacent processes dorsales), ligamenta interansale (margo caudalis of ansa costotransversaria of one vertebra with margo cranialis of ansa costotransversaria of following vertebra, largely limited to the vertebrae cervicales), ligamenta ventrolaterales (between crista ventrolateralis of one vertebra and processus caroticus of following vertebra), and ligamenta intercristales ventrales (between processes ventrales of vertebrae cervicales or thoracicae of some taxa).

See: J. D. Harris (1998: appendix 2, characters 58, 61–62); Makovicky and Sues (1998: appendix 1, character 36), concerning "pneumatic openings" in vertebrae cervicales; Azuma and Currie (2000: appendix 1, character 25); Currie and Carpenter (2000: appendix 1, character 53).

0844. Vertebrae cervicales communis, arcus vertebrae, zygapophyses craniales (dorsal perspective), position relative to corpus vertebrae:

a. overhang corpora parasagittally;
b. displaced from corpora laterally.

Note.—See: Makovicky (1995); Holtz (1994a: appendix 1, character 85), in reference to "anterior cervical zygapophyses elongate"; Makovicky and Sues (1998: appendix 1, character 35); Holtz (2000 [1998]: appendix I, character 155).

0845. Vertebrae cervicales communis, arcus vertebrae, processes transverses vertebrae (dorsal perspective), forma:

a. strongly caudal and triangular in profile;
b. essentially transverse, subtriangular.

Note.—See: Holtz (1994a: appendix 1, character 5).

0846. Vertebrae cervicales communis, arcus vertebrae, zygapophyses caudalis, length:

a. abbreviate; **b.** elongate.

Note.—See: Makovicky and Sues (1998: appendix 1, character 38); Holtz (2000 [1998]: appendix I, character 163).

0847. Vertebrae cervicales communis, arcus vertebrae, zygapophyses *caudales*, facies articularis, typus:

a. planar or simple unifacotyle;
b. bifacetate.

Note.—See: Gauthier (1986: text character 56); Chatterjee (1995: character 6, part). True gomphosis for this articulatio not confirmed among Neornithes.

Vertebrae Thoracicae et Sacrales

0848. Vertebrae thoracicae (dorsales), numerus modalis (**ordered**):

a. 11 or more; **b.** six to ten;
c. five or fewer.

Note.—See: Andrews (1897); Frankenberger (1947); Berger (1960b: table 4, character 4), regarding Cuculiformes; Sanz and Bonaparte (1992: character 5); Zhou et al. (2000); Sereno and Rao (1992); Chiappe and Calvo (1994: appendix I, characters 15–16); Chiappe (1995a: legend for fig. 1); Chiappe (1995b: character 16). Chatterjee (1999: appendix II, character 34, modified); Chiappe (1995b: character 15); Sanz et al. (1995, 1997: characters 14–15); Chiappe (1996b: character 14); Chiappe et al. (1996: appendix 1, character 14); Livezey (1998b: appendix A, character 114); Livezey (1996a: appendix 1, character 17); Livezey (1998b: appendix A, character 117); Hughes (2000: appendix 2, character 129); Chiappe (2001a: appendix 1, character 36); Currie and Chen (2001: 1711); Chiappe (2002: appendix 20.2, character 36); Norell and Clarke (2001: appendix I, character 54), treated similarly by J. A. Clarke (2002: appendix I, character 54), J. A. Clarke and Norell (2002: appendix 2, character 54), and J. A. Clarke (2004: appendix 1, character 54); Sereno et al. (2002); Zhou and Zhang (2002: appendix III, character 54). J. A. Wilson and Sereno (1998: appendix, character 70); G. Mayr et al. (2003: appendix 1, character 26); Zhou and Zhang (2003); G. Mayr and Ericson (2004: appendix I, character 33).

0849. Vertebrae thoracicae (dorsales), inclusion of vertebrae dorsalis decimus among vertebrae thoracicae verae, status:

a. absent, excluded; **b.** present, included.

Note.—See: J. D. Harris (1998: appendix 2, character 64); Currie and Carpenter (2000: appendix 1, character 55), concerning inclusion of element based on comparative morphology of associated costae (Currie and Zhao 1994a [1993a]), pertinent caveats applicable to this diagnosis indicated by Welles (1984). *Archaeopteryx* has 13, presumably includes the remiculus, fewer in Munich (approximately 10–11).

0850. Vertebrae thoracicae (dorsales), *corpus* vertebrae, facies lateralis corporis, foramen pneumaticum, status et forma (**unordered**):

a. absent;

b. present, large, positioned in mid centrum, entire recessus pneumatic;

c. present, large, positioned in mid centrum, but toti-pneumatic recessus found only in caudalmost vertebrae cervicales and rostralmost vertebrae thoracicae;

d. present, medium to large, positioned rostrad on centrum;

e. present, moderately large, variably recessed, ventrally positioned.

Note.—States exclude taxa having variable numbers of minute perforations in diverse positions on the lamina lateralis of the corpus vertebrae, arcus vertebrae, fovea costalis, or a recessus pneumaticus at margo between corpus and arcus (e.g., Dinornithiformes, *Phaethon*, *Balaeniceps*, *Gyps*, *Pandion*, *Sagittarius*, *Heliornis*, *Pezophaps*, *Cuculus*, *Centropus, Corythaixoides*, *Tyto*, *Steatornis*, *Pharomachrus*, *Momotus*). See: J. D. Harris (1998: appendix 2, character 66); Azuma and Currie (2000: appendix 1, character 38); Currie and Carpenter (2000: appendix 1, character 57); Dyke et al. (2003: appendix 1, character 23).

0851. Vertebrae thoracicae (dorsales), corpus vertebrae, facies lateralis corporis, recesses dorsocraniales pneumatici thoracicae ("pleurocoels"), status et forma (**ordered**):

a. absent; **b.** present, comprising one pair;

c. present, comprising two pairs, single diverticulae partitioned superficially by septa.

Note.—The term "pleurocoel" is properly restricted to true, essentially circular atria or depressiones that *penetrate* the corpus to admit diverticulae pneumaticae, features distinct from mere excavationes or depressiones. See: Livezey (1992b: appendix A, character 116, part); Russell and Dong (1994a [1993a]: table 2, character 27); Russell and Dong (1994b [1993b]: troödontid character 13); Holtz (1994a: appendix 1, character 51); Ericson (1997: fig. 16); J. D. Harris (1998: appendix 2, character 66); Xu et al. (1999a: character 32); Azuma and Currie (2000: appendix 1, character 38); Currie and Carpenter (2000: appendix 1, character 57); Holtz (2000 [1998]: appendix I, character 180); Chiappe (2001a: appendix 1, character 39); J. A. Clarke and Chiappe (2001: character 70); Chiappe (2002: appendix 20.2, character 39), limited to "grooves" and fossae but devoid of details; Dyke and Gulas (2002: appendix 1, character 34), regarding bilateral pairs of recessi among Galliformes; Maryanska et al. (2002: appendix 1, character 107); Zhou and Zhang (2002: appendix III, character 58); Dyke et al. (2003: appendix 1, character 23); Ji et al. (2003: 22), regarding *Shenzhouraptor*; J. A. Clarke (2004); G. Mayr and Ericson (2004: appendix I, character 30).

0852. Vertebrae thoracicae (dorsales), corpus vertebrae, facies lateralis corporis, recessi dorsocraniales pneumatici thoracicae, status et situs seriatum (**ordered**):

a. absent;

b. present, limited to cranial elements ("vertebrae pectorales") in thoracic series;

c. present, throughout thoracic series.

Note.—See: Holtz (1994a: appendix 1, character 51, part); J. D. Harris (1998: appendix 2, character 66, part); Rauhut (2003: character 106).

0853. Vertebrae thoracicae (dorsales), corpus vertebrae, facies lateralis corporis, eminentia costolateralis, fovea costalis (parapophyses), status:

a. absent; **b.** present, in centrum corporis.

Note.—See: Sanz et al. (1995, 1997: character 77); Novas (1996: appendix, character M3), with respect to "parapophyses" of "presacral vertebrae"; Xu et al. (2002a: supplement, character 82), in reference to "parapophyses of posterior trunk vertebrae" being "flush with neural arch" or "distinctly projected on pedicels."

0854. Vertebrae (dorsales) thoracicae (especially caudal elements in series), corpus vertebrae, facies lateralis corporis, eminentia costolateralis, fovea costalis (parapophyses) relative to processes transverses, situs dorsoventralis:

a. coplanar; **b.** (cranio)ventral.

Note.—See: Russell and Dong (1994a [1993a]: table 2, character 26), in reference to position of the "capitular facet" relative to "anteroventral lamina from transverse process in dorsal vertebrae"; Makovicky (1995); J. D. Harris (1998: appendix 2, character 67); Holtz (2000 [1998]: appendix I, character 182); Chiappe (2001a: appendix 1, character 40); Norell and J. A. Clarke (2001: appendix I, character 56), treated similarly by J. A. Clarke (2002: appendix I, character 56), J. A. Clarke and Norell (2002: appendix 2, character 56), and J. A. Clarke (2004: appendix 1, character 56); Chiappe (2002: appendix 20.2, character 40), in terms of craniocaudal position within corpora vertebrales thoracicae; Chiappe and Walker (2002: appendix 11.1, character 2); Xu (2002: suite I, character 66); Xu et al. (2002a: supplement, character 192) referred to character possibly related to this feature, specifically in terms of "zygapophyses of trunk vertebrae abutting one another above neural canal, opposite hyposphenes meet [*sic*] to form lamina . . . or zygapophyses placed lateral to neural canal and separated by groove for interspinous ligaments, hyposphenes separated"; Zhou and Zhang (2002: appendix III, character 56); Rauhut (2003: character 111); Ji et al. (2005: supplement, part I, character 56).

0855. Vertebrae thoracicae (dorsales), especially caudal elements in series, corpus vertebrae, facies lateralis corporis, eminentia costolateralis, lateral prominence relative to facies lateralis, arcus vertebrae, forma:

a. former approximately equal to latter, coplanar;

b. former exceeding latter, pedicellate.

Note.—See: Norell et al. (2001: appendix 1, character 105); J. M. Clark et al. (2002a: appendix 2.2, character 106); Vickers-Rich et al. (2002), concerning *Avimimus*; Xu (2002: suite II, character 137); Hwang et al. (2004: supplement, character 103); Xu and Norell (2004: supplement, character 103).

0856. Vertebrae thoracicae (dorsales), corpus et arcus vertebrae, facies lateralis corporis et arcus, canalis vertebrarterialis, sulcus vertebrarterialis medialis (**new term**), status:

a. absent or indistinct; **b.** present.

Note.—See: Chiappe and Calvo (1994: appendix II, character 21), listed "strong lateral grooves" in thoracic vertebrae as synapomorphy of Enantiornithes; Sanz et al. (1995, 1997: character 76), described as "strong lateral grooves." Until Mesozoic forms are studied, this character is only provisionally considered for Neoaves; may simply reflect the depth of the arcus vertebrae, lamina lateralis arcus, incisurae cranialis et caudalis in this segment. Evidently refers to a sulcuslike impression or aspect of the corpus vertebrae as it forms the medial wall of the canalis vertebrarterialis (the other enclosing structures being the capitulum and tuberculum costae, with intervening incisura capitulotubercularis; i.e., the conspicuous aspect of this feature may reflect, in part, the stage at which these taxa occupy in the transition between costae liberae and the apomorphic, apparently acostal vertebra cervicalis of most Neornithes.

0857. Vertebrae thoracicae (dorsales), cranial elements, corpus vertebrae, facies ventralis corporis, extreme dorsoventral compression combined with bilateral separation of uniquely broad cristae ventrales, producing a clipeolate aspectus (ventral view), status:

a. absent; **b.** present.

0858. Vertebrae thoracicae (dorsales), corpus vertebrae, facies lateralis corporis, bilateral compression, often accompanied by reduced or virtual absence of pneumaticity of elements, status et forma (**ordered**):

a. absent, corpus (sub)cylindrical;

b. present, manifested by concavitas lateralis, depressio ovalis, **new term**;

c. present, manifested by virtually laminar structure of corpus between facies articulares cranialis et caudalis.

Note.—This depressio (state "b") is deep, distinctly rimmed, and ovate. Corpora conforming to state "c" appear essentially laminar. Caudal vertebrae cervicales of *Pachyptila*, *Oceanites*, *Pelecanoides* differ from others in state "b" in showing shallow depressio or pneumatic recessus pneumaticus as opposed to apneumatic recessus corporis caudolateralis. Turnicidae and Pedionomidae show marginal depressiones which typically lack distinct ventral rima, possibly qualifying as one of the apomorphic states. See: Novas (1996: appendix, character M5), referred to "transversal compression" in association with "pronounced ventral keel"; Ericson (1997: table 1, characters 24, 27–28; table 2, character 21); Holtz (2000 [1998]: appendix I, character 175), a contrast between "cylindrical" with "hourglass-shaped" sagittal profiles; Norell and Clarke (2001: appendix I, character 58), treated similarly by J. A. Clarke (2002: appendix I, character 58), J. A. Clarke and Norell (2002: appendix 2, character 58), and J. A. Clarke (2004: appendix 1, character 58); Dyke and Gulas (2002: appendix 1, character 35); Ji et al. (2005: supplement, part I, character 58).

0859. Vertebrae thoracicae (dorsales), corpus vertebrae, forma (planum transversus):

a. subcircular or oval;

b. elliptical with axis majoris distinctly lateromedially oriented.

Note.—See: Makovicky and Sues (1998: appendix 1, character 43); Azuma and Currie (2000: appendix 1, character 35); Dyke and Gulas (2002: appendix 1, character 36); Zhou and Zhang (2002: appendix III, character 57); Rauhut (2003: character 105).

0860. Vertebrae thoracicae (dorsales), corpus vertebrae, marked craniocaudal trend of increasing dorsoventral depth of corpora, status:

a. absent; **b.** present.

Note.—See: Novas (1994 [1993]: character A) regarding truncation of corpus of caudal vertebrae thoracicae in Herrerasauridae.

0861. Vertebrae thoracicae (dorsales), arcus vertebrae, lamina dorsalis arcus, processus spinosus, marked reduction in height relative to arcus vertebrae, lamina dorsalis arcus, largely obliterating processes, status seriatum:

a. absent; **b.** present.

Note.—See: Livezey (1998b: appendix A, characters 118–119); Sereno et al. (1998: footnote 22, character 23).

0862. Vertebrae thoracicae (dorsales), corpus vertebrae, craniocaudal length markedly longer than element is wide lateromedially, status:

a. absent; **b.** present.

Note.—See: Norell and Clarke (2001: appendix I, character 57), treated similarly by J. A. Clarke (2002: appendix I, character 57), J. A. Clarke and Norell (2002: appendix 2, character 57), and J. A. Clarke (2004: appendix 1, character 57); Dyke et al. (2003: appendix 1, character 24); Ji et al. (2005: supplement, part I, character 57).

0863. Vertebrae thoracicae (dorsales), especially cranial elements, corpus vertebrae, facies ventralis corporis, crista (processus) ventralis (haemalis) corporis, status et situs:

a. absent or rudimentary throughout series;

b. present, typically well developed only on some cranial elements (vertebrae "cervicothoracicae") but well developed on at least some vertebrae thoracicae cum costae completae verae, long processes typically terminating in paired alae cristae ventralis.

Note.—Substantial individual variation; related to comparatively great development of the mm. longus colli ventralis, functionally associated with movement of the neck, especially underwater. Typically associated with comparatively prominent development of cristae ventrolaterales in caudalmost elements of vertebrae cervicales (sectio III) and cranialmost elements of vertebrae thoracicae (dorsales), if the latter pertain (see below).

See: Strauch (1985: character 14); Gauthier (1986); Sereno et al. (1998: footnote 22, character 22); Norell et al. (2001: appendix 1, character 104); J. M. Clark et al. (2002a: appendix 2.2, character 105); J. A. Clarke (2002: appendix I, character 53), J. A. Clarke and Norell (2002: appendix 2, character 53), and J. A. Clarke (2004: appendix 1, character 53), regarding "hypapophyses" on vertebrae thoracicae verae (having costae completae verae); Xu (2002: suite II, character 136); Zhou and Zhang (2002: appendix III, character 53); Rauhut (2003: character 107); Hwang et al. (2004: supplement, character 102); Xu and Norell (2004: supplement, character 102).

0864. Vertebrae thoracicae (dorsales), especially cranial elements, corpus vertebrae, facies ventralis corporis, crista (processus) ventralis corporis, status et/aut forma:

a. absent or rudimentary;

b. present and prominent.

Note.—See: Holtz (2000 [1998]: appendix I, character 166); Rauhut (2003: character 108). Partial redundancy with preceding character via necessary, repeated inclusion of "status."

0865. Vertebrae thoracicae, arcus vertebrae, foramen vertebrale, forma craniocaudalis *vs.* dorsoventralis corporis (**ordered**):

a. corpus much shorter than high;

b. corpus of subequal length and height;

c. corpus much longer than high.

Note.—See: Sanz and Bonaparte (1992: character 2); Chiappe and Calvo (1994: appendix I, character 17, part); Sanz et al. (1995); Chiappe (1995b: character 17); Sanz et al. (1995, 1997: character 16); Chiappe (1996b: character 15); Chiappe et al. (1996: appendix 1, character 15); Novas (1996: appendix, character 29); Novas (1997: appendix, character 31); Novas and Puerta (1997), with identical characters employed by Novas (1997); Chiappe et al. (1998: character 18); distinguished merely "small" *vs.* "wide"; Ji et al. (1998: supplement, character 18); Forster et al. (1998: supplement, character 29); Xu et al. (1999b: character 25); Holtz (2000 [1998]: appendix I, characters 173 and 176); Chiappe (2001a: appendix 1, character 37); Chiappe (2002: appendix 20.2, character 37); Rauhut (2003: character 112).

0866. Vertebrae thoracicae (dorsales), arcus vertebrae, lamina dorsalis arcus, recessus dorsocranialis pneumatici (**new term**), status:

a. absent; **b.** present.

Note.—Pneumatic nature of recessus provisionally inferred and variable in conspicuousness among taxa and among elements within individual specimens. This feature is paired and located at base of processus spinosus (where present). Important to distinguish this pair of (variably pneumatic) depressiones from the foramina pneumatica craniales of the arcus vertebrae in many taxa. See: Ericson (1997: table 1, character 23; table 2, character 19), regarding the "pleurocoelous" conditions of vertebrae thoracicae in some taxa; G. Mayr and Clarke (2003: appendix A, character 58).

0867. Vertebrae thoracicae (dorsales), arcus vertebrae, lamina dorsalis arcus, fovea interzygopophysialis (**new term**), foramina pneumatica, status:

a. absent; **b.** present.

Note.—Fovea is a variably deep enclosure which includes the area ligamentum elastici caudalis, which may extend dorsally along the margo caudalis of the processus spinosus in some taxa. The foramina pneumatica (if present) are located within bilaterally paired, variably distinct recesses lateral to basis caudalis of processus spinosus.

0868. Vertebrae thoracicae (dorsales), arcus vertebrae, lamina dorsalis arcus, processus spinosus, increase in length of processes from bases to margines dorsales, status:

a. absent, length subequal from basis to margo dorsalis of processes spinoses;

b. present, length significantly greater at margo dorsalis than basis processi, flabellate.

Note.—See: Chen et al. (1998); Rauhut (2003: character 110).

0869. Vertebrae thoracicae (dorsales), arcus vertebrae, lamina dorsalis arcus, processus spinosus, dorsoventral dimension relative to that of respective corpus:

a. former less than twice, typically equal to that of latter;

b. former twice that of latter.

Note.—See: Azuma and Currie (2000: appendix 1, character 36).

0870. Vertebrae thoracicae (dorsales), arcus vertebrae, lamina dorsalis arcus, processus spinosus, distinct craniocaudal increase in height *in seriatum* relative to arcus vertebrae, status et forma (**ordered**):

a. present, marked, typically equal to twice that of corpus vertebrae;

b. present, limited; **c.** absent.

Note.—See: J. D. Harris (1998: appendix 2, character 68); Sereno et al. (1998: footnote 22, character 23); Azuma and Currie (2000: appendix 1, character 37); Currie and Carpenter (2000: appendix 1, character 58); Holtz (2000 [1998]: appendix I, character 167).

0871. Vertebrae thoracicae (dorsales), arcus vertebrae, processus transversus vertebrae, dorsal orientation (defining angulus with processus spinosus < 90º) reaching maximum near middle of series, status:
a. present, conspicuous;
b. absent or moderate, axis of processes essentially perpendicular to medial planum throughout.
Note.—See: J. D. Harris (1998: appendix 2, character 59); Makovicky and Sues (1998: appendix 1, character 45); Holtz (2000 [1998]: appendix I, character 171), most of whom characterized vertebrae thoracicae by craniocaudal gradations in *combined* trends of dorsal orientation and elongation.

0872. Vertebrae thoracicae (dorsales), arcus vertebrae, lamina dorsalis arcus, processus spinosus, forma dorsoventralis *vs.* craniocaudalis:
a. equi-rectangular, height approximately equal to length;
b. tall-rectangular, height significantly greater than length.
Note.—See: Rauhut (2003: character 109). Also related: Xu and Norell (2004: supplement, character 206), concerning flabellate lateral aspect of processus spinosus.

0873. Vertebrae thoracicae (dorsales), arcus vertebrae, lamina dorsalis arcus, processus spinosus, margo aut apex dorsalis spinae, lamina transversalis dorsalis ("spine tables"), status:
a. present, expanded, "spine tables" developed;
b. absent, unexpanded, "spine tables" lacking.
Note.—See: Makovicky and Sues (1998: appendix 1, character 47); Holtz (2000 [1998]: appendix I, character 168); Norell et al. (2000: appendix 1, character 29); Norell et al. (2001: appendix 1, character 109); J. M. Clark et al. (2002a: appendix 2.2, character 111); Vickers-Rich et al. (2002), concerning *Avimimus*; Xu (2002: suite II, character 141); Xu et al. (2002a: supplement, character 86); Hwang et al. (2004: supplement, character 108); Xu and Norell (2004: supplement, character 108).

0874. Vertebrae thoracicae (dorsales), arcus vertebrae, lamina dorsalis arcus, processus spinosus, impressiones ligamentorum ossificantes, dorsoventral position relative to apex processi:
a. ventral to apex, typically at basis in area ligamentorum elastici;
b. coplanar with apex.
Note.—See: Makovicky and Sues (1998: appendix 1, character 48); Holtz (2000 [1998]: appendix I, character 169); Norell et al. (2001: appendix 1, character 110); J. M. Clark et al. (2002a: appendix 2.2, character 112); Xu (2002: suite II, character 142); Xu et al. (2002a: supplement, character 87); Hwang et al. (2004: supplement, character 109); Xu and Norell (2004: supplement, character 109).

0875. Vertebrae thoracicae (dorsales), arcus vertebrae, processus transversus vertebrae, craniocaudal gradual but distinct elongation of processes *in seriatum* among presynsacral elements, status:
a. absent, processes transverses essentially of uniform width throughout the presynsacral elements or moderately reversed grade;
b. present, processes transverses distinctly increasing in width throughout the presynsacral elements.
Note.—This *Gestalt* character requires specimens having articulated vertebrae thoracicae and synsacrae.

0876. Vertebrae thoracicae (dorsales), arcus vertebrae, processus transversus vertebrae (dorsal perspective), forma generalis (**unordered**):
a. craniolaterally directed and subrectangular in profile;
b. laterally directed and subrectangular in profile;
c. strongly caudally directed and triangular in profile.
Note.—See: Holtz (1994a: appendix 1, character 5); Holtz (2000 [1998]: appendix I, character 170).

0877. Vertebrae thoracicae (dorsales), cranial elements, arcus vertebrae, processus transversus vertebrae, forma generalis:
a. long and thin;
b. short, wide, and only slightly inclined.
Note.—See: Norell et al. (2001: appendix 1, character 108); J. A. Clarke (2002: appendix I, character 62), primarily with respect to dorsal inclination of processes in cranial synsacral elements; J. M. Clark et al. (2002a: appendix 2.2, character 110); Xu (2002: suite II, character 140); Xu et al. (2002a: supplement, character 85); Hwang et al. (2004: supplement, character 107); Xu and Norell (2004: supplement, character 107).

0878. Vertebrae thoracica (dorsales), arcus vertebrae et costa vertebralis, foramen (costo) transversarium (cranial perspective), forma (**unordered**):
a. elliptical (axis majoris dorsoventral) or subcircular;
b. elliptical (axis majoris lateromedial) or fissuriform;
c. occluded by membrana ossificans.
Note.—Variation in form a composite of prominence of processus transversus vertebrae, eminentia costolateralis, incisura capitulotubercularis, capitulum costae et tuberculum costae.

See: Romer (1956: fig. 140), regarding nonavian Theropoda.

0879. Vertebrae thoracica (dorsales), arcus vertebrae et costa vertebralis, foramen (costo)transversarium (cranial perspective), membrana ossificans dividing foramen diagonally into two primary ostia, status:

a. absent; **b.** present.

Note.—Foramen is homologue of spatium delimited by two articulationes vertebracostales, the dorsolateral member of which giving rise to processus transversus vertebrae. Vaguely delimited pair of foramina evidently serve as axial passages for neurovascular components.

0880. Vertebrae thoracicae (dorsales), arcus vertebrae, processus transversus vertebrae, ankylosis iliovertebralis (**new term**), status:

a. absent; **b.** present.

Note.—New term refers to ankylosis of two or three vertebrae dorsales immediately cranial to synsacrum with margo cranialis, ala (pars) preacetabularis ilii by bilaterally paired aponeuroses ossificantes. Aponeuroses ossificantes apparently associated with fasciae craniales origii m. iliotrochantericus caudalis. Distinguishable from comparatively widespread, splintlike aponeuroses by greater breadth, fascialike appearance, and cranial extent. See: Norell and Clarke (2001: appendix I, character 59), similarly by J. A. Clarke (2002: appendix I, character 59); J. A. Clarke and Norell (2002: appendix 2, character 59), and J. A. Clarke (2004: appendix 1, character 59); Zhou and Zhang (2002: appendix III, character 59); Ji et al. (2005: supplement, part I, character 59).

0881. Vertebrae thoracicae (dorsales), caudalmost element in series (sectio I of Boas 1934) in which processes costales are firmly synostotic with ala preacetabularis ilii, facies ventralis, foramina transversaria, division into two subforamina by dorsoventrally oriented pila, status:

a. absent; **b.** present.

0882. Vertebrae thoracicae (dorsales), arcus vertebrae, zygapophyses caudales, margines caudales, craniocaudal position relative to associated corpus vertebrae, facies articularis caudalis:

a. former coincident with latter;

b. former exceeding latter.

Note.—See: Makovicky and Sues (1998: appendix 1, character 46); Holtz (2000 [1998]: appendix I, character 172); Maryanska et al. (2002: appendix 1, character 108).

0883. Vertebrae thoracicae (dorsales), arcus vertebrae, zygapophyses craniales et caudales, articulationes interzygapophysiales, status:

a. absent; **b.** present.

Note.—See: Benton (1990a: 20), termed “accessory intervertebral articulations (hyposphene-hypantrum) in dorsal vertebrae.”

0884. Vertebrae thoracicae (dorsales), arcus vertebrae, zygapophyses craniales et caudales, articulationes interzygapophysiales relative to foramen vertebrale, situs lateromedialis:

a. dorsal to foramen vertebrale, forming lamina;

b. lateral to foramen vertebrale, zygapophyses separated latermedially by area ligamentorum elastici.

Note.—See: Norell et al. (2001: appendix 1, character 92); J. M. Clark et al. (2002a: appendix 2.2, character 108); Xu (2002: suite II, character 247); Hwang et al. (2004: supplement, character 105); Xu and Norell (2004: supplement, character 105).

0885. Vertebrae thoracicae (dorsales), arcus vertebrae, lamina lateralis arcus, foramina pneumatica, status (**unordered**):

a. present, paired, comprising foramina cranialis et caudalis or networks thereof, often immediately adjacent to margines of processes transversariae;

b. present, single, restricted to foramen cranialis or network of foramina craniales;

c. present, single, restricted to foramen caudalis or network of foramina caudales;

d. absent, neither foramen cranialis or caudalis typical.

Note.—Where both foramina present, evidently interrelated, separated by variably developed strut or lamina supporting the processus transversus.

See: Ostrom (1976a); Currie and Zhao (1994b [1993b]: fig. 17), in reference to infraprezygapophysial fossa in *Sinraptor*; Forster et al. (1998: supplement, character 30); Livezey (1998b: appendix A, character 116); Xu et al. (1999b: character 26); Xu et al. (2000: supplement, character 17). Provisional codings are: foramina pneumatica absent (*Allosaurus*, *Compsognathus*, Ornithomimosauria, Troödontidae, Alvarezsauridae, Enantiornithes, *Patagopteryx*, Ornithurae) *vs*. present (*Protarchaeopteryx*, *Archaeopteryx*, Oviraptorosauria, Velociraptorinae, Dromaeosauridae).

0886. Vertebrae thoracicae (dorsales), arcus vertebrae, lamina lateralis arcus, incisura caudalis arcus, dorsoventral osseus occlusion enclosing foramina neurovascularia, status et numerus (**unordered**):

a. absent; **b.** present, single;

c. present, two, vertically aligned, including notarium, if present.

Note.—Small, evidently *a*pneumatic, with dense margines and uniform diameter, probably serves as canalis neurovascularia. Weakly developed in some specimens of *Ciconia*. See: Ericson (1997: table 1, character 26).

0887. Vertebrae thoracicae (dorsales), arcus vertebrae, facies ventralis, (prominent) processus ventralis, status:

a. absent; **b.** present.

Note.—See: Norell et al. (2000: appendix 1, character 28).

0888. Vertebrae thoracicae (dorsales) et sacrales, caudalmost elements (cranial to vertebrae synsacrales), corpus vertebrae, facies articularis caudalis (of penultimate element) et facies articularis cranialis (of ultimate element), typus (**unordered**):

a. amphiplatyan; **b. procoelous**;

c. amphicoelous, both surfaces variably, often slightly concave, with rounded margins;

d. heterocoelous, surfaces saddle-shaped, comprising articulationes sellares;

e. opisthocoelous, cranial element with facies articularis caudalis concave and rounded, whereas caudal element with facies articularis cranialis convex and rounded.

Note.—States for *Archaeopteryx* and *Ichthyornis* based on literature (W. K. Parker 1888a; Beddard 1898a; L. D. Martin 1987; Baumel and Witmer 1993: annotation 113). In some taxa having a notarium (e.g., Pelecanidae), articulatio cranialis involves the notarium, forming an articulatio notariosynsacralis. Most taxa classified as amphicoelous may be “quasi-amphicoelous,” i.e., approaching amphicoely, with immediate precursor being either heterocoely or opisthocoely. Osteological remains in this character may be misleading given the possible presence of menisci intervertebrales fibrocartilagines (or anuli fibroses) in these (typically synovial) articulationes intercorporalia (Barkow 1856), minutia largely obscured where juncturae are synostotic.

See: Strauch (1978: character 34), reanalyzed by Björklund (1994: appendix) and Chu (1995); Ericson (1997: table 1, character 22); Novas (1997: appendix, character 5); Novas and Puerta (1997), with identical characters used by Novas (1997); J. D. Harris (1998: appendix 2, character 65); J. A. Wilson and Sereno (1998: appendix, characters 59 and 92); Azuma and Currie (2000: appendix 1, character 34); Currie and Carpenter (2000: appendix 1, character 56); Holtz (2000 [1998]: appendix I, characters 177 [“typical” vertebrae thoracicae] and 184 [caudalmost vertebrae thoracicae or cranialmost vertebrae synsacrales]), “amphiplatyan” *vs.* “biconvex” (character 177) or “procoelous” (character 184); Romer (1956: fig. 117); J. A. Clarke and Chiappe (2001: character 61); Ji et al. (2001), regarding unnamed dromaeosaurid NGMC 91-A, referred to “thoracics are platycoelous”; Norell and Clarke (2001: appendix I, character 55); J. A. Clarke (2002: appendix I, character 55), J. A. Clarke and Norell (2002: appendix 2, character 55), and J. A. Clarke (2004: appendix 1, character 55); Goedert and Cornish (2002), regarding Plotopteridae; Zhou and Zhang (2002: appendix III, character 55); G. Mayr and Clarke (2003: appendix A, character 57); Dyke and van Tuinen (2004: appendix 1, character 38); G. Mayr (2004b: appendix 1, character 26), in reference to opisthocoely; Ji et al. (2005: supplement, part I, character 55).

0889. Vertebrae thoracicae, vertebra synsacralis primus (**new term**), modal craniocaudal position relative to ala (pars) preacetabularis ilii, margo cranialis, situs craniocaudalis:

a. caudal; **b.** coincident or cranial;

x. noncomparable because notarium articulates with synsacrum (Pelecanidae).

0890. Vertebrae thoracicae (dorsales) et sacrales, vertebra synsacralis primus (**new term**), corpus vertebrae, pronounced lateromedial (bilateral) compression, status:

a. absent;

b. present, principally indicated by subcristate facies ventralis of the corpora vertebrae involved.

Note.—Coding here involves merging of two characters proposed by Ericson (1997: table 1, characters 27–28) and differs in intermediate codings for several taxa—*Pedionomus*, *Chionis*, *Thinocorus*, and *Stercorarius*. See also: Murray and Vickers-Rich (2004: table 9, character 8), regarding Dromornithidae.

0891. Vertebrae thoracicae (dorsales) et sacrales, caudalmost elements (cranial to vertebrae synsacrales), craniocaudal reduction of columna vertebralis cranial to sacral elements relative to length of femur, status (**unordered**):

a. absent; **b.** present, “camerate”;

c. present, “camellate.”

Note.—See: Bakker et al. (1988); Novas (1992: character B); Holtz (1994a: appendix 1, character 93); J. D. Harris (1998: appendix 2, character 69); Holtz (2000 [1998]: appendix I, character 181); Britt (1993) investigated anatomy of pneumaticity, histologically defined the generalities above, but exceptions have been reported (H.-D. Sues, pers. comm.).

Notarium

Note.—Where notarium is absent (e.g., *Iberomesornis*, *Concornis, Lithornis*) all associated characters are treated as noncomparable.

0892. Notarium, status et numerus vertebrae ankylosae (**ordered**):

a. absent;

b. present, modally composed of two vertebrae;

c. present, modally composed of three vertebrae;

d. present, modally composed of four vertebrae thoracicae;

e. present, modally composed of caudalmost vertebra cervicalis and first three vertebrae thoracicae;

f. present, modally composed of five vertebrae.

Note.—Purportedly present also in *Archaeopteryx* (polymorphic), *Apsaravis* (polymorphic), and *Gobipteryx* (L. D. Martin 1987). Juncturae notarii involves variably complete ankylosis of vertebrae, with extreme conditions of smoothly united synostosis in some taxa, with variably complete ankylosis of the juncturae notarii—e.g., synostoses intercorporales, intertransversaria, et interspinalis (comparatively poorly developed in some taxa, e.g., *Anseranas*). Aponeuroses et ligamenta ossificans intervertebrales have been reported in nonavian Theropoda, including Velociraptorinae (Norell and Makovicky 1999). Ankyloses of vertebrae immediately cranial to the synsacrum in Pelecanidae and Trochilidae do not constitute notaria *sensu stricto*. Like canalis synsacri, synostosis intervertebralis notarii preserves an open canalis notarii. Variable ankylosis among two to five vertebrae thoracicae in Rheidaeis not considered herein to be a notarium verae.

See: Barkow (1856); Boas (1934); Rydzewski (1935); Storer (1982), regarding functional and systematic implications of notaria and "co-ossified" vertebrae in birds; Houde (1988: table 27, character 39) regarding similar structures in mosasaurs and cetaceans. Extreme of six vertebrae incorporated into the notarium reported by Baumel and Witmer (1993: 90) was not confirmed. Two USNM specimens of *Anseranas* had reasonably well-united "notaria" comprising two and three vertebrae (evidently vertebrae thoracicae II–III and II–IV, respectively), having discernable divisions between processes spinoses and a fenestra intercristalis. Cladistic applications include: Ericson (1997: table 1, character 25; table 2, character 18); Livezey (1997a: appendix 1, character 56; *corrigenda*, Livezey 1998a); D. A. Winkler et al. (1997: appendix 1, character 17), regarding "ossified hypaxial tendons" in Ornithischia; Livezey (1998b: appendix A, character 115); Norell and Clarke (2001: appendix I, character 60), treated similarly by J. A. Clarke (2002: appendix I, character 60), J. A. Clarke and Norell (2002: appendix 2, character 60), and J. A. Clarke (2004: appendix 1, character 60); Dyke and Gulas (2002: appendix 1, character 38); Dyke et al. (2003: appendix 1, character 26). Sanz et al. (1996) did not note the presence or absence of a notarium in *Eoalulavis*, but a four-element notarium composed of vertebrae thoracicae and separated from the synsacrum by one vertebra was evidently present; Zhou and Zhang (2002: appendix III, character 60); G. Mayr and Clarke (2003: appendix A, character 56); J. A. Clarke (2004); Dyke and van Tuinen (2004: appendix 1, character 37); G. Mayr (2004a: appendix 1, character 32); G. Mayr and Ericson (2004: appendix I, character 31); Novas et al. (2004: appendix, character 12), regarding "ossified hypaxial tendons" in Ornithischia; Ji et al. (2005: supplement, part I, character 60).

0893. Notarium (if present), crista spinosa notarii, fenestrae interspinoses (**new term**), status:

a. essentially absent, crista distinctly laminar without delimitation of incorporated elements;

b. present, crista not distinctly laminar and showing delimitation of incorporated elements;

x. noncomparable, lacking notarium (other Neornithes).

0894. Notarium (if present), lamina transversa notarii, fenestrae intertransversariae, status modalis et forma (**unordered**):

a. present, large, often emarginate laterally and irregular in outline;

b. present, moderate, orbiculate;

c. minute or absent;

x. noncomparable, notarium absent (other Neornithes, including Dinornithiformes, *Aptornis*).

0895. Notarium (if present), corpus notarii, crista ventralis notarii, fenestrae intercristales, status:

a. typically absent, cristae ventrales demarcated ventrally by incisurae cristae, ligamenta intercristales of adjacent vertebrae notarii not ossified;

b. typically present, ligamenta intercristales of adjacent vertebrae notarii (often robustly) ossified;

x. noncomparable, lacking notarium (other Neornithes).

0896. Notarium (if present), arcus notarii, foramina (intervertebralia) interarcuales, status et forma (**unordered**):

a. present, large, diameter distinctly greater than that of fovea costalis;

b. present, small, diameter approximately equal to that of fovea costalis;

c. present, obsolete, reduced to minute perforations or evidently absent;

x. noncomparable, lacking notarium (other Neornithes).

Note.—This "foramen" is actually delimited by the incisura cranialis of one incorporated vertebra and the incisura cranialis of the following vertebra, and formed by the lamina lateralis arcus of two vertebrae notarii *in seriatum*, not formed within the corpus notarii (as given in the *Nomina*). States provisionally sequenced by relative size of foramina, beginning with that characteristic of elements not ankylosed into notarium.

Vertebrae Synsacrales (Synsacrum)

Note.—Partitions among vertebrae incorporated into the synsacrum correspond to two parallel suites of names, that of the *Nomina* and the sectiones of Mivart and Clarke (1879) and Boas (1929, 1934). A multi-organ treatment of the lumbosacral region was produced by Holmdahl (1925, 1926). This incorporation of elements comprises several juncturae synsacri—synostosis intercorporis, synostosis intertransversaria, et synostosis interspinalis—essentially identical to those involved with notaria (where present).

The caudalmost vertebra cranial to and free from the synsacrum is the vertebra thoracica prosynsacralis (**new term**). Proceeding from cranialmost to caudalmost synsacral elements, these sectiones are: vertebrae thoracicae (sectio I), vertebrae lumbares (sectio II), vertebrae [eu]sacrales (sectio III), and vertebrae caudales stabiles (sectio IV). Vertebrae caudal to the synsacrum are the remaining, caudalmost vertebrae caudales liberae (terminating with the pygostylus, where present), delimited from the synsacrum by the symphysis postsynsacralis and beginning with the vertebra caudalis postsynsacralis (**new term**).

Vertebrae acetabulares are a subset of vertebrae (eu)sacrales (sectio III of Boas 1934), and distinguished (Baumel and Witmer 1993: annotation 141b) by the presence of processes costales acetabulares (**emended term**), an apparent homologue (du Toit 1912–1913; Radu 1975; Komárek 1979) of the typically much thicker "sacral ribs" (Romer 1956) of other Archosauromorpha. Nomenclatural differences occur in the literature, e.g., Archey (1941: 26) refers to the vertebrae possessing homologues of "sacral ribs" to be preacetabular, whereas acetabular vertebrae lack both processes transversariae et costales.

Superficial consideration of geometry and position of the structure in basal Archosauria, however, suggest that if the costa propria is incorporated to a significant extent, the contribution mostly or entirely comprises the capitulum costae and proximalmost corpus costae (in addition to the proximalmost processus costalis). This applies as well to Sauropoda (Campos and Kellner 1999). If a vestigium of the tuberculum costae is involved in the "sacral rib," it seems limited to a small dorsalmost lamina immediately ventral to the corresponding, incorporated processus transversaria. A modicum of counterevidence that argues for incorporation of extremitas vertebralis costae within "sacral ribs" are the small foramina in the midregion of the junctura iliocostalis, hiatae that may correspond to incisura capitulotubercularis vestigialis for each (eu)sacral costo-vertebral segmentum. With the possible exception of the ratites, however, the homologues of "sacral ribs" of other Reptilia and at least some Amphibia do not appear to include costae propriae or processes transversariae, but instead (as given in current name) represent variably enlarged processes costales. Pending study of ontogenetic series, however, this assessment must remain hypothetical.

0897. Vertebrae synsacrales (maximally comprising vertebrae thoracicae, lumbares, sacrales, et caudales), numerus modalis (**ordered**):

a. two; **b.** three or four;
c. five or six; **d.** seven to nine;
e. ten to 13; **f.** 14 to 18;
g. 19 or more.

Note.—See: van Oort (1904, 1905); Boas (1934); Ostrom (1976a); Thulborn (1984: 126–127, character 7); Gauthier (1986: 13, unindexed synapomorphy of Ornithurae); Houde (1988: table 27, character 40); Siegel-Causey (1988: character 106); Novas (1992: character 14); Sanz and Bonaparte (1992); Holtz (1994a: appendix 1, character 121); Novas (1994 [1993]: appendix, character 14); Elzanowski (1995: 38); Sanz and Bonaparte (1992: character 6); Chiappe and Calvo (1994: appendix I, character 18); Russell and Dong (1994b [1993b]: troödontid character 14); Chiappe (1995a: legend for fig. 1), Chiappe (1995b: character 18); Elzanowski (1995: character C7); Sanz et al. (1995, 1997: character 17); Chiappe (1996b: character 16); Chiappe et al. (1996: appendix 1, character 16); Livezey (1997a: appendix 1, character 57; *corrigenda*, Livezey 1998a); Sues (1997: appendix 1, character 25; fig. 6); Chiappe et al. (1998: character 20); Forster et al. (1998: supplement, character 31); Ji et al. (1998: supplement, character 20); Livezey (1998b: appendix A, character 120); Makovicky and Sues (1998: appendix 1, character 49); J. A. Wilson and Sereno (1998: appendix, character 2); Chatterjee (1999: appendix II, character 36); Xu et al. (1999b: character 27); Holtz (2000 [1998]: appendix I, character 185); Xu et al. (2000: supplement, character 18); Chiappe (2001a: appendix 1, character 41); J. A. Clarke and Chiappe 2001: character 62); Cracraft and Clarke (2001: appendix 2, character 20); Hutchinson (2001a: appendix 1, character 1); Norell and Clarke (2001: appendix I, character 61); Norell et al. (2001: appendix 1, character 111); Chiappe (2002: appendix 20.2, character 41); J. M. Clark et al. (2002a: appendix 2.2, character 113); J. A. Clarke (2002: appendix I, character 61); J. A. Clarke and Norell (2002: appendix 2, character 61); Maryanska et al. (2002: appendix 1, character 109); Xu (2002: suite II, character 143); Xu et al. (2002a: supplement, character 88); Zhou and Zhang (2002: appendix III, character 61); Zhou and Zhang (2003); G. Mayr and Clarke (2003: appendix A, characters 55 and 91), pertaining to counts of vertebrae presynsacrales et synsacrales, respectively; Rauhut (2003: character 113); J. A. Clarke (2004: appendix 1, character 61); Dyke and van Tuinen (2004: appendix 1, characters 36 and 65), regarding counts of vertebrae presynsacrales et synsacrales, respectively; G. Mayr (2004a: appendix 1, character 48); Hwang et al. (2004: supplement, character 110); Xu and Norell (2004: supplement, character 110); Ji et al. (2005: supplement, part I, character 61).

0898. Vertebrae synsacrales, incorporated vertebrae thoracicae synsacrales, i.e., sectio I of Boas (1934), numerus modalis:

a. six to eight; **b.** three to five.

Note.—Tallies of incorporated "thoracic" vertebrae excluded weakly or partially ankylosed elements. See: Sereno et al. (1993: legend for fig. 3a), as synapomorphy of Dinosauria.

0899. Vertebrae synsacrales, incorporated vertebrae thoracicae synsacrales, i.e., sectio I of Boas (1934), caudally diminishing processes ventrales caudad to synostosis pubicus, status:

a. absent; **b.** present.

0900. Vertebrae synsacrales, incorporated vertebrae thoracicae synsacrales, i.e., sectio I of Boas (1934), irregularly fenestrated crista ventralis synsacri, status:

a. absent; **b.** present.

Note.—Limited to cristae in this sectio synsacralis.

0901. Vertebrae synsacrales, vertebrae thoracicae synsacrales—sectio I of Boas (1934)—processes costales et transverses displaced dorsad, compressed ventromedial to medioventrally compressed alae preacetabulares iliorum so as to effect a virtually impervious, osseus lamina transversus, precluding a craniocaudally conductive canalis or sulcus synsacri, status:

a. absent; **b.** present.

0902. Vertebrae synsacrales, incorporated vertebrae acetabulares or "eusacrales" synsacri (**new term**)—sectio III of Boas (1934)—processes transverses, caudolateral orientation and terminal divergence of *two* adjacent vertebrae to form intumescentia lateralis postacetabularis (**new term**) and (typically) an intermediate or distal, enclosed fenestra, status:

a. absent; **b.** present.

Note.—See: Boas (1934: fig. 4); J. A. Clarke (2002: appendix I, character 62), J. A. Clarke and Norell (2002: appendix 2, character 62), and J. A. Clarke (2004: appendix 1, character 62), regarding vertebrae caudal to vertebrae thoracicae synsacrales and cranial to vertebrae "eusacrales" aut acetabulares, i.e., sectio II of Boas (1934), but possibly equivalent to vertebrae acetabulares.

0903. Vertebrae synsacrales, corpus vertebrae, vertebra synsacralis primus (**new term**), facies articularis cranialis, forma in planum transversus (**ordered**):

a. bilaterally compressed, dorsoventral dimension substantially (at least 1.5 times) greater than lateromedial dimension;

b. subcircular, subrectangular, or weakly bilobate, dorsoventral and lateromedial dimensions being approximately equal;

c. dorsoventrally compressed, lateromedial dimension being substantially (at least twice, often three times) greater than dorsoventral dimension.

Note.—See: Makovicky and Sues (1998: appendix 1, character 50); J. A. Wilson and Sereno (1998: appendix, character 68), pertaining to Sauropoda; Holtz (2000 [1998]: appendix I, character 186); Norell and Clarke (2001: appendix I, character 62). Structurally related character—Makovicky and Sues (1998: appendix 1, character 51); Holtz (2000 [1998]: appendix I, character 187)—craniocaudal decline in corporal widths among synsacral elements—proved intractable among Neornithes; Zhou and Zhang (2002: appendix III, character 62); Murray and Vickers-Rich (2004: table 9, character 9); Ji et al. (2005: supplement, part I, character 62).

0904. Vertebrae synsacrales preacetabularis, processes transverses relative to adjacent foramina (fenestrae) intertransversaria, forma transversa (**ordered**):

a. former less than or equal to latter;

b. former greater than latter, but latter retaining diameters meriting reference to latter as fenestrae;

c. former much greater than latter, reducing diameter of foramina intertransversaria to prominent pori;

x. noncomparable, by occlusion of foramina (*Aepyornis*).

0905. Vertebrae synsacrales preacetabularis, processes transverses, angulus craniocaudalis with respect to axis craniocaudalis of columna vertebralis, situs craniocaudalis (**ordered**):

a. distinctly caudad, i.e., angulus cranialis obtuse, angulus caudalus acute (< 90º);

b. essentially perpendicular (~ 90º);

c. distinctly craniad, i.e., angulus cranialis acute, angulus caudalis obtuse (> 90º).

0906. Vertebrae synsacrales preacetabularis, cranialmost incorporated element (i.e., caudalmost vertebrae thoracicae), processes transverses, termini laterales, longitudinal junctura via crista lateralis, synostosis with facies ventralis of ala (pars) preacetabularis ilii, status:

a. absent; **b.** present.

Note.—Crista lateralis is typically limited to the notaria of some taxa.

0907. Canalis synsacri, ostium cranialis, forma modalis (**unordered**):

a. essentially circular;

b. distinctly oval, with axis majoris oriented lateromedially;

c. distinctly oval, with axis majoris oriented dorsoventrally;

d. distinctly bilobate, with axis majoris oriented dorsoventrally, lobulae of approximately equal size;

e. distinctly bilobate, with axis majoris oriented dorsoventrally, dorsal lobulus substantially smaller than ventral lobulus.

Note.—Critical to examine completely cleaned, adult specimens with immediately cranial, semiankylosed vertebrae thoracicae detached.

0908. Extremitas cranialis synsacri (cranialmost incorporated element, typically one of caudalmost vertebrae thoracicae), corpus vertebrae, facies articularis cranialis, concavito-convexity of facies articularis, typus (**unordered**):

a. "**amphiplatyan**," including both facies articulares being flat;

b. "**procoelous**," including concave facies articularis cranialis;

c. "**opisthocoelous**," including orbiculate, distinctly convex facies articularis caudalis of corpus vertebralis;

d. "**heterocoelous**."

Note.—See: Thulborn (1984: 126–127, character 5); Gauthier (1986); L. D. Martin (1987); Chiappe et al. (1996: appendix 1, character 76); Novas (1996: appendix, character 5); Novas (1996: appendix, character 19); Novas (1997: appendix, character 21, part); Novas and Puerta (1997), see identical characters in Novas (1997); Chiappe et al. (1998: character 21); Ji et al. (1998: supplement, character 21); perhaps redundant with corresponding character of extremitas caudalis synsacri, i.e., descriptive in combination of heterocoely of vertebrae (syn)sacrales; J. A. Wilson and Sereno (1998: appendix, character 92), concerning caudal vertebrae thoracicae among Sauropoda; Holtz (2000 [1998]: appendix I, character 184), in reference to "amphiplaty" *vs*. "procoely" of "first sacral" vertebrae; Chiappe (2001a: appendix 1, character 42); Cracraft and Clarke (2001: appendix 2, character 44); Chiappe (2002: appendix 20.2, character 42); Xu et al. (2002a: supplement, character 91), with respect to facies articularis caudalis of caudalmost vertebra sacralis; Ericson (1997: table 1, character 22; table 2, character 19).

0909. Extremitas cranialis synsacri (cranialmost incorporated element, typically one of caudalmost vertebrae thoracicae), corpus vertebrae, facies articularis cranialis, forma (cranial perspective) *sensu* outline of facies(iae) articularis(es) verae (**unordered**):

a. subrectangular and semi-bilobate, wider than deep, margo ventralis more deeply incised (sulcus caroticus) than margo dorsalis, entire surface so delimited involved in articulatio intervertebralis;

b. subcircular, squarish, or cordiform by dorsal incisura;

c. noncircular-elliptical or nonsquare-rectangular, significantly wider than deep.

0910. Extremitas cranialis synsacri, caudalmost vertebrae thoracicae synsacri, dorsal exposure of facies lateralis synsacri such that single foramen intervertebrale and part of vertebrae synsacrales ventral to processes costales are exposed dorsocraniad to acetabulum, status:

a. absent; **b.** present;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—See: Stephan (1979), a comprehensive atlas of Spheniscidae.

0911. Extremitas cranialis synsacri, facies visceralis synsacri, vertex ventrocranialis of facies articularis, ventrocranially prominent, bifurcated hamulus, status:

a. absent; **b.** present.

Note.—Evidently effects supplementary, ventral stabilization of articulatio synsacralis against extreme dorsoventral flexion.

0912. Facies dorsalis synsacri, crista spinosa synsacri, synostosis to form essentially continuous, dorsal, axial lamina, status:

a. absent;

b. present, in majority of taxa limited in distinctness caudal to acetabulum.

Note.—See: Sues (1997: fig. 6), regarding *Chirostenotes*; Holtz (2000 [1998]: appendix I, character 188), regarding preacetabular crista in nonavialians; Livezey (1998b: appendix A, character 124), regarding preacetabular crista in gruiforms; Hughes (2000: appendix 2, character 130), regarding prominentia postacetabulares in cuculiforms. Tsuihiji (2004) related bifurcationes of spinae dorsales vertebralia cervicales of *Rhea* as evolutionarily related to those of Sauropoda.

0913. Facies dorsalis synsacri, crista spinosa synsacri, height relative to width of associated processus transversus:

a. greatly elevated—height significantly greater than width of associated processus transversus;

b. depressed or unremarkably prominent—height less than or approximating width of associated processus transversus.

Note.—See: Livezey (1998b: appendix A, character 121).

0914. Facies dorsalis synsacri, crista spinosa synsacri, lateral synostoses between facies lateralis cristae and alae preacetabulares iliorum, facies ventrales, areae articulares vertebrales, largely or completely occluding ostium cranialis synsacri of canalis synsacralis (cranial perspective), status:

a. absent; **b.** present in adults.

0915. Facies visceralis synsacri—sectiones III–IV of Boas (1934)—comparative qualitative differentiation between sectiones III and IV, and modification of processes transverses, forma (**unordered**):

a. former distinguishable from latter, but processes costales not extending laterally toward acetabulum;

b. former indistinguishable from latter, elements uniform or form a gradual morphocline;

c. former distinguishable from latter, the former moderately laterally extensive, forming junctura with well-developed crista iliaca intermedia, the latter reaching a point near the acetabulum;

d. former distinguishable from latter, the former greatly laterally extensive and forming distal terminus of junctura dorsal to acetabulum;

e. former distinguishable from latter, but all vertebrae postacetabulares greatly laterally extensive and cranial members opposite acetabulum extend to rima caudalis acetabuli;

x. noncomparable (Rheidae).

Note.—Processes transverses et crista iliaca intermedia (where forming a supportive strut) vary considerably depending on the relative breadth of the pelvis, appearing comparatively prominent in taxa with broad pelves. See: Strauch (1985).

0916. Vertebrae acetabulares synsacri (**resurrected term**, cf. du Toit 1912–1913; Radu 1975; Komárek 1979)—the osteological estimate of vertebrae "eusacrales" diagnosable fundamentally by neuroanatomical means, and those elements corresponding most closely to those of sectio III of Boas (1934)—numerus modalis (**ordered**):

a. four or five; **b.** two or three; **c.** one;
x. noncomparable (Cuculidae, Brachypteracidae, Rhamphastidae, Jyngidae, Picidae).

Note.—Authors varied in the delimitation of these nominal vertebrae, most equating synsacral vertebrae having prominent processes transversales directed toward the acetabulae as "true" sacral vertebrae. The vertebrae acetabulares of Baumel (1988), with the true "sacral" or vertebrae eusacrales; because of the neuroanatomical alternative for diagnosis of "eusacral" vertebrae, herein these elements were diagnosed using osteological criteria. However, several taxa proving intractable by these means, e.g., Trochilidae, Menuridae. Boas (1934) evidently attributed a single presumptive element to the sacral vertebrae, referring to this *a priori* series as "sectio III." Among the Dinosauria, usually synsacrum is formed first by one to two "dorsal sacral" vertebrae, to which usually three to four "true sacrals" (i.e., those immediately medial to the acetabulum) ankylose; therefore, approximately five synsacral vertebrae are present, and typically these articulate or join via synostosis with both ilia et costae. At least in the paleontological literature, "sacral" vertebrae typically are synonomized with those in direct articulation with the ossa ilii (i.e., possess suturae iliovertebrales); other, adjacent vertebral elements tend to "join" to compose the synsacrum definitivum.

The latter diagnoses (qualitative assignments based on structural differences) were performed here, but many taxa proved difficult to characterize in this fashion. Omissions of tallies of elements in the virtually uniform sectio II of Boas (1934) avoided redundancy of encoded tallies of totals and all subparts of integral totals for the synsacrum. See: Currie and Chen (2001: 1712), in reference to *Sinosauropteryx*.

0917. Vertebrae acetabulares (i.e., those having disproportionately elongated processes costales bilaterally oriented toward acetabulae—sectio III of Boas (1934), facies visceralis synsacri, numerus modalis (**ordered**; basal state "b"):

a. zero; **b**. **one**; **c.** two;
d. three; **x.** noncomparable (ratites).

Note.—See: Baumel and Witmer (1993: annotation 141b).

0918. Vertebrae acetabulares—sectio III of Boas (1934), facies visceralis synsacri, pairs having foramina transversaria, numerus modalis (**ordered**):

a. zero; **b.** one; **c.** two;
d. three; **x.** noncomparable (ratites).

Note.—See: Boas (1934: fig. 4); Livezey (1998b: appendix A, character 126), concerning processes costales and transverses and variably deep foramina enclosed thereby. Distinct from fenestrae intertransversaria.

0919. Vertebrae thoracicae synsacri, caudalmost incorporated elements, i.e., those composing pila preacetabularis synsacri (**new term**), facies ventralis, margo caudalis, narrow but distinct transverse jugum, status:

a. absent; **b.** present.

0920. Vertebrae thoracicae synsacri, facies ventralis, lamina transversa synsacri, robust linkage among processes transverses vertebrales regardless of density of associated synostosis iliosynsacralis, i.e., lamina present regardless of union with facies ventralis of ala preacetabularis ilii, status:

a. absent or tenuous; **b.** present, robust.

Note.—Most obvious examples found among large-bodied taxa of Spheniscidae.

0921. Vertebrae acetabularis synsacri, processes costales, corpus bulbosus et lamina immediately proximal to synostosis with ala postacetabularis ilii, facies ventralis, crista iliaca intermedia, status:

a. absent; **b.** present;
x. noncomparable (Dromornithidae).

0922. Vertebrae acetabularis synsacri, processes costales, lamina immediately proximal to synostosis with ala postacetabularis ilii, facies ventralis, crista iliaca intermedia, status:

a. absent; **b.** present.

0923. Vertebrae acetabulares synsacri, processus costalis, lateral extension of two or three synostotic processes to unite with incisura ilioischiadica, margo cranialis, on pila acetabularis dividing acetabulum from spatium ilioischiadicum, status:

a. absent, principally by lateral limits of processes or caudal limit of margo cranialis of spatium ilioischiadicum;
b. present.

0924. Vertebrae acetabulares synsacri, processus costalis, extreme lateral prominence of single pair of processes associated with narrow, essentially sublinear isthmus synsacri (**new term**) medial to the acetabuli, status:
a. absent; **b.** present.

0925. Vertebrae acetabulares synsacri, corpus et arcus vertebralis, robustness relative to preceding vertebrae sacrales (lumbares et thoracicae) and following (caudales), forma:
a. subequal; **b.** distinctly greater.
Note.—See: Xu (2002: suite II, character 22).

0926. Facies dorsalis synsacri, caudal (posterior, distal) elements (i.e., elements caudal to level of processes antitrochanterici), pronounced lateromedial compression of elements, with corresponding narrowing of facies dorsales of synsacrum caudally, status:
a. absent; **b.** present.
Note.—See: Cracraft (1974: character 14); Cracraft (1985: character 27); Bledsoe (1988: appendix, character 35); Novas (1996: appendix, characters M7 and 2 [part]), including associated formation of "pronounced ventral 'keel'"; K. Lee et al. (1997: appendix 1, character 19).

0927. Facies dorsalis synsacri, caudal (posterior, distal) elements, pronounced lateromedial compression of elements, associated with close proximity or contact between ala postacetabularis ilii, crista spinalis (dorsalis) synsacri, status:
a. absent; **b.** present.
Note.—See: Cracraft (1982: series 2, character 1); Cracraft (1985: character 27); Cracraft (1988: series XI, character 1); Maryanska et al. (2002: appendix 1, character 110), in terms of fusion of sacral spines.

0928. Facies dorsalis synsacri, pars postacetabularis, distinct concavitas delimited by crista dorsolateralis, status:
a. absent; **b.** present.

0929. Vertebrae synsacrales, incorporated vertebrae caudales synsacrales (vertebrae caudales stabiles)—sectio IV by Boas (1934)—numerus modalis:
a. three to six;
b. seven to eight, rarely nine.
Note.—Tallies of "sacral" vertebrae, the series cranial to the vertebrae caudales stabiles, were based on structural diagnoses, notably prominence of interposed cristae iliacae intermediae supporting the acetabulum (cf. Van Oort 1905), as opposed to the presumptive assignment of a single vertebra sacralis as evidently done by Boas (1934).

0930. Vertebrae caudales stabiles synsacri—sectio IV of Boas (1934)—facies dorsalis synsacri, crista spinosa synsacri, inclusion of medial fenestrae interspinales dorsales, status:
a. absent; **b.** present.
Note.—These perforations are medial and unpaired along midline of crista dorsalis synsacri planum synsacralis, marking hiatae between processes spinoses (dorsales) within osseus lamina between margines dorsales of alae (partes) postacetabulares iliorum; often co-occur with bilateral fenestrae intertransversariae.

0931. Vertebrae caudales stabiles synsacri—sectio IV of Boas (1934)—facies visceralis synsacri, processes costales et transversales, pars distales, pronounced sigmoidal curvature with 90° torsion and broadening of processes immediately medial to suturae iliosynsacralis, status:
a. absent; **b.** present.

0932. Vertebrae caudales stabiles synsacri—sectio IV of Boas (1934)—facies dorsalis synsacri, crista spinosa synsacri, mediodorsal separation of cristae spinosae (dorsales) from margines dorsales of alae (partes) postacetabulares iliorum by elongate fissurae dorsales iliorum (**new term**), status:
a. absent; **b.** present.

0933. Vertebrae synsacrales, cranialmost vertebrae caudales synsacri, facies lateralis vertebrae, penetration and visibility through foramen ilioischiadicum (lateral perspective), status:
a. absent; **b.** present;
x. noncomparable (Aepyornithiformes, Dinornithiformes).

0934. Vertebrae caudales stabiles synsacri—sectio IV of Boas (1934)—facies dorsalis synsacri, crista spinosa synsacri, height of processes relative to combined heights of corresponding arcus et corpus vertebrales:
a. distinctly greater; **b.** distinctly less;
x. noncomparable, vertebrae in sectio lacking (Rheidae).

0935. Extremitas caudalis synsacri, processes transverses, termini laterales, eminentia angulares (**new term**), status:
a. absent;
b. present, defining small triangular points extending beyond margo caudalis of ala postacetabularis ilii.
Note.—Similar, but more-robust and less-angular eminentiae characterize some Coraciiformes (e.g., *Brachypteracias* and *Leptosomus*).

0936. Extremitas caudalis synsacri, vertebra synsacri ultima (**new term**), modal craniocaudal position relative to ala postacetabularis ilii, margo caudalis ilii at medial extreme (i.e., relative to margo medialis of incisura caudalis pelvis):
a. cranial;
b. coincident, typically interposed between medial termina of pilae postrenales;
c. largely or completely caudal;
x. noncomparable (Rheidae).

Note.—New term refers to caudalmost *synostotic* vertebrae *synsacri verae*.

0937. Extremitas caudalis synsacri, vertebra synsacri ultima (**new term**), facies ventralis, processes transverses distinctly paddle-shaped (i.e., termina distales of processes transverses spatulate), typically producing lobate margo caudalis of extremitas caudalis synsacri, and enclosing comparatively conspicuous, dorsally exposed foramina intertransversaria, status:

a. absent; **b.** present.

Note.—See: Hughes (2000: appendix 2, character 131). Essentially describes the tenuous synostosis and dorsal exposure of the last ankylosed vertebra caudalis synsacri.

0938. Extremitas caudalis synsacri, corpus vertebrae, facies articularis cranialis et caudalis, forma (plana transversalia):

a. approximately circular;

b. dorsoventrally compressed.

Note.—See: Sues (1997: appendix 1, character 26); Xu et al. (1999a: character 34).

0939. Extremitas caudalis synsacri (sectio IV of Boas 1934), caudal (posterior, distal) elements, differentiation (primarily ventral prominence of corpus and craniocaudal broadening and change in orientation of processes transverses) relative to more-cranial elements, and structurally associated with ala (pars) postacetabularis ilii, facies ventralis, recessus caudalis fossae, lamina ventralis, margo cranialis (if recessus present) or pila postrenalis, status et numerus vertebrae (**ordered**):

a. absent;

b. present, affecting one vertebra;

c. present, affecting two vertebrae;

x. noncomparable, ala postacetabularis ilii not articulating with vertebrae (ratites).

Note.—See: Payne and Risley (1976: character 30), regarding depth of recessus among Ardeidae; Livezey (1998b: appendix A, character 122), pertaining to heterogeneity of processes transverses of sectiones vertebrae caudales III et IV of Boas (1934) are treated; Livezey (1998b: appendix A, character 125), in which craniocaudal breadths, dorsal planarity of interacetabular and postacetabular vertebrae were contrasted.

0940. Extremitas caudalis synsacri—sectiones I–IV of Boas (1934)—processes transverses vertebrae, comparatively vertical orientation, status:

a. absent; **b.** present.

0941. Facies dorsalis synsacri, fenestrae intertransversariae, status et forma modalis (**ordered**, basal state “b”):

a. absent;

b. present (at least vertebrae caudales stabiles), comparatively small;

c. present (at least vertebrae caudales stabiles), comparatively large;

x. noncomparable (Struthionidae, Rheidae, Apterygidae, Gaviidae, Podicipedidae).

Note.—See: Strauch (1978: character 56), reanalyzed by Björklund (1994: appendix) and Chu (1995); G. Mayr and Ericson (2004: appendix I, character 68).

0942. Facies dorsalis synsacri, zygapophyses craniales et caudales, synostosis resulting in aspect (dorsal perspective) of jugum zygapophysialis sinuosis (**new term**), status:

a. absent; **b.** present.

Note.—See: Norell et al. (2001: appendix 1, character 115); J. M. Clark et al. (2002a: appendix 2.2, character 114); Xu (2002: suite II, character 236), in terms of “fused zygapophyses forming a sinuous ridge”; Hwang et al. (2004: supplement, character 111); Xu and Norell (2004: supplement, character 111).

0943. Facies lateralis synsacri, recessus dorsocranialis pneumatici (“pleurocoelae”) synsacri, status:

a. absent throughout;

b. present, at least in cranialmost elements;

x. noncomparable (Neornithes).

Note.—See: Russell and Dong (1994a [1993a]: table 2, character 28); Holtz (1994a: appendix 1, character 48); Norell and Makovicky (1997); Forster et al. (1998: supplement, character 38); J. D. Harris (1998: appendix 2, character 70); Makovicky and Sues (1998: appendix 1, character 44); Xu et al. (1999a: character 35), regarding pleurocoels of “sacral vertebrae”; Xu et al. (1999b: character 32); Azuma and Currie (2000: appendix 1, character 99); Currie and Carpenter (2000: appendix 1, character 59); Holtz (2000 [1998]: appendix I, character 183); Norell et al. (2001: appendix 1, character 113); J. M. Clark et al. (2002a: appendix 2.2, character 116); Maryanska et al. (2002: appendix 1, character 112); Xu (2002: suite II, character 145); Xu et al. (2002a: supplement, character 90); Rauhut (2003: character 115); Hwang et al. (2004: supplement, character 113); Xu and Norell (2004: supplement, character 113).

0944. Facies lateralis synsacri (sectio IV of Boas 1934), exposure of corpus vertebrae of included elements ventral to ala postacetabularis ilii, margo ventralis, status et forma (**unordered**):

a. absent;

b. present, limited, exposure pertains only to ventral portions of vertebrae;

c. present, extreme, facies laterales of caudalmost vertebrae almost completely ventral to margo ventralis of ala postacetabularis ilii.

0945. Facies lateralis synsacri—sectio IV of Boas (1934)—extreme bilateral compression of all elements caudal to processus antitrochantericus, including absence of processes transverses et costales vertebrae, status:

a. absent; **b.** present.

Note.—See: Strauch (1978: character 53), reanalyzed by Björklund (1994: appendix) and Chu (1995), in reference to "lumbar vertebral parapophyses."

0946. Facies dorsalis et visceralis synsacri, lamina transversa synsacri, margo lateralis laminae transversae, forma marginalis (**unordered**):

a. "unilobate" or "hourglass-shaped"—i.e., variably wide and linear cranially, variably narrowing closely cranial to acetabulae, wide or attaining greatest breadth opposite processes antitrochanterici, narrowing again to terminate with approximately linear segmenta caudalis;

b. "funnel-shaped"—i.e., broadest cranially and tapering essentially monotonically caudad;

c. "narrowly linear"—i.e., margines laterales synsacri essentially straight and synsacrum comparatively narrow throughout;

d. "broadly linear"—i.e., margines laterales synsacri essentially straight and synsacrum comparatively broad throughout.

Note.—Largely a function of the gradation in lengths of processes transverses, margo lateralis synsacri typically is evaluated primarily from ventral (visceral) perspective (especially cranial portion), whereas caudal to acetabulum this character can be evaluated from either dorsal or ventral perspectives (notable exceptions being bilaterally compressed taxa, streamlined for cursorial or natatorial locomotion).

0947. Facies visceralis synsacri, bulla intumescentia lumbosacralis (**new term**), size relative to adjacent vertebrae synsacrales:

a. negligibly differentiated;

b. distinctly enlarged, mediolaterally expanded for more than one-half the craniocaudal length of the synsacrum;

x. noncomparable (Gaviidae, Podicipedidae).

Note.—See: Breazile and Kuenzel (1993: annotation 1); Kuhlenbeck (1975) for ratites; Hughes (2000: appendix 2, character 130), regarding cuculiforms. Canalis synsacri (vertebralis) enlarged where containing the intumescentia lumbosacralis (also related to medulla spinalis, pars cervicalis, intumescentia cervicalis), and formerly distinguished nomenclaturally as cranium inferior (ischiadicus), e.g., Barkow (1856).

0948. Facies visceralis synsacri, bulla intumescentia lumbosacralis (**new term**), extreme ventrocranial position in which intumescentia extends craniad to adjoin cranialmost synostotic vertebra thoracica synsacri et margo cranialis synsacri, and exposed (lateral perspective) ventrad to alae preacetabulares iliorum, status:

a. absent; **b.** present.

0949. Facies visceralis synsacri, corpus synsacri, intumescentia lumbosacralis, forma (in excess of general enlargement):

a. variably concave, forming a variably conspicuous shallow sulcus (ventralis corporis) intumescentialis (**new term**), and bordered by parallel, linear margines ventrales;

b. planar or slightly convex or medially alar, latter forming crista ventralis synsacri;

x. noncomparable (Dromornithidae).

Note.—See: Maryanska et al. (2002: appendix 1, character 111); Ji et al. (2003a: 22).

0950. Facies visceralis synsacri, corpus synsacri, crista ventralis synsacri, comprising prominent processes variably synostotically united at ventral termini by arcus and thereby enclosing one or more fenestrae intercristales, status:

a. absent, including some having similar structures in other sectiones of the columna vertebralis;

b. present, limited to cranialmost vertebrae thoracicae synsacri.

0951. Facies visceralis synsacri, corpus synsacri, facies ventralis synsacri, forma:

a. carinate, possessed of crista ventralis synsacri;

b. gently rounded, flat, or distinct, longitudinal, sulcus ventralis corporis.

Note.—See: Sanz and Bonaparte (1992: character 7), with respect to "hypapophyses in sacral vertebrae"; Makovicky (1995); Chiappe et al. (1996: appendix 1, character 77); Novas (1996: appendix, character 2, part); Novas (1997: appendix, characters 2 and 22, part); Novas and Puerta (1997), repeated identically by Novas (1997); Chiappe et al. (1998: character 22); Ji et al. (1998: supplement, character 22), with respect to "caudal portion of the synsacrum forming a prominent ventral keel"; Chiappe (2001a: appendix 1, character 43); Norell et al. (2001: appendix 1, character 112); Chiappe (2002: appendix 20.2, character 43); J. M. Clark et al. (2002a: appendix 2.2, character 115); Xu (2002: suite II, character 114); Xu et al. (2002a: supplement, character 89), citing Novas (1997), who distinguished two types of corpora lacking cristae ventrales, those convex or rounded, and those flattened; Rauhut (2003: character 114); Hwang et al. (2004: supplement, character 112); Xu and Norell (2004: supplement, character 112).

0952. Facies visceralis synsacri, corpus synsacri, comparatively great lateromedial compression and synostosis among elements rendering foramina transversaria reduced in diameter, and in which

crista ventralis, processus caroticus, et processus costalis rendered obsolete, status:
a. absent; **b.** present;
x. noncomparable (Rheidae).

0953. Facies lateralis synsacri, vertebrae acetabulares (i.e., those having disproportionately elongated processes costales oriented toward acetabulae—sectio III of Boas (1934)—foramina intervertebralia, forma *sensu* numerus modalis per parum (**ordered**):
a. zero foramina, facies lateralis synsacri acetabularis et postacetabularis forming an imperforate lamina;
b. one foramen, presumably common foramen passing between each pair of vertebrae, the ventral member evidently subject to loss (especially caudally), admitting ramus ventralis of respective couplet in plexus sacralis nervosum;
c. one distinct foramen dorsally with conspicuously reduced vestigium indicative of ventral member;
d. two distinct foramina passing between each pair of vertebrae.
Note.—Often visible only by craniolateral view through acetabulum.

0954. Facies visceralis synsacri, vertebrae acetabulares (i.e., those having disproportionately elongate processes costales oriented toward acetabulae—sectio III of Boas (1934)—lateral extent relative to rima acetabularis (**ordered**):
a. essentially extend(s) laterad to rima acetabularis;
b. approaches closer than one-half distance between columna vertebralis and rima acetabularis but distinctly proximad to rima acetabularis;
c. approaches less than one-half distance between columna vertebralis and rima acetabularis;
x. noncomparable (Dromornithidae).
Note.—See: Baumel and Witmer (1993: annotation 141b).

0955. Facies visceralis synsacri, vertebrae acetabulares (i.e., those having disproportionately elongated processes costales—sectio III of Boas (1934)—cranial and caudal components of orientation toward acetabulae (**ordered**):
a. cranial or craniodorsal to acetabulum, variably coalesced at synostosis with ilium, pars acetabularis;
b. caudodorsal to acetabulum, synostotic as single composite with ilium;
c. caudal to acetabulum, synostotic as single composite with ilium et ischium, pars acetabularis.

0956. Facies visceralis synsacri, vertebrae acetabulares et caudales stabiles synsacri, processes costales et foramina transversariae, *prominence and continuity* from acetabulum to margo caudalis of extremitas caudalis synsacri, status et forma (**ordered**):
a. absent, limited to segment immediately caudal to acetabulum;
b. present, small; **c.** present, large.
Note.—Presumptively basal polarity typically assigned on basis of dorsoventral compression of elements in middle elements of sectio comprising vertebrae caudales stabiles, wherein closure of foramina transversariae.

0957. Facies visceralis synsacri, vertebrae acetabulares (i.e., those having disproportionately elongated processes costales—sectio III of Boas (1934)—and vertebrae caudales stabiles synsacri immediately caudal, distinctive aspect comprising prominently ventral processes costales (most ventral in cranial elements in series and receding dorsad caudally), extending laterad to margo caudalis of rima acetabularis, and caudal elements joined synostotically to ala postacetabularis ilii by processes costales progressively truncated and through irregular osseus lamina to point craniocaudally equal to pila postrenalis, and together forming a densely perforated, sloping system of struts roofing a recessus interacetabularis (**new term**), status:
a. absent; **b.** present;
x. noncomparable (ratites).
Note.—A particularly diagnostic feature is the dorsal lamina uniting the processes costales incorporated into this complex; see also "lamina procostalis caudae" (**new term**).

0958. Facies visceralis synsacri, vertebrae acetabulares (i.e., those having disproportionately elongated processes costales sectio III of Boas (1934)—processes costales, uniquely robust aspect in which elements between acetabulae are strongly synostotic and form a dense pila interacetabularis (**new term**), status:
a. absent;
b. present, typically extending (cranio)ventrad to ilii, pars acetabularis.

Vertebrae caudales stabiles

Note.—*Eoalulavis* evidently lacked preservation of any vertebrae caudales. This, together with poor discernability of elements of the synsacrum, renders coding of any characters of the vertebrae caudales unfeasible in this taxon.

0959. Vertebrae caudales synsacri (stabiles)—sectio IV of Boas (1934)—facies dorsalis of extremitas caudalis synsacri, marked bilateral sulci interilii (**new term**) formed by exceptionally prominent crista spinosa (dorsalis) synsacri at its terminus caudalis, juxtaposed with adjacent ventrally depressed processes transverses vertebrales bordered by lateral, medially sloping alae postacetabulares iliorum, status:
a. absent; **b.** present.

Note.—This unique feature is accompanied by an unusually extensive absence of dorsal lamina ilii, thereby exposing processes transverses in dorsal perspective.

0960. Synsacrum, vertebrae caudales, bilateral compression of elements and absence of processes transversariae, status:
a. absent; **b.** present.

0961. Vertebrae caudales synsacri (stabiles)—sectio IV of Boas (1934)—foramina transversaria, numerus parum modalis (**ordered**):
a. zero; **b.** one or two;
c. three or four; **d.** five or more.
Note.—See: Boas (1934: fig. 4); Livezey (1998b: appendix A, characters 125–126), concerning processes costales and transverses and variably deep foramina enclosed thereby. Distinct from fenestrae intertransversaria (above). Rare occurrence of bilateral asymmetry in presence of foramina (i.e., only one side of a given vertebra possesses foramen).

0962. Synsacrum, vertebrae caudales stabiles, columna extending at least partly ventrad to margo ventralis alae ilii postacetabularis, status (**ordered**):
a. absent, synsacrum enclosed (lateral perspective) bilaterally by ossa ilii;
b. present, only exposed in part;
c. present, completely exposed caudad, columna curving ventrad at extremitas caudalis alae ilii postacetabularis.

0963. Vertebrae caudales synsacri (stabiles)—sectio IV of Boas (1934)—proximal and distal synostosis of ventrally displaced processes transverses forming a semilaminar aspect (ventral perspective), thereby forming lamina procostalis caudae (**new term**), status:
a. absent; **b.** present.

0964. Vertebrae caudales synsacri (stabiles)—sectio IV of Boas (1934)—facies visceralis, hiatus postacetabularis synsacri (**new term**), status:
a. absent; **b.** present.
Note.—Absent vertebrae synsacrales are probably cartilaginous in life and variably indicated by ossified, vestigial ligamenta or processus dorsales. Vertebrae immediately cranial to hiatus are vestigia, and those caudal to the hiatus are vestigia along facies dorsalis symphysialis iliorum postacetabulares, the caudal (posterior, distal) elements approximating normality at terminus caudalis symphysialis. See: Gadow (1885) regarding anatomical variation among modern Rheidae.

0965. Vertebrae caudales synsacri stabiles—sectio IV of Boas (1934)—extremitas caudalis synsacri (caudalmost incorporated element), corpus vertebrae, facies articularis caudalis, forma superficialis:
a. concave or planar; **b.** convex.
Note.—See: Chiappe et al. (1996: appendix 1, character 78); Novas (1996: appendix, character 1), also purportedly characterizes cranialmost vertebra postsynsacralis; Novas (1996: appendix, character 20); Novas (1997: appendix, characters 1 and 21); Novas and Puerta (1997), see identical characters in Novas (1997); Chiappe et al. (1998: character 23); Ji et al. (1998: supplement, character 23); perhaps redundant with corresponding character of extremitas cranialis synsacri, i.e., descriptive in combination of heterocoely of vertebrae (syn)sacrales; Chiappe (2001a: appendix 1, character 44); Norell et al. (2001: appendix 1, character 114); Chiappe (2002: appendix 20.2, character 44); J. M. Clark et al. (2002a: appendix 2.2, character 117); Xu (2002: suite II, character 146); Hwang et al. (2004: supplement, character 114); Xu and Norell (2004: supplement, character 114).

0966. Vertebrae caudales synsacri (stabiles)—sectio IV of Boas (1934)—single element transitional between vertebrae caudales stabiles et liberae, processes transverses, synostosis with margines mediales of narrowly separated, parallel, elongated processes dorsolaterales, ala postacetabularis ilii, status:
a. absent; **b.** present.

0967. Vertebrae caudales synsacri (stabiles)—sectio IV of Boas (1934)—et cranial vertebrae caudales liberae, facies laterovisceralis (related to dorsoventral compression of elements), bilateral foramina (recesses) pneumatica ("pleurocoels") immediately basal to processes costales, status:
a. absent;
b. present, at least on cranialmost elements.
Note.—Evidently effects reduction in buoyancy related to subaquatic locomotion in most plesiomorphic Neornithes. See: Maryanska et al. (2002: appendix 1, character 115).

Vertebrae caudales cunctes (stabiles et liberae)

0968. Vertebrae caudales cunctes (i.e., stabiles et liberae), numerus modalis (**ordered**):
a. 61 or more; **b.** 45–60; **c.** 31–44;
d. 26–30; **e.** 16–25; **f.** ten to 15;
g. nine; **h.** seven or eight;
i. five or six; **j.** four.
Note.—Tallies include pygostylus (if present) as single element. See: Andrews (1897); Van Oort (1905); Strauch (1978: character 31), reanalyzed by Björklund (1994: appendix) and Chu (1995); Houde (1988: table 27, character 41); Cracraft (1986: appendix, characters 10–11, and 72); Gauthier (1986: 12–14), unindexed synapomorphies of Avialae, Aves, and Ornithurae; Cracraft (1988: series I, character 11; series II, character 4; series III, character 2); Sanz

and Bonaparte (1992: character 8); Sereno and Rao (1992); Chiappe and Calvo (1994: appendix I, character 21); Chiappe (1995a: legend for fig. 1); Chiappe 1995b: character 21); Elzanowski (1995: character O10); Sanz et al. (1995: appendix 2, character 20); Chiappe (1996: character 19); Chiappe et al. (1996b: appendix 1, character 19); Livezey (1996a: appendix 1, character 18); Novas (1996: appendix, character 30); Novas (1997: appendix, character 32); Novas and Puerta (1997); Livezey (1998b: appendix A, character 127); Makovicky and Sues (1998: appendix 1, character 55); Hou et al. (1996: character 29); Chiappe et al. (1998: character 29); Ji et al. (1998: supplement, character 29); Forster et al. (1998: supplement, character 33); Chatterjee (1999: appendix II, characters 37 and 39); Chiappe et al. (1999); Xu et al. (1999b: character 29, modified); Azuma and Currie (2000: appendix 1, character 21); Holtz (2000 [1998]: appendix I, character 190); Zhou et al. (2000); Chiappe (2001a: appendix 1, character 52); Currie and Chen (2001: 1712), in reference to *Sinosauropteryx*; Norell et al. (2001: appendix 1, character 122); Sereno (2001: table 2, character 42); Chiappe (2002: appendix 20.2, character 52); J. M. Clark et al. (2002a: appendix 2.2, character 124); Maryanska et al. (2002: appendix 1, character 119); Sereno et al. (2002), regarding *Sinornis*; Xu (2002: suite II, character 153); Xu et al. (2002a: supplement, character 98); Zhou and Zhang (2002: appendix III, character 63); Ji et al. (2003: 22); Rauhut (2003: character 117); Zhou and Zhang (2003), for *Jeholornis*; Hwang et al. (2004: supplement, character 121); Xu and Norell (2004: supplement, character 121); Ji et al. (2005: supplement, part I, character 203).

Vertebrae caudales liberae

***Note*.**—Virtually all vertebrae caudales among nonavialian Theropoda qualify as "liberae" because of the rudimentary synsacrum possessed by these taxa, whereas a fundamental structural distinction between vertebrae caudales stabiles et liberae pertains to the Neornithes. As previously, unless another state is given specifically, *Iberomesornis*, *Concornis* can be assumed to undetermined.

0969. Vertebrae caudales liberae (*sensu stricto*, sectio cranialis), numerus modalis (**ordered**):

a. 45 or more; **b.** 31–44; **c.** 26–30;
d. 16–25; **e.** ten to 15; **f.** nine;
g. seven or eight; **h.** five or six; **i.** four.

***Note*.**—Counts here include pygostylus (if present) as one additional element. See: Norell and Clarke (2001: appendix I, character 63), who used eight as breakpoint for Ornithurae, treated similarly by J. A. Clarke (2002: appendix I, character 63), J. A. Clarke and Norell (2002: appendix 2, character 63), and J. A. Clarke (2004: appendix 1, character 63); Zhou and Zhang (2002: appendix III, character 63); G. Mayr and Ericson (2004: appendix I, character 34); Ji et al. (2005: supplement, part I, character 63).

0970. Vertebrae caudales liberae (sectio cranialis), corpus vertebrae, facies lateralis corporis, processus costalis, status:

a. present, vestigial; **b.** absent.

***Note*.**—See related character under "costae." Costae verae of vertebrae caudales, including articulationes capitulae et tuberculae costarum, represent plesiomorphy of basalmost Reptilia, confirmed only among seymouriamorphs (Romer 1956: 269).

0971. Vertebrae caudales liberae (sectio cranialis), locus transitionalis (i.e., morphological "transition point") principally diagnosed by means of conformational changes (e.g., craniocaudally from short corpora and long processes transverses to long corpora and truncate or absent processes transverses), status:

a. present; **b.** absent or indistinct.

***Note*.**—See: Gauthier (1986); J. D. Harris (1998: appendix 2, character 77), emphasizing mere distinctness of transition; Norell et al. (2001: appendix 1, character 116); J. M. Clark et al. (2002a: appendix 2.2, character 118); Maryanska et al. (2002: appendix 1, character 113); Xu (2002: suite II, character 147); Xu et al. (2002a: supplement, character 92); Brochu (2003); Hwang et al. (2004: supplement, character 115); Xu and Norell (2004: supplement, character 115); Ji et al. (2005: supplement, part I, character 204), dichotomy in comparative uniformity in widths of corpora vertebrales I–VI, presumably a corollary of variation in "transition point."

0972. Vertebrae caudales liberae (sectio cranialis), corpora vertebrales, morphological locus transitionalis (**new term**) of elements, principally diagnosed by means of conformational changes in processes transverses, ordinal meristics of last vertebra caudalis craniad to locus, situs:

a. comparatively distal, caudad to tenth element in series, i.e., vertebra caudalis decimus;
b. comparatively proximal, coincident with or craniad to vertebra caudalis decimus;
x. noncomparable because locus transitionalis not evident (Neornithes).

***Note*.**—Gatesy and Dial (1996) analyzed the functional implications of the functional and structural hiatus within the tails of modern Aves. Locus transitionalis ("transition" point) ideally includes qualitative changes in processes spinoses, processes transverses, processes ventrales, and corpora vertebrales; given different "points" corresponding to some or all of these aspects, it may be necessary to delimit several such "loci."

See: Novas (1997: appendix, characters 33–35) and Novas and Puerta (1997) delimited vertebrae caudales 1–23 *vs*. 1–12 for processes spinoses, 16–25 *vs*. 12 for processes transverses, and 17 *vs*. ten for processes ventrales. See also: Russell (1972); Gauthier (1986: text characters 20, 40, and 71); Russell and Dong (1994a [1993a]: table 2, character 31); Russell and Dong (1994b [1993b]: list B, character 4); Holtz (1994a: appendix 1, character 107); Novas (1996: appendix, character 32); Forster et al. (1998: supplement, character 35); J. D. Harris (1998: appendix 2, character 78); Xu et al. (1999b: character 30); Holtz (2000 [1998]: appendix I, character 197); Azuma and Currie (2000: appendix 1, character 19); Currie and Carpenter (2000: appendix 1, character 66); Xu et al. (2000: supplement, character 21); Norell et al. (2001: appendix 1, character 117); J. M. Clark et al. (2002a: appendix 2.2, character 119); Xu (2002: suite II, character 148); Xu et al. (2002a: supplement, character 93); Hwang et al. (2004: supplement, character 116); Xu and Norell (2004: supplement, character 116).

0973. Vertebrae caudales liberae (sectiones intermedius et caudalis), arcus vertebrae, facies lateralis, vertebrae cum processes transverses, numerus modalis (**ordered**):

a. 16 or more; **b.** 12–15;

c. 11 or fewer.

Note.—See: Gauthier (1986); Makovicky and Sues (1998); Rauhut (2003: character 118).

0974. Vertebrae caudales liberae (sectiones intermedius et caudalis), arcus vertebrae, facies dorsalis, vertebrae cum processes (dorsales) spinoses, numerus modalis:

a. 11 or more; **b.** fewer than 11.

Note.—See: Rauhut (2003: character 119).

0975. Vertebrae caudales liberae (sectiones intermedius et caudalis), combined length relative to that of sectio cranialis, forma:

a. subequal;

b. substantially greater, length of former at least 130% of that of latter;

x. noncomparable (Dromornithidae).

Note.—See: Novas (1996: appendix, character A3), who delimited as less than 175% *vs*. greater than 200%; Novas (1997: appendix, character 37); Novas and Puerta (1997), using criterion of 130%, and see identical characters in Novas (1997); Forster et al. (1998: supplement, character 40); Xu et al. (1999b: character 34); Xu et al. (2000: supplement, character 23); Xu (2002: suite I, character 49). Assumed herein that sectiones intermedius et caudalis correspond to vertebrae caudales caudal to the "transition" point.

0976. Vertebrae caudales liberae (sectio intermedius), arcus vertebrae, processus spinosus, margo cranialis, forma:

a. linear;

b. angular (margo convex), sectio dorsalis more-strongly inclined caudad than sectio ventralis within elements.

Note.—See: Rauhut (2003: character 123), with respect to "cranial mid-caudal elements."

0977. Vertebrae caudales liberae, arcus vertebrae, foramina transversaria, numerus modalis parum (**ordered**):

a. zero; **b.** one or two;

c. three or four.

Note.—See: Boas (1934: fig. 4); Livezey (1998b: appendix A, character 126), concerning processes costales and transverses and variably deep foramina enclosed thereby, latter distinct from fenestrae intertransversaria.

0978. Vertebrae caudales liberae (especially cranial elements), arcus vertebrae, zygapophyses craniales (and associated cylindrical derivations), prominence, or cranial extent relative to corpus vertebrae ("centrum") of the preceding element, forma (**ordered**):

a. extremely elongate—typically approximating three to ten times the length of associated corpus;

b. moderately elongate—extending at least to midpoint of preceding corpus vertebrae;

c. truncate or absent—extending no more than one-quarter of the length of the preceding corpus vertebrae.

Note.—The "rodlike" elongations of the zygapophyses craniales of Dromaeosauridae and allies are bilateral, distally bifurcated amplexes (clasps), stabilizing with torus dorsalis of preceding vertebra, zygapophyses caudales rendered obsolete (P. J. Currie, pers. comm.).

See: Sanz and Bonaparte (1992: character 9); Novas (1994 [1993]: appendix, character 41); Novas (1996: appendix, character 34); Novas (1997: appendix, character 36); Novas and Puerta (1997), identically treated by Novas (1997); Chiappe et al. (1998: character 24); Ji et al. (1998: supplement, character 24); Forster et al. (1998: supplement, character 41); Xu et al. (1999b: character 35); Holtz (2000 [1998]: appendix I, character 198); Xu et al. (2000: supplement, character 24), with respect to "prezygapophyses of distal caudal vertebrae"; Chiappe (2001a: appendix 1, character 46); Ji et al. (2001), regarding unnamed dromaeosaurid NGMC 91-A; Norell and Clarke (2001: appendix I, character 66), treated similarly by J. A. Clarke (2002: appendix I, character 66), J. A. Clarke and Norell (2002: appendix 2, character 66), and J. A. Clarke (2004: appendix 1, character 66); Chiappe (2002: appendix 20.2, character 46), using criterion of 25% longer than corpus; Xu et al. (2002a: supplement, character 97), allocating taxa by criterion of zygapophyses craniales having lengths between one-third and entire length of corresponding corpora vertebrales (states a', b', and c'); Ji et al. (2003a: 22); Ji et al. (2005: supplement, part I, character 66).

0979. Vertebrae caudales liberae (cranial elements), "highly modified" forma:

a. present;

b. absent, corpora comparatively typical, taller, ovate in planum transversus.

Note.—Shape encoded here is such that elements so conformed can be rested on end; processus dorsalis last caudal to element IX in which dens is distinctively rectangular in planum transversus.

See: Carroll (1997: 312), possibly redundant in part with other, earlier works, and clearly comprising several distinct characters. Included in part by Holtz (1994a: appendix 1, character 36); Makovicky and Sues (1998: appendix 1, character 52); Holtz (2000 [1998]: appendix I, character 194), in reference to highly modified, boxlike proximal vertebrae caudales; Norell et al. (2001: appendix 1, character 118); J. M. Clark et al. (2002a: appendix 2.2, character 120); Xu (2002: suite II, character 149); Xu et al. (2002a: supplement, character 94), in which a third state pertaining to a carinate processus ventralis was appended (see under processus ventralis); Hwang et al. (2004: supplement, character 117); Xu and Norell (2004: supplement, character 117).

0980. Vertebrae caudales liberae, processes transverses, median length relative to craniocaudal width of processes, forma (**ordered**):

a. obsolete, median length less than width;

b. truncate, median length approximately equal to width;

c. moderate, median length of majority of elements approximately twice as great as width;

d. elongate, median length of majority of elements approximately three times as great as width;

x. noncomparable, processes transverses lacking on vertebrae caudales (*Apteryx*).

Note.—See: Livezey (1998b: appendix A, character 128); Norell and Clarke (2001: appendix I, character 65), treated similarly by J. A. Clarke (2002: appendix I, character 65), J. A. Clarke and Norell (2002: appendix 2, character 65), and J. A. Clarke (2004: appendix 1, character 65); Zhou and Zhang (2002: appendix III, character 65); Ji et al. (2005: supplement, part I, character 65).

0981. Vertebrae caudales liberae (cranial elements), facies ventralis corporis, sulcus ventralis (**new term**), status:

a. absent; **b.** present.

Note.—See: Rowe and Gauthier (1990); Holtz (2000 [1998]: appendix I, character 193); Rauhut (2003: character 120).

0982. Vertebrae caudales liberae (cranial elements), facies ventralis corporis, processus ventralis, status:

a. absent; **b.** present, carinate.

Note.—See: Novas (1997: appendix, character 23), identically treated by Novas and Puerta (1997), regarding elongation of "haemal arches of proximal caudals"; Xu et al. (2002a: supplement, character 94); Rauhut (2003: character 121).

0983. Vertebrae caudales liberae, vertebra caudalis postsynsacralis (**new term**), corpus vertebrae, distinct bilateral compression, status:

a. absent; **b.** present.

Note.—New term refers to cranialmost element of vertebrae caudalis liberae after Baumel (1988). See: Chiappe et al. (1998: character 26); Ji et al. (1998: supplement, character 26); Chiappe (2001a: appendix 1, character 48); Chiappe (2002: appendix 20.2, character 48).

0984. Vertebrae caudales liberae (cranial elements), corpus vertebrae, facies articularis cranialis et caudalis, forma transversa (**unordered**):

a. subcircular; **b.** cordiform;

c. rectangular.

Note.—See: Ostrom (1976a); Gauthier (1986: text characters 20, 40, and 77); Novas (1996: appendix, character 35); Sues (1997: appendix 1, character 27); Xu et al. (1999a: character 36); Holtz (1994a: appendix 1, character 36); Holtz (2000 [1998]: appendix I, character 194); Rauhut (2003: character 127).

0985. Vertebrae caudales liberae, corpus vertebrae, facies articularis cranialis et caudalis, conformation and nature of articulatio intervertebralis, typus:

a. amphicoelous; **b.** procoelous.

Note.—See: Chiappe et al. (1996: appendix 1, character 89); Novas (1996: appendix, characters M6 and 19); Novas (1997: appendix, character 21, part); Novas and Puerta (1997), see identical characters in Novas (1997); Chiappe et al. (1998: character 25); Ji et al. (1998: supplement, character 25); Forster et al. (1998: supplement, character 42); Chiappe (2001a: appendix 1, character 47); Chiappe (2002: appendix 20.2, character 47). "Procoely" represents a craniocaudal isomeriform of "opisthocoely," in which facies articularis cranialis is concave and facies articularis caudalis is convex. A discus intervertebralis (perhaps related to intercentra) is interposed at the juncturae caudae between the corpora of vertebrales caudales liberae (Barkow 1856; Radu 1975), rendering interpretations of corresponding facies articulares based on skeletons subject to variance not readily interpretable using typically prepared skeletal specimens and fossils.

0986. Vertebrae caudales liberae (caudal—posterior, distal—elements), corpus vertebrae, facies ventralis corporis (exclusive of serially variable processus haemalis or "chevron bones"), crista(e) [processus] ventralis corporis, status et forma:

a. present, bicarinate;

b. absent, essentially cylindrical.

Note.—See: Russell and Dong (1994b [1993b]: troödontid character 16, part); J. D. Harris (1998: appendix 2, character 73), equating "ventral groove" with a "double ventral keel"; Azuma and Currie (2000: appendix 1, character 20); Currie and Carpenter (2000: appendix 1, character 62); Currie and Chen (2001); Zhou and Zhang (2002: appendix III, character 64); G. Mayr and Clarke (2003: appendix A, character 59). Chevron bones clearly present in "pretransitional" vertebrae caudales in most basal taxa, in caudalmost prepygostylous element in terminal taxa.

0987. Vertebrae caudales liberae (caudal/distal elements), corpus vertebrae, craniocaudal length relative to dorsoventral height, forma:

a. great, corpus "elongate";

b. small, corpus "short."

Note.—See: Sues (1997: appendix 1, character 28); Makovicky and Sues (1998: appendix 1, character 58), who contrasted "craniocaudally truncated, cylindrical elements with "flattened and platelike"; Xu et al. (1999a: character 37); Ji et al. (2003a: 22); Rauhut (2003: character 126).

0988. Vertebrae caudales liberae ("distal" elements), corpus vertebrae, craniocaudal pattern of relative elongation *in serriatum*, status (**ordered**):

a. length of distal elements *markedly* less than that of proximal elements;

b. length of distal elements approximately equal to that of proximal elements;

c. length of distal elements more than 130% that of proximal elements.

Note.—See: Makovicky and Sues (1998: appendix 1, character 54); Holtz (2000 [1998]: appendix I, character 200); Maryanska et al. (2002: appendix 1, character 118).

0989. Vertebrae caudales liberae (cranialmost elements), arcus vertebrae, lamina lateralis arcus, incisura caudalis arcus, closure of margo caudalis to produce foramina caudalis arcus (**new term**), status:

a. absent, incisura remains open caudally;

b. present, incisura closed by osseus arcus to produce entire foramen.

0990. Vertebrae caudales liberae, arcus vertebrae, lamina dorsalis arcus, processus spinosus (arcus), status et forma (**unordered**):

a. present, a variably dorsally elongate spina or bilaterally compressed carina;

b. present, a craniocaudally compressed, terminally bilobate processus;

c. present, a moderately small boss, torus, or tuberculum;

d. absent, lamina dorsalis arcus essentially flat, or concave with sulcus.

Note.—See: Gauthier (1986); Russell and Dong (1994a [1993a]: table 2, character 30); Novas (1996: appendix, character 31); Makovicky and Sues (1998: appendix 1, character 56), the latter two identically emphasizing caudal (distal) vertebrae caudales; Norell et al. (2001: appendix 1, character 120); J. M. Clark et al. (2002a: appendix 2.2, character 122); Maryanska et al. (2002: appendix 1, character 116), regarding bilobate apices; Xu (2002: suite II, character 151); Xu et al. (2002a: supplement, character 96), in reference to conformation of "neural spines" on *distal elements* as "low ridge," "absent," or "midline sulcus"; Hwang et al. (2004: supplement, character 119); Xu and Norell (2004: supplement, character 119).

0991. Vertebrae caudales liberae (cranial elements), arcus vertebrae, processus spinosus, forma *sensu* craniocaudal inclination relative to facies dorsalis of arcus vertebrae:

a. caudad, typically rodular;

b. essentially perpendicular or craniad, typically rodular, infrequently laminar.

Note.—See: Novas (1992: character D); J. D. Harris (1998); Holtz (2000 [1998]: appendix I, character 179); Rauhut (2003: character 124).

0992. Vertebrae caudales liberae, arcus vertebrae, lamina dorsalis arcus, processus spinosus (arcus), vertebrae caudales possessing processes spinoses, situs:

a. extending beyond vertebra caudalis (X) decimus;

b. limited to elements cranial to vertebra caudalis (X) decimus;

x. noncomparable because of limited number of vertebrae caudales (Neornithes).

Note.—See: Holtz (2000 [1998]: appendix I, character 192); Norell et al. (2000: appendix 1, character 30); Maryanska et al. (2002: appendix 1, character 117).

0993. Vertebrae caudales liberae, arcus vertebrae, lamina dorsalis arcus (dorsal perspective), processus spinosus (arcus), distinctive diagonally cruciate ("X-shaped") forma:

a. absent; **b.** present.

Note.—See: Holtz (2000 [1998]: appendix I, character 156).

0994. Vertebrae caudales liberae (especially cranial elements), arcus vertebrae, lamina dorsalis arcus, processus spinosus (arcus), forma apicalis:

a. unipartite or only weakly bilobate;

b. deeply bifurcate, producing widely divergent, bilateral alae bordering deep medial incisura.

Note.—See: Russell and Dong (1994a [1993a]: table 2, character 29).

0995. Vertebrae caudales liberae, arcus vertebrae, lamina dorsalis arcus, processus spinosus (arcus), separation into cranial and caudal spina aut alae, status:

a. absent, i.e., processus spinosus singular, undivided;

b. present, i.e., processus spinosus divided into cranial and caudal subparts.

Note.—See: Makovicky (1995); Norell et al. (2001: appendix 1, character 119); J. M. Clark et al. (2002a: appendix 2.2, character 121); Xu (2002: suite II, character 150); Xu et al. (2002a: supplement, character 95); Rauhut (2003: character 125); Hwang et al. (2004: supplement, character 118); Xu and Norell (2004: supplement, character 118).

0996. Vertebrae caudales liberae, arcus vertebrae, lamina dorsalis arcus, processus spinosus (arcus), excavationes cranialis et caudalis (**new terms**), foramina accessoriae (**new term**), status:

a. absent; **b.** present.

Note.—See: J. D. Harris (1998: appendix 2, character 74); Currie and Carpenter (2000: appendix 1, character 63), with respect to "subsidiary foramina in proximal and distal excavations in neural spines."

0997. Vertebrae caudales liberae, arcus vertebrae, processus transversus vertebrae, status ossium *in seriatum* (**ordered**):

a. present virtually throughout cauda, processes transverses present in elements including vertebrae caudales XV and more-caudal members;

b. present only proximally, processes transverses absent in elements XV and beyond;

c. vestigial and limited to cranialmost few elements, or absent.

Note.—See: Holtz (1994a: appendix 1, character 87); Holtz (2000 [1998]: appendix I, character 196); Maryanska et al. (2002: appendix 1, character 114); Zhou and Zhang (2002: appendix III, character 65).

0998. Vertebrae caudales liberae, arcus vertebrae, processus transversus vertebrae, angulus craniocaudalis (dorsal perspective) with respect to facies lateralis corporis:

a. approximately perpendicular;

b. distinctly acute, resulting in marked caudal angulation;

x. noncomparable (palaeognathous Neornithes, Podicipedidae).

0999. Vertebrae caudales liberae, arcus vertebrae, processus transversus vertebrae, angulus dorsoventralis (craniocaudal perspective) relative to facies lateralis corporis (**ordered**):

a. dorsally obtuse, processes angling distinctly ventrad;

b. approximately coplanar with planum transversus;

c. dorsally acute, processes angling markedly dorsad;

x. noncomparable (palaeognathous Neornithes, Podicipedidae).

1000. Vertebrae caudales liberae, arcus vertebrae, processus transversus vertebrae (dorsal perspective), craniocaudal gradation in lateromedial lengths, status:

a. gradation absent or obsolete;

b. present, cranialmost elements are relatively narrow, middle elements are relatively long, and distal elements are relatively narrow, resulting in "spatulate" profile of ossa caudae in dorsal view;

x. noncomparable (palaeognathous Neornithes, Podicipedidae).

1001. Vertebrae caudales liberae, arcus vertebrae, processus transversus vertebrae, abrupt disappearance of processes transverses in vertebra propygostyli, status:

a. absent, no abrupt disappearance;

b. present, abrupt deviation from conformational trend within columna vertebralis in complete absence of processus transversus;

x. noncomparable (palaeognathous Neornithes, Podicipedidae).

1002. Vertebrae caudales liberae, arcus vertebrae, foramina intervertebralia, persistence in adult, status (**ordered**):

a. absent throughout vertebrae caudales stabiles et liberae;

b. present in vertebrae caudales stabiles only;

c. present in both vertebrae caudales stabiles et liberae.

Note.—As these foramina are typically found in juvenile birds in many taxa (Baumel and Witmer 1993: annotation 143a), persistence into adulthood may be considered paedomorphic.

1003. Vertebrae caudales liberae, caudal (posterior, distal) elements, zygapophyses craniales, length relative to those of associated corpora vertebrae and (if elongated) interlocking or ankylosis among series of vertebrae (**ordered**):

a. zygapophyses craniales obsolete or completely absent;

b. zygapophyses craniales present but manifest only slight elongation, extend less than one-half length of associated corpus vertebralis, "interlocking" among vertebrae minimal;

c. zygapophyses craniales manifest moderate elongation, extend more than one-half but less than one length of associated corpus vertebralis, "interlocking" among vertebrae moderate;

d. zygapophyses craniales manifest pronounced elongation, extend significiantly more than length of associated corpus vertebralis, *cartilaginous* extensions, et ligamenta or tendines, effecting rigidity in vertebrae caudales VII and more-distad elements;

e. zygapophyses craniales manifest extreme elongation, *ossified* extensions et ligamenta or tendines, having lengths up to combined lengths of 14 corpora vertebrales effecting extreme "interlocking" or stabilization among elements.

Note.—See: Gauthier (1986); Novas (1992: character E), with respect to elongation in which zygapophyses craniales overlap almost half of preceding vertebra; Sereno et al. (1993: legend for fig. 3a); Holtz (1994a: appendix 1, character 106); Russell and Dong (1994b [1993b]: troödontid character 15); Sereno et al. (1994: footnote 12); Chiappe (1995a: legend for fig. 1); Chiappe et al. (1996: appendix 1, character 85); Currie (1995: appendix, character 24, part), with respect to "ossified caudal rods" of both processes ventrales ("chevron bones") and zygapophyses craniales ("prezygapophyses"); Novas (1996: appendix, character 34); Sereno et al. (1996: footnote 45, character 58); Makovicky and Sues (1998: appendix 1, character 53); Holtz (2000 [1998]: appendix I, character 199); Chiappe (2001a: appendix 1, character 45); Ji et al. (2001), regarding unnamed dromaeosaurid NGMC 91-A; Norell et al. (2001: appendix 1, character 121); Chiappe (2002: appendix 20.2, character 45); J. M. Clark et al. (2002a: appendix 2.2, character 123); Xu (2002: suite II, character 152); Zhou and Zhang (2002: appendix III, character 66); Rauhut (2003: character 122). Baumel and Witmer (1993: annotation 132) cited *Diomedea* as being exceptional among Neornithes in the presence of zygapophyses on vertebrae caudales liberae. Holtz (2000 [1998]: appendix I, character 199), relating lengths of "prezygapophyses" to those of "centra," considered the presence of a pygostylus as a fifth state ("4" or "e") a separate character; Hwang et al. (2004: supplement, character 120); Xu and Norell (2004: supplement, character 120).

1004. Vertebrae caudales liberae, arcus vertebrae, zygapophyses caudales, status et forma (**ordered**):

a. present, elongate;

b. present, truncate; **c.** absent.

Note.—See: Gauthier (1986: 13, unindexed synapomorphy of Ornithurae); Holtz (2000 [1998]: appendix I, character 195).

1005. Vertebrae caudales liberae, corpus et arcus vertebrae, foramina pneumatica, status et locus (**unordered**):

a. absent entirely;

b. present in corpus vertebrae, facies lateralis corporis et/aut basis (typically margo cranialis) of processes transversae;

c. present in arcus vertebrae, lamina dorsalis et/aut processus spinosus.

Note.—See: Sereno et al. (1996: footnote 45, character 55); J. D. Harris (1998: appendix 2, character 72); Currie and Carpenter (2000: appendix 1, character 61); Holtz (2000 [1998]: appendix I, character 191).

1006. Vertebrae caudales liberae, cranialmost elements in series, processus ventralis corporis, forma (*sensu* dorsoventral length relative to craniocaudal width):

a. much longer (up to three times) craniocaudally than deeper dorsoventrally;

b. slightly deeper (at most) dorsoventrally than long craniocaudally.

Note.—See: Novas (1996: appendix, characters 21 and 33); Chiappe et al. (1998: character 27); Ji et al. (1998: supplement, character 27); Forster et al. (1998: supplement, character 39), with respect to "proximal haemal arches"; Chiappe (2001a: appendix 1, character 49); Chiappe (2002: appendix 20.2, character 49).

1007. Vertebrae caudales liberae, two caudalmost vertebrae propygostylae (**new term**), corpora vertebrales, markedly distinct, elongate, cranially hamulate, rounded processes ventrales, status:

a. absent; **b.** present.

Note.—Nomenclatural revision after Baumel (1988). Whether this character can be evaluated in taxa lacking pygostylus is unresolved.

Processes chevroniformes caudae

Note.—In addition to the uncertain homology of the "chevron bones" of (primarily) nonavialian theropods and sauropod dinosaurs, a formal nomenclature for these structures and features thereof (e.g., "bases," "bends," "projections," "bridges," and "cranial and caudal pairs") remains to be proposed. It appears, however, that "chevron bones" represent homologues of the processes ventrales of the vertebrae caudales that retain their bilateral composition (and enclosed canalis vascularis). At least among Aves possessed of these structures, each of the pairs of processes ventrales involved typically is ankylosed in close proximity to the terminus cranialis of one corpus vertebrae while extending craniad to articulate with the terminus caudalis of the corpus vertebrae immediately cranial to the latter; this bivertebral association is related to the traditional view of these structures as related to "intercentra" (Baumel and Witmer 1993: annotation 144).

Reference to "poorly developed" state of "hypocentra" of vertebrae caudales of Galliformes by Andors (1992: table 2, character 24) may relate to the processes ventrales; see also Russell and Dong

(1994b [1993b]: troödontid character 16, part) regarding creation of pons by "haemal arches"; Novas (1996: appendix, character 34). Nevertheless, these structures are listed by some workers so as to suggest an inference of homology with costae of the vertebrae caudales. Also, substantial redundancy and synonymous characters persist in the literature, principally a reflection of the absence of a standardized nomenclature and inconsistent reference to what constitutes "proximal" or "distal" elements. As serial homologues, "chevron bones," like the vertebrae caudales with which these are associated, undergo changes *in serriatum*; e.g., "chevron bones" of *Sinosauropteryx* are carinate on cranial vertebrae caudales, but are "Y-shaped" (having basal or dorsal transverse struts) caudally. Here the formal name for "chevron bones" is the processus (ventralis) *chevroniformis* (**new term**) in Neornithes limited to vertebrae caudales liberae, each comprising cranial and caudal counterparts bridging the articulatio intervertebralis.

1008. Vertebra caudalis liberus propygostylus, processes ventrales chevroniformes, forma et situs modalis (**ordered**):

a. extensive or complete, columna vertebralis distal to sacrum (i.e., cauda), elongate (at least as long as processes spinoses vertebrae), robust (exclusive of cranialmost), well-defined facies articulares cranialis et caudalis, enclosing supracentral triangular fenestra;

b. widespread distribution among vertebrae caudales in comparatively elongate caudae, but diminution in size evident;

c. present on all vertebrae caudales propygostyli;

d. limited to and diminutive on one to three vertebrae pygostylae;

e. absent throughout series.

Note.—See: Van Oort (1904) for review; Baumel and Witmer (1993: annotation 144), concerning presence in Neornithes; Currie and Chen (2001); Chiappe and Walker (2002: appendix 11.1, character 3); Ji et al. (2003b). See separately coded retention of "chevron bones" on pygostyli. Determination of vertebrae propygostyli can be challenging, in that these penultimate caudal units show a continuum of synostosis with the pygostylus, and typically differ structurally from more-cranial vertebrae caudales liberae by the presence or prominence of processes ventrales.

1009. Vertebrae caudales liberae, processus ventrales propriae aut processes ventrales chevroniformes, "V-shaped" or bipartite-cuneate conformation, status and positions of elements bearing such, and those of associated sitae transitionales (i.e., "transition points") between elements possessing and those devoid of these structures, status et forma (**unordered**):

a. present, extending essentially throughout series;

b. present, limited to intermediate elements, beginning with element between vertebrae caudales X and XVII;

c. present, limited to caudal (posterior, distal) elements, beginning with element beyond vertebra caudalis XVII;

d. absent throughout series;

x. noncomparable (Dromornithidae).

Note.—Vernacular name of this is point of **"chevron transition"** in caudal vertebrae; we propose a formal name of situs transitionalis processi chevroniformes (**new term**). In those taxa possessed of "chevron bones" in the caudalmost elements, these structures are incorporated into the pygostylus (if present). Homology with other sectiones vertebrales (e.g., "ossified caudal rods extending lengths of prezygapophyses and chevrons") likely; partial redundancy of codings pertaining to "transition point" in vertebrae caudales based separately on processes transverses, processes ventrales, etc.

See: Gauthier (1986); Holtz (1994a: appendix 1, character 109); Sereno et al. (1994: footnote 12); Currie (1995: appendix, character 24, part); Sereno et al. (1996: footnote 45, character 26); J. A. Wilson and Sereno (1998: appendix, character 41), contrasting "Y-shaped" *vs*. craniocaudally "forked" conformations among Sauropoda; Xu et al. (1999b: character 100); Holtz (2000 [1998]: appendix I, character 204); Xu et al. (2000: supplement, character 80); Ji et al. (2001), regarding unnamed dromaeosaurid NGMC 91-A; Norell and Clarke (2001: appendix I, character 64), J. A. Clarke (2002: appendix I, character 64), J. A. Clarke and Norell (2002: appendix 2, character 64), and J. A. Clarke (2004: appendix 1, character 64), providing only a binary, presence–absence treatment. Gatesy (2002) considered the functional implications of phylogenetic patterns in the pygostylus avium. Carroll (1997: 312) regarded synapomorphy of dromaeosaurs to include "chevrons longer than deep"; Ji et al. (2005: supplement, part I, character 64).

1010. Vertebrae caudales liberae (exclusive of pygostylus, if present), processes ventrales chevroniformes of distal elements in series (evidently caudal to "transition point"), forma (**unordered**):

a. simple and curving in profile;

b. shafts cylindrical in profile cranially, much reduced caudally;

c. brevi-cuneate or vestigial, limited to several vertebrae caudales propygostyli;

x. noncomparable (palaeognathous Neornithes, Dromornithidae).

Note.—See: Russell and Dong (1994a [1993a]: table 2, character 32); Russell and Dong (1994b

[1993b]: troödontid character 16); Xu et al. (1999a: character 38).

1011. Vertebrae caudales liberae (especially cranialmost elements, exclusive of pygostylus, if present), processes ventrales chevroniformes, bases (extremitates proximales) of processes chevroniformis, processus cranialis typically bearing facies articularis, status:

a. absent; **b.** present.

Note.—See: Sereno et al. (1996); Rauhut (2003: character 128).

1012. Vertebrae caudales liberae (exclusive of pygostylus, if present), processes ventrales chevroniformes of middle and distal elements in series (evidently caudal to "transition point"), forma:

a. bilaterally compressed, dorsoventrally expanded **or** lacking cranial and caudal projections, being less than twice as long craniocaudally as deep dorsoventrally;

b. dorsoventrally compressed into a thin horizontal lamina **or** possessing cranial and caudal projections, being more than twice as long craniocaudally as deep dorsoventrally.

Note.—See: Ostrom (1976a); Gauthier (1986: text characters 20, 40, and 77); Holtz (1994a: appendix 1, character 47); Russell and Dong (1994a [1993a]: table 2, character 33); Forster et al. (1998: supplement, character 36); Xu et al. (1999b: character 31); Holtz (2000 [1998]: appendix I, character 209); Xu et al. (2000: supplement, character 22); Ji et al. (2001), about dromaeosaurid NGMC 91-A; Xu et al. (2003).

1013. Vertebrae caudales liberae (exclusive of pygostylus, if present), processes ventrales chevroniformes, proximal examples, forma:

a. dorsoventrally elongate;

b. dorsoventrally depressed;

x. noncomparable (Neornithes).

Note.—See: J. A. Wilson and Sereno (1998: appendix, character 41), contrasting "Y-shaped" *vs.* craniocaudally "forked" conformations among Sauropoda; Sereno (1999: character 147); Holtz (2000 [1998]: appendix I, character 207); Maryanska et al. (2002: appendix 1, character 123); Suzuki et al. (2002: character 7).

1014. Vertebrae caudales liberae (exclusive of pygostylus, if present), processes ventrales chevroniformes, terminus proximalis, forma (planum transversus):

a. craniocaudally short, cylindrical;

b. craniocaudally elongate, bilaterally flattened and laminar;

x. noncomparable because of vestigial form and distribution of processes (Neornithes).

Note.—See: Norell et al. (2001: appendix 1, character 123); J. M. Clark et al. (2002a: appendix 2.2, character 125); Xu (2002: suite II, character 154); Xu et al. (2002a: supplement, character 99); Hwang et al. (2004: supplement, character 122); Xu and Norell (2004: supplement, character 122).

1015. Vertebrae caudales liberae (exclusive of pygostylus, if present), distal elements (mid-caudal to lesser extent), processes ventrales chevroniformes, forma generalis:

a. gently curved, rodular;

b. sharp bend in distal portion producing perpendicular ("L-shaped") angulus;

x. noncomparable because of vestigial form and distribution of processes (Neornithes).

Note.—See: J. D. Harris (1998: appendix 2, character 76); Currie and Carpenter (2000: appendix 1, character 65); Holtz (2000 [1998]: appendix I, character 208); Rauhut (2003: characters 129–130).

1016. Vertebrae caudales liberae (exclusive of pygostylus, if present), processes ventrales chevroniformes of distal elements, pons (crus) basalis, status:

a. absent; **b.** present;

x. noncomparable (Neornithes).

Note.—See: J. A. Wilson and Sereno (1998: appendix, character 87), regarding distribution among Sauropoda; Holtz (2000 [1998]: appendix I, character 206), in reference to "bridge of bone dorsal to haemal canal."

1017. Vertebrae caudales liberae (exclusive of pygostylus, if present), processes ventrales chevroniformes, paired caudal and cranial chevron bases (where processes exist), status:

a. absent, unibasic; **b.** present, bibasic;

x. noncomparable (Dromornithidae).

Note.—See: Holtz (2000 [1998]: appendix I, character 205). Typically, the craniocaudal pairs of attachments between the processes et corpora vertebrales reflects the "intercentral position" of the former with respect to the adjacent vertebrae "bridged" by the processus.

1018. Vertebrae caudales liberae (exclusive of pygostylus, if present), processes ventrales chevroniformes of distal elements, termini cranialis et/aut caudalis, status et forma (**ordered**):

a. absent, both termini "simple";

b. present, terminus cranialis bifurcate;

c. present, both termini cranialis et/aut caudalis of processes ventrales "bifurcate";

x. noncomparable (ratites, Dromornithidae, *Aptornis*).

Note.—See: J. D. Harris (1998: appendix 2, character 75); Currie and Carpenter (2000: appendix 1, character 64); Holtz (2000 [1998]: appendix I, character 210); Norell et al. (2001: appendix 1, character 124); J. M. Clark et al. (2002a: appendix 2.2, character 126); Xu (2002: suite II, character 256); Xu et al. (2002a: supplement, character 201), regarding "cranial and caudal bifurcations"; Hwang et al. (2004:

supplement, character 123); Xu and Norell (2004: supplement, character 123).

Pygostylus

Note.—Referred to as "coccyx" in many classical works, especially in reference to other, evidently nonhomologous terminal composites of the cauda in Tetrapoda. See classic osteological review by Van Oort (1904), including a figurative overview of variation in form and synostoses pygostyli among neornithine taxa (Van Oort 1904: pls. I–II). Ontogeny of the vertebrae caudales and pygostylus was detailed by several authors, e.g., Van Oort (1904: pls. III–V) and Steiner (1938). Also see the myological study of the uropygial apparatus by Baumel (1988). The proposal by de Beer (1956) that the intermediate state of ratites is not homologous with that of carinates has been refuted.

As in most skeletal complexes comprising several variably united, distinct components, the pygostylus presents several sources of possible error, including confusion concerning differences in the processes ventrales chevroniformes at the cranioventral apex of the structure. For analytical purposes, for characters critical for both Neornithes and Mesozoic Theropoda lacking pygostyli, states for Neornithes were inferred as the number of vertebrae caudales stabiles et liberae and augmented by the number of synostotic elements judged to be incorporated into the pygostylus by means of fetal ankylosis.

1019. Pygostylus (synostosis pygostyli), status et typus (**ordered**):

a. absent—juncturae caudae (specifically vertebrae caudales liberae) are articulationes;

b. present, partial—synostoses pygostyli present, but juncturae intervertebrales (especially cranially) are discernable and weak synostoses (hypothesized herein to embody partial apomorphic reversal), with synostotic elements lacking extensive lamina pygostyli;

c. present, complete—synostoses intervertebrales firmly uniting all included vertebrae, terminal unit having extensive lamina pygostyli.

Note.—Presence of pygostylus is equivalent to presence of terminal juncturae caudae being synostoses intervertebralis caudalis or synostoses pygostyli. Conditions in ratites are variously interpreted as (*i*) a distinct, nonhomologous, partial complexus juncturarum; (*ii*) partial or complete homologues of pygostyli verae of neognathous taxa interpreted as intermediate precursory states or paedomorphic variants of latter; or (*iii*) partial reversals from pygostyli verae of neognathous taxa (Cracraft 1986; Gauthier 1986). The present study inferred that palaeognathous taxa, and (independently) a minority of neognathous taxa (e.g., Diatrymidae, Dromornithidae), are most likely to represent hypothesis (*ii*).

See: Cracraft (1974); Thulborn (1984: 126–127, character 8); Cracraft (1986: appendix, character 12); Gauthier (1986: 14, unindexed synapomorphy of Aves); Cracraft (1988: series II, character 5); Sanz and Buscalioni (1992: character 14); Sereno and Rao (1992); Chiappe and Calvo (1994: appendix I, character 20); Holtz (1994a: appendix 1, character 106, terminal state); Chiappe (1995a: legend for fig. 1); Chiappe (1995b: character 20); Elzanowski (1995: characters O1 and PG1); Sanz et al. (1995, 1997: character 19); Chiappe (1996b: character 18); Chiappe et al. (1996: appendix 1, character 18); Hou et al. (1996: characters 30–31); Chiappe et al. (1998: character 28); Forster et al. (1998: supplement, character 34); Ji et al. (1998: supplement, character 28); Rotthowe and Starck (1998: appendix, character 2); Zhou and Hou (1998: fig. 7.8); Chatterjee (1999: appendix II, character 38); Barsbold et al. (2000b), regarding presence in an oviraptorosaurid; Holtz (2000 [1998]: appendix I, character 199, state "e"); Chiappe (2001a: appendix 1, character 50); Norell and Clarke (2001: appendix I, character 67), treated similarly by J. A. Clarke (2002: appendix I, character 67), J. A. Clarke and Norell (2002: appendix 2, character 67), and J. A. Clarke (2004: appendix 1, character 67); Chiappe (2002: appendix 20.2, character 50); Maryanska et al. (2002: appendix 1, character 120), in reference to Oviraptorosauria; Sereno et al. (2002: fig. 8.2), regarding *Sinornis*; Vickers-Rich et al. (2002), concerning *Avimimus*; Zhou and Zhang (2002: appendix III, character 67); Ji et al. (2003a: 22); Ji et al. (2005: supplement, part I, character 67).

1020. Pygostylus (if present), incorporated vertebrae caudales, numerus modalis (**ordered**):

a. three or fewer; **b.** four;
c. five or six; **d.** seven or more;

x. noncomparable by indistinguishability or absence of elements (Dromornithidae).

Note.—See: Steiner (1938); Baumel and Witmer (1993: annotation 145); Chiappe (2001a: appendix 1, character 51); Norell and Clarke (2001: appendix I, character 68); Chiappe (2002: appendix 20.2, character 51); J. A. Clarke (2002: appendix I, character 68) and J. A. Clarke and Norell (2002: appendix 2, character 68), considering forma as well as numerus; Maryanska et al. (2002: appendix 1, character 120); Zhou and Zhang (2002: appendix III, character 68); J. A. Clarke (2004: appendix 1, character 68); Ji et al. (2005: supplement, part I, character 68).

1021. Pygostylus (if present), apex pygostyli et lamina pygostyli, margo dorsalis (lateral perspective), forma (**unordered**):

a. tumid, typically caudodorsally oriented;

b. acuminate, typically caudodorsally oriented;

c. carinate, typically ventrally oriented;

d. rounded, laminate, typically dorsocaudally oriented;
x. noncomparable (Rheidae, Dromaiidae, Apterygidae, Tinamidae, Dromornithdae).
Note.—See: Van Oort (1904); Baumel (1988); Chu (1998: appendix 1, character 67), regarding "dorsal expansion"; Hughes (2000: appendix 2, character 133), concerning angulus of junctura at apex.

1022. Pygostylus (if present), basis pygostyli, processus ventralis (ventral perspective), partitions, status et forma ventralis (**unordered**):
a. absent, cylindrical;
b. present, unipartite, presenting a lamina;
c. present, bipartite, presenting a concavitas;
x. noncomparable (Rheidae, Dromaiidae, Apterygidae, Tinamidae, Dromornithdae).
Note.—See: Van Oort (1904); Baumel (1988).

1023. Pygostylus (if present), basis pygostyli, facies ventralis, medial eminentia cuneata (**new term**), status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes, Dromornithdae).

1024. Pygostylus (if present), corpus pygostyli, crista ventralis (lateral perspective), forma marginalis (**unordered**):
a. convex;
b. essentially linear or slightly concave;
c. sigmoid or at least partly concave;
x. noncomparable (Dinornithiformes, Rheidae, Dromaiidae, Apterygidae, Tinamidae, Dromornithdae).
Note.—See: Baumel (1988); Hughes (2000: appendix 2, characters 134–135), regarding angulus between basis pygostyli et margo caudalis. By nomenclature used herein, corresponds to margo ventralis, lamina pygostyli immediately caudal to angulus ventrocaudalis pygostyli.

1025. Pygostylus, corpus pygostyli, canalis vascularis (ventral perspective), ventral perforation, forming medial fovea (sulcus) vascularis (**new term**), status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes, Rheidae, Dromaiidae, Apterygidae, Tinamidae, Dromornithidae).
Note.—See: Van Oort (1904); Baumel (1988).

1026. Pygostylus, corpus pygostyli, processus transversus, status et forma (**unordered**):
a. present, as variably distinct processes in one or more component elements;
b. present, coalesced to form variably prominent alae transversae;
c. present, mere vestigia or rudimenta of variable and indistinct form;
d. absent;
x. noncomparable (Dromornithidae).
Note.—See: Van Oort (1904); Burt (1930); Baumel (1988). In the pygostylus, the coalescence of processes transversae produces a variably prominent, bilateral pair of craniocaudally oriented cristae or alae; where present, these alae are dorsal to the discus pygostyli (where present).

1027. Pygostylus (if present), corpus pygostyli, foramina transversaria, status:
a. absent; **b.** present;
x. noncomparable (Dromornithidae).

1028. Pygostylus (if present), corpus pygostyli (lateral perspective), foramen intercristatus dorsalis (**new term**), status modalis:
a. present; **b.** absent;
x. noncomparable (Rheidae, Dromaiidae, Apterygidae, Dromornithidae).
Note.—See: Van Oort (1904); Baumel (1988); G. Mayr and Clarke (2003: appendix A, character 61); Dyke and van Tuinen (2004: appendix 1, character 40).

1029. Pygostylus (if present), corpus pygostyli (cranial perspective), canalis (vertebralis) pygostyli, modal status and degree of craniocaudal penetrance:
a. present, craniocaudally extensive;
b. present, craniocaudally limited;
c. obsolete, subfoveate; **d.** absent;
x. noncomparable (Rheidae, Dromaiidae, Apterygidae, Tinamidae, Dromornithidae).
Note.—See: Van Oort (1904); Baumel (1988).

1030. Pygostylus, lamina pygostyli (lateral perspective), foramen intervertebrale, status:
a. present; **b.** absent;
x. noncomparable (Rheidae, Dromaiidae, Apterygidae, Tinamidae, Dromornithidae).
Note.—See: Van Oort (1904); Baumel (1988).

1031. Pygostylus (if present), margo caudalis, tuberculum pygostyli (**new term**) et discus pygostyli, status et forma (**ordered**):
a. tuberculum et discus absent, lamina pygostyli planar with lateral eminentia or crista;
b. variably conformed, bilateral tuberculae present, but lateral extent is less than that of processes transverses of caudalmost vertebra caudalis craniad to pygostylus;
c. discus pygostyli present, a rounded, well-developed transverse lamina that equals or exceeds in lateral extent that of processes transverses of caudalmost vertebra caudalis craniad to pygostylus;
x. noncomparable, by absence of pygostylus (Rheidae, Dromaiidae, Apterygidae, Tinamidae, Dromornithidae).
Note.—Tuberculae and discus serve as expanded area for insertiones m. depressor caudae in scansorial birds. See: Richardson (1942) and Bock and Miller (1959) for functional review of anatomy of

scansorial birds; Richardson (1972); G. Mayr et al. (2003: appendix 1, character 25); G. Mayr and Clarke (2003: appendix A, character 60); Dyke and van Tuinen (2004: appendix 1, character 39); G. Mayr (2004d: appendix I, character 7); G. Mayr (2005a: appendix 1, character 7).

1032. Pygostylus (if present), margo caudalis, discus pygostyli (if present), foliate, bi-alar structure in combination with elongate processus cranialis, status:

a. absent; **b.** present;

x. noncomparable (Dromornithidae).

Juncturae Columnae Vertebralis

Note.—See: Ametov (1971).

1033. Articulationes intervertebrales thoracicae (dorsales), incorporation of articulationes interzygapophysiales (**new term**), status et forma (**ordered**):

a. absent;

b. present, "hyposphene" simple and unilaminar;

c. present, "hyposphene" wide, incorporating medially curved area.

Note.—Articulationes above are those between zygapophyses caudales of cranial elements with synlateral zygapophyses craniales of next (following or correspondingly caudal) vertebrae; such juncturae occur in vertebrae cervicales and thoracicae, functionally restrict or dorsal flexion of the columna vertebralis (Boas 1933). These also are referred to as examples of "hyposphene-hypantra construction" in the paleontological literature.

See: Gauthier (1986: 13, unindexed synapomorphy of Ornithurae); Currie and Zhao (1994b [1993b]), with respect to *Sinraptor*; Novas (1994 [1993]: appendix, character 29); Sereno et al. (1993: legend for fig. 3a); Elzanowski (1995: 38, character unindexed); Chiappe et al. (1996: appendix 1, character 84); Novas (1996: appendix, character M4); Novas (1996: appendix, character 74); Novas and Puerta (1997), identical in Novas (1997: appendix, character 75); Chiappe et al. (1998: character 19); Ji et al. (1998: supplement, character 19); Forster et al. (1998: supplement, character 37); Holtz (2000 [1998]: appendix I, character 174); Chiappe (2001a: appendix 1, character 38); Chiappe (2002: appendix 20.2, character 38); Norell et al. (2001: appendix 1, character 106); J. M. Clark et al. (2002a: appendix 2.2, character 107); Xu (2002: suite II, character 138); Xu et al. (2002a: supplement, character 83), with respect to "trunk vertebrae"; Rauhut (2003: characters 103–104); Hwang et al. (2004: supplement, character 104); Xu and Norell (2004: supplement, character 104).

1034. Junctura atlantoaxialis, typus definitivum:

a. articulatio; **b.** synostosis.

Note.—Apomorphic state subject to polymorphic or ontogenetic variation within Dromornithidae (P. Murray, pers. comm.). See: Murray and Vickers-Rich (2004: table 9, character 3).

1035. Juncturae notarii, synostosis notariosynsacralis, status:

a. absent; **b**. present;

x. noncomparable by absence of notarium (see character regarding status).

Note.—Sole apomorphic taxon—Pelecanidae—was first noted by Barkow (1856), remains problematic as may represent instead a cranially extensive synsacrum; other Neornithes possessing notaria have at least one vertebra thoracica interposed between notarium and synsacrum (Boas 1933).

1036. Juncturae synsacri, comparative integrity reflected by extent of synostoses intercorporis, intertransversaria, et interspinalis, with ancillary support provided by sutura iliosynsacrales et synostoses interiliospinales, status (**ordered**):

a. absent or incomplete, synostoses lacking, variably extensive;

b. present, weakly to moderately reinforced by ligamenta; incipient juncturae present in which suturae are discernable between included elements;

c. present, juncturae well developed and reinforced in which suturae are indiscernable between included elements.

Note.—Treatments of synostosis synsacri in Mesozoic taxa are essentially binary. See: Boas (1933); Romer (1956); Baumel and Raikow (1993: annotation 76); Forster et al. (1998: supplement, character 32); J. D. Harris (1998: appendix 2, character 71); Xu et al. (1999b: character 28); Azuma and Currie (2000: appendix 1, character 100), emphasizing lamina interiliospinalis; Currie and Carpenter (2000: appendix 1, character 60); Xu et al., 2000: character 19), i.e., "absent or partial" (*Allosaurus*, *Archaeopteryx*, Oviraptorosauria, Dromaeosauridae, Velociraptorinae, Ornithomimosauria, Troödontidae, Tyrannosauridae, *Sinornithosaurus*) *vs*. "present" (Alvarezsauridae, Enantiornithes, *Patagopteryx*, Ornithurae, Neornithes). However, this complex requires more-detailed characterization using the six juncturae synsacrales involved (Baumel and Raikow 1993). Among modern birds, especially conspicous in large-bodied taxa and high, curved crista spinosa dorsalis synsacri, the synostosis interspinalis is complete and without fenestrae interspinales.

1037. Juncturae synsacri, symphysis postsynsacralis, inclusion of junctura (articulatio aut synostosis) intertransversariae, status:

a. absent; **b.** present;

x. noncomparable (Rheidae, Casuariidae, Apterygidae, Tinamidae, Podicipedidae).

Note.—See: Barkow (1856).

1038. Juncturae synsacri, cranialmost vertebra caudalis liberae (primus), articulatio (sutura aut synostosis) iliosynsacralis, status et typus (**ordered**):

a. absent;

b. present, represented by articulatio, specifically between processes transversariae et ala postacetabularis ilii;

c. present, represented by synostosis, specifically between processes transversariae et ala postacetabularis ilii;

x. noncomparable (Rheidae, Casuariidae, Apterygidae, Tinamidae, Podicipedidae).

Note.—See: Boas (1933).

1039. Junctura synsacri, synostosis interiliospinalis and resultant form of crista iliosynsacralis, canalis (ilio)synsacralis, et sulci (ilio)synsacrales (containing mm. epaxialii), status et typus (**ordered**):

a. absent and not delimiting sulci—synostosis interiliospinalis lacking throughout length of synsacrum, margines dorsales of alae (partes) preacetabulares iliorum failing to approach the crista spinosa synsacri and terminating sufficiently laterad (typically with irregular margo medialis) so as to dorsally expose fenestrae intertransversarae and fail to delimit distinct sulci iliosynsacrales medial to the alae [partes] preacetabulares iliorum;

b. absent but delimiting sulci—synostosis interiliospinalis lacking throughout the length of the synsacrum, margines dorsales of alae (partes) preacetabulares iliorum failing to reach mediad to crista spinosa synsacri, but sufficiently extensive to delimit sulci iliosynsacrales that are dorsally exposed and distinct medial to the alae [partes] preacetabulares iliorum;

c. present, incomplete, and perforate—synostosis interiliospinalis and resultant crista iliosynsacralis limited to the synsacrum preacetabularis, and perforated by an ostium caudalis (**new term**) of canalis iliosynsacralis (synsacri) that is exposed dorsally immediately cranial to margo caudalis of ala preacetabularis ilii;

d. present, incomplete, and imperforate—synostosis interiliospinalis and resultant crista iliosynsacralis limited to the synsacrum preacetabularis, and lacking an ostium caudalis (**new term**) of canalis iliosynsacralis (synsacri) immediately cranial to margo caudalis of ala preacetabularis ilii;

e. present, complete—synostosis and resultant crista iliosynsacralis extending the entire length of the synsacrum, such that ostium caudalis (**new term**) of canalis iliosynsacralis (synsacri) is concealed dorsally by margo caudalis of ala postacetabularis ilii, ostia comparatively cranial and approximately coincident with vertex cristae iliorum.

Note.—In nonavian Theropoda, vertebrae synsacrales do not show synostoses iliosynsacrales, but instead synostoses iliocostales. See: Boas (1933); Payne and Risley (1976: fig. 1); Ericson (1997: table 1, character 29); Livezey (1997a: appendix 1, character 80; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, character 262); Azuma and Currie (2000: appendix 1, character 60); Norell and Clarke (2001: appendix I, character 159), treated similarly by J. A. Clarke (2002: appendix I, character 160), J. A. Clarke and Norell (2002: appendix 2, character 160), and J. A. Clarke (2004: appendix 1, character 160); Maryanska et al. (2002: appendix 1, character 150); Zhou and Zhang (2002: appendix III, character 159); Dyke et al. (2003: appendix 1, character 71), referred to as "two large and depressed foramina between . . . anterior iliac crests," employed again by Dyke (2003: table 1); G. Mayr and Clarke (2003: appendix A, character 92); Dyke and van Tuinen (2004: appendix 1, character 65); G. Mayr and Ericson (2004: appendix I, character 66); Ji et al. (2005: supplement, part I, character 159).

1040. Junctura synsacri, crista iliosynsacralis extending the majority of the length of the synsacrum, such that ostium caudalis (**new term**) of canalis postiliosynsacralis (synsacri) (**new term**) is (*i*) present, (*ii*) largely concealed dorsally by margo caudalis of ala postacetabularis ilii, (*iii*) ostia comparatively expansive, irregularly shaped, caudal, and passing dorsad to synsacrum bilaterally along midline of regio dorsalis of alae postacetabulares iliorum, status:

a. absent; **b.** present.

1041. Junctura synsacri, crista spinosa synsacri, dorsoventral curvature, magnitude and craniocaudal extent, status:

a. marked throughout length; **b.** obsolete.

1042. Junctura caudae, junctura propygostyli, typus:

a. articulatio; **b.** synostosis;

x. noncomparable by absence of pygostylus (Dromornithidae).

1043. Junctura caudae (vertebrae caudalis liberae), articulatio zygapophysialis, articulatio between zygapophysialis cranialis of caudal member and torus dorsalis of adjacent cranial element, status:

a. absent; **b.** present.

Note.—See: Boas (1933). Problematic assessments not infrequent in that the prominence of the zygapophyses and associated articulationes varies significantly (e.g., Ciconiiformes).

Costae

Note.—Given the information on sterna, costae vertebrales et sternales, et gastralia in *Confuciusornis*, evidence of same for the Münich *Archaeopteryx* presents a confusing or very plesiomorphic stage in a transformation series leading to *Confuciusornis* and

Neornithes. A reasonably parsimonious scenario would posit *Archaeopteryx* as having a lateromedially broad, craniocaudally short acarinate sternum comprising two cartilagines metasternae; only bilateral articulationes with ossa coracoidea are inferred. Numerous costae vertebrales (a pair per vertebra cervicalis aut thoracica) are suspended craniad or caudad to the sternum, none in articulation with the sternum or even oriented toward the element, and none is shown in association with vertebrae sternales (despite the appearance of a facies articularis intercostalis on extremitas ventralis costae in at least some costae vertebrales thoracicae). Instead, some articulate with an elongate series of gastralia, the latter enclosing the ventrum caudal to the abbreviate sternum. A similar arrangement apparently pertains to *Compsognathus*.

Variations in actual morphology or preservational artefacts suggest that gastralia relate differently with primordia sternales. For example, a newly discovered dromaeosaurid (Norell and Makovicky 1997: fig. 3) shows a series of gastralia, each comprising an elongate pars bilaterally paired ligamenta gastraliorum laterales and abbreviated gastralia mediana aligning ventrad with ligmentum gastraliorum medianis or a primordium sternalis (Ostrom 1969: fig. 53), and evidently including rostral articulationes sternogastralia (margo caudalis metasternalis aut cartilagines quasi-xiphoideae; **new term**) et caudal pubogastralia (**new term**). Superficial examination of fossil specimens of adults (e.g., Romer 1956: fig. 141C) suggest that the angularly articulating gastralia medianae of vertebrae caudales represent the primordia of processes chevroniformes caudales.

Gastralia evidently were numerous and manifested substantial serial variation in form in *Deinonychus* (Ostrom 1969: 87) and *Compsognathus* (Ostrom 1978: 89). Ostrom (1969: fig. 53) reconstructed a comparatively complex system of costal segments for *Deinonychus*, in which either side of vertebrae thoracicae articulate with a “dorsal rib” (costa vertebralis), followed progressively ventrad by a “lateral rib” (costa intermedia), and a “sternal rib” (costa sternalis), the latter in articulation with a rudimentum inferred to be a homologue with the sternum. The recurrence of costae intermediae in a Dromaeosauridae, typical of Crocodylia (Romer 1956: fig. 141C) but unsubstantiated among other Archosauria, is questionable given the preservational complexities of costae and gastralia. Even if confirmed in *Deinonychus*, it is unlikely that these intermediae segments would be homologous with those of Crocodylomorpha (Romer 1956: fig. 153C).

This condition evidently underwent evolutionary transformations in which the sternum elongated and articulated with progressively caudal costae—either directly with costae vertebrales that subsequently underwent a partitioning into vertebral and sternal subparts, or as bipartite complexes comprising a costa vertebralis with gastralium in articulation—or a similar caudal progression involving neomorphous vertebrae sternales and the apparent loss of the gastralia adjacent to the lengthening sternum (Claessens 2004). A possible role of gastralia in the formation of the primitive sternum is suggested by the coalescence of cranial gastralia in some *Tyrannosaurus* (Brochu 2003), and a wide, sparsely substantiated distribution of gastralia (e.g., Crocodylia, Ornithomimosauria, Oviraptorosauria) investing ventral cartilagines metasternae (**new term**) and (to a limited degree) ventral spatia intercostales (**new term**) and ossa pubis (symphysis pubica) in propubic taxa, the latter properly considered to form a shield or *cuirasse*. *Confuciusornis* appears to represent an intermediate stage of this transformation, one that also reveals the gastralia themselves to be two-parted. Ultimately, Aves possess extensive sternum with bipartite costal complexes in articulation, with the complete absence of gastralia.

A less conspicuous evolutionary trend in the morphology of costae vertebrales involves two aspects of the extremitas vertebralis costae: (*i*) a progressively dorsal shift of the capitulum, accompanied by (*ii*) a decrease in width and depth of the incisura capitulotubercularis (Romer 1956: fig. 140). This trend is evident only at a scale encompassing all Theropoda (Romer 1956), which, where accompanied by a caudodorsal shift of the capitulum, attains a marked apomorphy in vertebrae thoracicae of Crocodylia, in which both capitulum and tuberculum costae have separate facies articulares on margo lateralis of the processus transversus (i.e., costae do not articulate with the corpus vertebrae).

See: W. K. Parker (1864); Behrens (1880); F. A. Lucas (1889); Duerden and FitzSimmons (1922).

Costae vertebrales

Note.—Where truly no capitulum is present, resulting in a single processus articularis vertebralis costae, the element is termed **holocephalus**. In most Theropoda and all Aves, however, both capitulum and tuberculum are conserved, the costa accordingly termed **dichocephalus** (Romer 1956).

1044. Costa vertebralis, extremitas dorsalis (vertebralis) costae, tuberculum costae, status:
a. present, variably elongate; **b.** obsolete.

1045. Costa vertebralis, extremitas dorsalis costae, capitulum costae, “processus cranialis” (**provisional term**), status:
a. absent; **b.** present.

Note.—See: Russell and Dong (1994a [1993a]: table 2, character 36); J. D. Harris (1998: appendix 2, character 80), in reference to “processes that protrude beyond the cranial facet of the cervical centrum to which it articulates"; Azuma and Currie (2000: appendix 1, character 23).

1046. Costa vertebralis, extremitas dorsalis costae, angulus costae, status:
a. absent or only subtly detectable;
b. present, distinct, margo caudalis costae typically rounded.
Note.—Dinornithiformes subtly apomorphic.

Costae completae verae

1047. Costae completae verae, numerus modalis per latus (**ordered**; plesiomorphy in bold):
a. three; **b.** four; **c. five**;
d. six; **e.** seven; **f.** eight;
g. nine or more.
Note.—Some taxa taken or confirmed by illustrations given by Fürbringer (1888). See: F. A. Lucas (1889); Andrews (1897); Poplin and Mourer-Chauviré (1985); Wellnhofer (1992); J. M. Clark et al. (1999); Chiappe et al. (1999); Norell and Clarke (2001: appendix I, character 53, part); Zhou and Zhang (2002: appendix III, character 53); Ji et al. (2003b); Ji et al. (2005: supplement, part I, character 53).

1048. Costa completae verae, cranialmost (first) in series, costa vertebra, abrupt, irregular craniocaudal (especially margo caudalis) broadening ventral to midpoint of costa that provides lateral support to adducted os coracoscapularis, status:
a. absent;
b. present, variably prominent and conformed.

1049. Costa vertebralis, extremitas dorsalis costae, tuberculum costae, length relative to that of capitulum costae (**ordered**):
a. obsolete, facies articularis vertebralis essentially sessile on corpus costae, resulting in shallow, fissuriform incisura capitulotubercularis and largely occluding the canalis vertebrarterialis;
b. present but comparatively truncate, length distinctly less than one-half that of capitulum, resulting in variable, moderately deep incisura capitulotubercularis and a moderately large canalis vertebrarterialis;
c. present and elongate, length approximately one-half or more that of capitulum, resulting in deep incisura capitulotubercularis and maintaining a variably spacious canalis vertebrarterialis.

1050. Costa vertebralis, extremitas dorsalis costae, capitulum et collum (especially) costae, facies medialis or (less frequently) facies lateralis, large foramen pneumaticum or cluster of smaller foramina pneumatica, variably delimited within recessus (variably involving incisura capitulotubercularis), status:
a. present; **b.** absent.
Note.—This foramen or (more typically) cluster of foramina is readily visible with costae in articulation with the vertebrae, unlike the foramen pneumaticum in the incisura capitulotubercularis (latter obvious only from perspective of extremitas proximalis). Single, minute foramen apneumaticum most likely a foramen neurovascularia and not treated included within state "a." See: J. D. Harris (1998: appendix 2, character 81); J. A. Wilson and Sereno (1998: appendix, character 97), pertaining to distribution among Sauropoda.

1051. Costa vertebralis, extremitas dorsalis costae, tuberculum costae, facies articularis vertebralis, forma:
a. essentially circular, unifaceted, and approximately of equal size to that of capitulum costae;
b. elongate, bifaceted, and distinctly larger than that of capitulum costae.

1052. Costa vertebralis, extremitas dorsalis costae, angulus costae, position relative to tuberculum costae:
a. immediately lateral;
b. significantly lateral, separated by essentially straight segment of collum costae.

1053. Costa vertebralis, corpus costae, facies lateralis, craniocaudal width relative to that of adjacent spatium intercostalis (**ordered**):
a. distinctly less, wherein the respective sulci pulmonales are comparatively wide, accommodating expanded tori intercostales of the lung, suggesting enhanced respiratory capacity;
b. approximately equal;
c. greater, typically with some adjacent costae in direct contact, forming articulationes intercostales vertebrales.

1054. Costa vertebralis, corpus costae, facies lateralis, extremitas dorsalis costae, modal craniocaudal breadth relative to that of pars ventralis (**new term**), status (**ordered**):
a. markedly broader;
b. moderately broader;
c. essentially of uniform width throughout corpus;
d. partes dorsalis et ventralis both broadened relative to collum;
e. significant segment distinctly narrowed dorsally;
x. noncomparable (*Cacatua*, *Opisthocomus*).
Note.—Involving corpus ventral to processes uncinatus or homologous locus, this feature largely reflects the marginal extensions of corpus costae, margo cranialis (especially) and margo caudalis, or the lack thereof, and hence shows substantial individual, ontogenetic variation. Apparently related to the support of the overlying scapula and extremitas distalis of processes uncinates costarum.

1055. Costa vertebralis, second member of series (without sternal counterpart, at least in most taxa), corpus costae, facies lateralis, distinct broadening essentially throughout in which corpus approaches twice the craniocaudal width of adjacent costae, status:

a. absent; **b.** present.

Note.—See: Kirby (1980) and associated character of adjacent costa sternalis; related to increased complexity of mm. scalenus, levatores costarum, and intercostales externi.

1056. Costa vertebralis, corpus costae, facies medialis, margo cranialis dorsal to processus uncinatus or homologous locus, foramina pneumatica, status:

a. absent; **b.** present.

Note.—See: Livezey (1997a: appendix 1, character 59; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, character 129).

1057. Costae vertebrales, corpus costae, processus uncinatus, status (**ordered**):

a. absent; **b.** rudimentary or vestigial;

c. present, joined with corpus costae, margo costalis, by synostosis or sutura (latter sometimes tenuous).

Note.—So-called "uncinate processes" of Crocodylomorpha are not homologous to the processes uncinates avium, both on structural and distributional bases. Costal flanges of Crocodylia emerge from margines costarum and appear to be an intrinsic extension of corpus (spinae in costae cervicales, alae in costae thoracicae). Typical of the structures found in Crocodylomorpha—cristae (spinae) marginis costae (**new term**)—one vertebra lies in longitudinal, dorsal articulation with the corpus costae of preceding vertebrae in the cervical series. Moreover, calcified, dermal accretions develop on margines caudales costarum vertebrae of Crocodylia that are consistent with candidates for homologues with the processes uncinates of "higher" Theropoda. Consequently, the nonhomologous "uncinate" structures of Crocodylomorpha are exclued from formal analysis here. If "uncinatus" is to be retained nomenclaturally for both classes of structures, the term should be emended by "cranialis" and "caudalis" for Crocodylomorpha and higher Tetrapoda, respectively.

Absence in basal avialians is likely a preservational artifact related to weak union of processus with margo costae, whereas absence in Anhimidae and Diatrymidae is apparently by apomorphic reversal. Variation in the persistence of a distinct sutura costouncinata in adults is problematic; "unfused," apparently by reversal and replacement by ligamenta in triangular arrangement (Ghetie et al. 1976) in some neognathous Neornithes (e.g., Gaviiformes, Podicipediformes, Sphenisciformes). The frail suturae in many taxa also exacerbate this state of affairs through variation in preservation; e.g., "absence" of processes uncinates in Aeypyornithidae reported by Andrews (1897) almost certainly resulted from loss after prolonged exposure of the suturae ligamentosae.

In many taxa, articulationes intercostales synoviales accessoriae (**new term**)—articulationes between processes uncinates of one or more pairs of costae with adjacent, caudal costae of respective elements, distinct from articulationes intercostales or articulations (i.e., synchondrosis intercostalis) between associated costae vertebrales et sternales—occur to varying degrees (i.e., with respect to numbers of costae involved and number of costae in articulation with a given processus uncinatus. Although such occur in a variety of taxa (e.g., Phoenicopterygiformes, most Falconiformes), the presence of such articulationes in diving taxa (e.g., Spheniscidae, Phalacrocoracidae, Anhingidae, Podicipedidae, Gaviidae, and Alcidae) may support the cavitas thoracicus against submarine hydrodynamic pressures.

See: Marsh (1880: pl. IX); Cracraft (1986: appendix, characters 30 and 32); Gauthier (1986: 13, for Ornithurae; 14, unindexed synapomorphy of Aves); Cracraft (1988: series II, character 14; series IV, character 9); Cracraft and Mindell (1989: table 1, character 9), in reference to sutura costouncinata, distinct from articulationes intercostales effected by contact between the processus uncinatus of one costa with the next, more-caudal costa in the costal series on the same latus; Andors (1992: table 2, character 25); Sanz and Bonaparte (1992: character 10); Chiappe and Calvo (1994: appendix I, character 22); Chiappe (1995b: character 22); Sanz et al. (1995, 1997: character 21); Chiappe (1996b: character 20); Chiappe et al. (1996: appendix 1, character 20), in reference to "ossified" uncinate processes; Hou et al. (1996: character 20); Norell and Makovicky (1997, 1999); J. M. Clark et al. (1999: fig. 14); Holtz (2000 [1998]: appendix I, character 202); Zhou and Wang (2000); Chiappe (2001a: appendix 1, character 53); Cracraft and Clarke (2001: appendix 2, character 22); Ji et al. (2001), regarding dromaeosaurid NGMC 91-A; Norell and Clarke (2001: appendix I, character 69), treated similarly by J. A. Clarke (2002: appendix I, character 69), J. A. Clarke and Norell (2002: appendix 2, character 69), and J. A. Clarke (2004: appendix 1, character 69); Xu et al. (2002a: supplement, character 101); Norell et al. (2001: appendix 1, character 126); Chiappe (2002: appendix 20.2, character 53); J. M. Clark et al. (2002a: appendix 2.2, character 128); Xu (2002: suite II, character 156); Zhou and Zhang (2002: appendix III, character 69); Ji et al. (2003a: 22); Xu et al. (2003). For recent taxa, see: Livezey (1986: appendix 1, character 91); Ericson (1997: table 2, character 20); Livezey (1997a: appendix 1, character 58; *corrigenda*, Livezey 1998a); J. M. Clark et al. (1999), regarding oviraptorosaurid *Citipati*; Zhou et al. (2000), regarding *Caudipteryx*; Hwang et al. (2002), regarding *Microraptor*; G. Mayr and Clarke (2003: appendix A, character 74); Hwang et al. (2004: supplement, character 125); G. Mayr (2004a: appendix 1, character 39); Novas et al. (2004), regarding ornithopod *Talenkauen*; Xu and Norell (2004: supplement, character 125); Ji et al. (2005: supplement, part I, character 69).

1058. Costae vertebrales, corpus costae, processus uncinatus, sutura costouncinatus, dorsoventral length (as proportion of costa vertebralis completae), forma:

a. less than one-third;

b. equal to or greater than one-third;

x. noncomparable by genuine absence (as opposed to weakly ankylosed and lost) of processus uncinatus (Anhimidae).

1059. Costae vertebrales, corpus costae, processus uncinatus, modal proportion ($\equiv Pr$) of costae vertebrales (including costae incompletae, completae verae, et completae spuriae) bearing processus uncinatus (**ordered**, basal polarity provisionally designated as state "c"):

a. $Pr \leq$ one-quarter;

b. one-quarter < Pr < one-half;

c. one-half $\leq Pr$ < three-fourths;

d. $Pr \geq$ three-fourths;

x. noncomparable by apparent absence of processus (Anhimidae).

Note.—In most taxa, the first and (in many) second cranialmost pairs of costae, in addition to several of the caudalmost pairs of costae (apparently universally in costae in articulation with vertebrae synsacrales, lack a processus uncinatus.

1060. Costae vertebrales (especially longest, most robust elements), corpus costae, processus uncinatus, augmentation by diminutive, acuminate spinus uncinatus (**new term**) dorsally on each costae, status:

a. absent; **b.** present;

x. noncomparable (Anhimidae).

1061. Costa vertebralis, cranialmost pair of costae incompletae cervico-thoracicae, corpus costae, distinct craniocaudal broadening largely through irregular laminar expansion of processus uncinatus, and typically enclosing one or two foramina, status:

a. absent; **b.** present.

Note.—See: Livezey (1998b: appendix A, character 131). Evidently associated with medial supportive surface for the scapus scapulae and origiones of m. serratus profundus. Adjacent costae often manifesting decreased broadening of similar derivation.

1062. Costa vertebralis, corpus costae, processus uncinatus (lateral perspective), trabecula dorsocaudalis, trabecula caudodorsalis, et angulus basalaris processi (**new term**), forma (**ordered**):

a. single, spinous trabecula dorsocaudalis (**new term**) of uniform width (some with limited broadening distally) and devoid of basal broadening or discernable basis or angulus basalaris processi (**new term**) of the element;

b. trabeculae dorsocaudalis lacking, with variably pronounced angulus basilaris processi;

c. strongly angular in lateral perspective including basis trabeculae dorsocaudalis, prominent, broad lobus caudoventralis on basis trabecularis;

d. strongly angular in lateral perspective, including basis essentially rectangular trabeculae dorsocaudal caused by combined effect of prominent, broad, lobus caudoventralis having rectangular margo ventralis and broad, rectangular terminus caudoventralis on extremitas dorsalis trabeculae;

e. essentially comprising only a dorsoventrally elongated crista homologous with the angulus basilaris lacking a distinct trabecula dorsocaudalis;

x. noncomparable (Anhimidae, Opisthocomidae).

Note.—Autapomophy of *Opisthocomus* may represent terminal state in this transformation series, herein treated as a separate character. Also, basal polarity may be state "b." Unique bilobate processus uncinatus of Cathartidae was figured by Shufeldt (1909: fig. 15).

1063. Costa vertebralis, corpus costae, processus uncinatus, conformation as broadly based, craniocaudally restricted crista, lacking typical dorsocaudally oriented lobus, status:

a. absent; **b.** present.

1064. Costa vertebralis, corpus costae, pars ventralis, broad conformation such that secondary, articulationes intercostales accessoriae effected between margines of many adjacent costae, status:

a. absent; **b.** present.

1065. Costa vertebralis, corpus costae, processus uncinatus, strongly hamulate, virtually dorsal orientation processi (lateral perspective), status:

a. absent; **b.** present.

1066. Costa vertebralis, caudalmost costa completae verae, length relative to that of associated (articulating) costa sternalis:

a. costa vertebralis ranging from approximately twice as long to equally long as costa sternalis;

b. costa vertebralis distinctly shorter than associated costa sternalis.

Note.—Elongation of costae sternales, along with elongate sternum and typically elongate processes uncinates (some articulating with two costae), perhaps associated with respiratory volume during dives.

See: Norell et al. (2001: appendix 1, character 128); J. M. Clark et al. (2002a: appendix 2.2, character 130), contrasting "lateral gastral segment" *vs.* "medial" or "distal" *vs.* "proximal"; Xu (2002: suite II, character 158), for Mesozoic taxa; Hwang et al.

(2004: supplement, character 127); Xu and Norell (2004: supplement, character 127).

1067. Costa vertebralis, extremitas ventralis costae, distinct lateromedial expansion and enhanced robustness immediately adjacent to articularis intercostalis (similarly evident in costae sternales), status:
a. absent; **b.** present.

1068. Costa vertebralis, extremitas ventralis costae, facies articularis intercostalis, status et typus (**ordered**):
a. absent or obsolete;
b. present, poorly differentiated;
c. present, well differentiated.
Note.—Absence *sensu stricto* limited to costae incompletae or costae completae spuriae. Conditional on transformation pertaining to sternum, costae, et gastralia, the modest facies discernable in *Archaeopteryx* may represent facies articulares costogastrales (**new term**).

Costae sternales

Note.—Crocodylia, and perhaps other basal Archosauria, possess tripartite costae comprising vertebral (dorsal, ossified), intermediate (calcified), and sternal (ventral, calcified) subsections. At some point between Crocodylia and basalmost Avialae (i.e., within Saurischia), ontogenetic sequences suggest that the intermediate segment was joined with the sternal segment at or about the point at which both subsections became truly ossified. See: Claessens (2004), regarding critical distinctions between gastralia (typically tripartite) and costae verae (typically bipartite).

1069. Costae sternales, ossified (as opposed to cartilaginous or calcified) and involving articulatio costosternalis, status:
a. absent; **b.** present.
Note.—See: Gauthier (1986: 13, unindexed synapomorphy of Ornithurae); Sanz and Bonaparte (1992); Chiappe and Calvo (1994); D. A. Winkler et al. (1997: appendix 1, character 15); J. M. Clark et al. (1999); Ji et al. (2001), regarding unnamed dromaeosaurid NGMC 91-A; Norell et al. (2001: appendix 1, character 127); J. M. Clark et al. (2002a: appendix 2.2, character 129); Xu (2002: suite II, character 157); Xu et al. (2002a: supplement, character 102); Hwang et al. (2004: supplement, character 126); Novas et al. (2004: appendix, character 11); Xu and Norell (2004: supplement, character 126).

1070. Costa sternalis (caudalmost costa completae verae), extremitas dorsalis costae, prominent, caudally directed lobus immediately dorsocaudal to facies articularis intercostalis, status:
a. absent; **b.** present;
x. noncomparable (*Aptornis*).
Note.—Given that Pelecanidae is one of a minority of taxa surveyed in which costae completae spuriae were lacking, this lamina may represent the synostotic vestigium of the extremitas distalis of such a costa caudalis in which the articulatio ventralis was of typus intercostalis. An alternative origin for this feature is suggested by an osseous arcus synostotic to the same costa in Cariamidae, evidently the unilateral vestigium of a more-caudal costa sternalis.

1071. Costa sternalis, caudalmost element(s) completae, corpus costae, forma generalis (lateral perspective):
a. monotonic, singly curved; **b.** sigmoid.

1072. Costa sternalis (cranialmost member in articulation with sternum), extremitas dorsalis costae, facies articularis intercostalis, distinctly broadening relative to corpus, status:
a. absent; **b.** present.
Note.—See: Kirby (1980), and related character of cranialmost costa vertebralis in same group (Picidae). Not to be confused with more-typical articulation between vertebral and sternal components of costae completae verae. Related to increased complexity of mm. scalenus, levatores costarum, et intercostales externi.

1073. Costa sternalis, extremitas ventralis costae, margo caudalis, elongate, hemicircular foramen enclosed within corpus costalis, status:
a. absent; **b.** present.
Note.—Frequency of this condition, which can be bilaterally asymmetrical, is not known.

1074. Costa sternalis, extremitas ventralis costae, facies medialis, immediately proximal to facies articularis sternalis, large foramen pneumaticum or cluster of foramina pneumatica, status:
a. present; **b.** absent.
Note.—Single, minute foramen (apparently apneumatic and most likely a foramen neurovascularia) not treated as state "b"; such minute foramina may be located on facies cranialis or facies caudalis of the extremitas ventralis, or on the facies articularis sternalis itself. See: Livezey (1998b: appendix A, character 132).

1075. Costa sternalis, extremitas ventralis costae, facies articularis sternalis, distinctly bicapitate conformation:
a. absent; **b.** present.
Note.—Contrary to some reports—Baumel and Raikow (1993: annotation 83); Baumel and Witmer (1993: annotation 157)—purported differences among neognathous taxa, e.g., Anatidae, *Gallus*, *Gavia*, Accipitridae, and Passeriformes, were not ascertained.

1076. Costa sternalis, extremitas ventralis costae, facies articularis sternalis, distinct dorsoventral terminal broadening, status:

a. absent;

b. present, dorsoventral breadth of terminus costae at least twice that of midpoint of corpus costalis of respective costa sternalis.

Note.—Related to expansion accommodating bicapitate facies articularis of some taxa.

Costae sternales incompletae

1077. Costa sternalis incompletae (**new term**), i.e., lacking associated costa vertebralis and for which articulatio costosternalis is replaced by synchondrosis intercostalis sternales (**new term**) with margo caudalis of preceding costa sternalis, status:

a. absent or distinctly rare;

b. typically present, sometimes with additional suborbiculate or crescentiform vestigium attached to margo caudalis of extremitas dorsalis costae of the costa incompletae.

Note.—Important to distinguish from more-widespread costae incompletae deriving from caudal costae *vertebrales* which show variably positioned and extensive juncturae with margo caudalis of preceding costa. Juncturae intercostales *sternales* often involve variably prominent *angulae articulares* (**new term**) on the margines caudales of the associated costae completae verae supported laterally by processus lateralis sterni (e.g., Meleagrididae); some retain vestigia of facies articularis intercostalis, suggesting possibility of an associated costa vertebralis vestigialis.

Costae completae spuriae

1078. Costae completae (caudales) spuriae, numerus modalis per latus (**ordered**):

a. zero; **b.** one;

c. two or (uncommonly) three;

d. four or more.

Note.—Costae completae spuriae apparently are limited to elements caudal to the costa completae verae (hence inclusion of the supplemental modifier "caudales"), many of which are syndesmotic dorsally with ala [pars] preacetabularis ilii, forming suturae iliocostales and delimiting one or more foramina and defining a truncated rudiment of a canalis vertebrarterialis synsacralis (**new term**). Problems arise in theropods lacking true sternum. Naïve model of *Archaeopteryx* in Münich implied that two may be present, with one vertebra lacking costa between costae vertebrales thoracicae et four vertebrae synsacrales.

See: Gauthier (1986: text character 27); Cracraft and Clarke (2001: appendix 2, character 26).

1079. Costae incompletae (caudales) spuriae, cranialmost or immediately following one or two elements synostotic with synsacrum having foramen capitulotubercularis completely enclosed within costa by synostosis, status modalis:

a. present; **b.** absent.

1080. Costae completae (caudales) spuriae, articulationes intercostales distales (**new term**), status modalis:

a. present; **b.** absent;

x. noncomparable where costae completae (caudales) spuriae lacking (see character for status).

Note.—"Costae completae spuriae cum articulationes intercostales" are such costae having ventral (distal) articulationes with the preceding costa (instead of the sternum); "costae completae spuriae sine articulationes intercostales" are such elements that lack ventral (distal) articulations, i.e., are caudal "floating" ribs. Accordingly, comparability with theropods lacking sterni is problematic. In taxa manifesting such costae, variation in details are typical (Duerden and FitzSimons 1922). Also, if more than one costae completae (caudales) spuriae is typical of a taxon, the status of articulationes distales evidently characterized all such elements uniformly (i.e., mixtures of "floating" and "intercostal" termini were not typical of any taxon). Substantial variation is evident within taxa, in part representative of the method of osteological preparation employed. As a result, only the examples found in the palaeognathous birds and a minority of anseriforms, in which costae were perpendicular to the columna vertebralis, was the absence of such articulationes considered both genuine and typical; apparent examples of costae incompletae caudal to the costae completae verae also appeared to be limited to these taxa.

Costae incompletae (cervicales)

Note.—Vertebrae cervicales communis, corpus et arcus vertebrae, facies lateralis corporis et arcus, canalis vertebrarterialis, appear to exhibit a transformation series in which typically conformed segmenta proximales of costae cervicales (i.e., collum costalis or incisura capitulotubercularis) are converted into the canalis vertebrarterialis. Based on examination of selected Theropoda, four principal stages in this series are evident: (*i*) canalis vertebrarterialis proprius absent, incisura capitulotubercularis of costae vertebrales typically conformed (*Alxasaurus*); (*ii*) canalis vertebrarterialis proprius absent, incisura capitulotubercularis of costae vertebrales essentially complete but manifesting marked ventral angling (*Sinraptor*); (*iii*) canalis vertebrarterialis proprius present, incisurae capitulotuberculares costorum vertebralium with marked ventral angling and with articulationes costotransversariae replaced by synostoses costotransversariae, but variably truncated corpora costales ventral to these juncturae remain; and (*iv*) canalis vertebrarterialis proprius present, incisura capitulotubercularis of costae vertebrales with marked ventral angling and with articulationes costotransversariae replaced by synostoses costotransversariae, and vestigia of corpora costales ventral to these juncturae, if any persist, are limited to caudalmost vertebrae cervicales (e.g., Neornithes). See: Baumel and Witmer (1993: annotations 134b and 148).

1081. Costae incompletae (cervicales), numerus modalis (**ordered**):

a. 11 or more; **b.** five to ten; **c.** four;
d. three; **e.** two; **f.** one.

Note.—Regarding state "b" and (to lesser extent) subsequent states, most elements persist into adulthood but evidently ultimately joined by synostosis (cranialmost) or suturae (middle members) (some caudalmost elements remaining in articulationes), beginning as far craniad as second vertebrae cervicales communis. See: Andrews (1897); Gauthier (1986: text character 55); Holdaway (1991: appendix 5.1, character 273); Sanz and Bonaparte (1992: character 3); Sereno et al. (1993: legend for fig. 3a); Russell and Dong (1994a [1993a]: table 2, character 25), regarding shape of "cervical ribs"; Russell and Dong (1994b [1993b]: list A, character 3); Chiappe et al. (1996: appendix 1, character 73), regarding "cervical ribs fused to centra in adults"; and Holtz (2000 [1998]: appendix I, character 165), regarding "cervical ribs" being "unfused to centra" *vs*. "fused to centra" of adult nonavian theropods; Norell and Clarke (2001: appendix I, character 54), characterizing number of "dorsal vertebrae" having "free" ribs (counts seem extraordinarily high); Maryanska et al. (2002: appendix 1, character 106), relating lengths of "cervical ribs" to respective "centra"; Ji et al. (2005: supplement, part I, character 54).

Processes costales are limited to those vertebrae synsacrales bearing costae, in turn are limited in Neornithes to the cranialmost elements (if any). Character equivalent to status et typus of vertebrae thoracicae synsacrales cum costales (**new term**), here limiting included vertebrae to those firmly synostotic with synsacrum proprius (i.e., no sutura intervertebralia remaining distinct in adults); costae synsacrales including vestigia of costae sternales apparently do not occur, hence the inclusion of the modifier "incompletae" in the character description. Evidently, costae spuriae (i.e., those lacking articulationes sternales) cranial to the costae completae verae comprised only the costae vertebrales (i.e., lacked even vestigial costae sternales and hence were exclusively costae incompletae); these cranial elements also did not articulate with another rib (i.e., lacked articulationes intercostales distales) and hence were true "floating" ribs. Intraspecific variation was complicated further by confusion between processes costales and fragmentary costales incompletae.

1082. Costa (verae) vertebralis atlantis et axialis, status:

a. present; **b.** absent.

Note.—Verae indicates costae articulate and are not synostotic or reduced to processus costalis. In Crocodylia, extremitas dorsalis of costa atlantis lack an incisura capitulotuberculata and appear unicapitate, articulating with corpus vertebrae ventrally, abutting its costal counterpart along axis ventromedianis.

1083. Costae (vertebrales) incompletae synsacrales, numerus modalis per latus (**ordered**):

a. zero; **b.** one;
c. two; **d.** three.

Note.—See: Strauch (1978: character 53), reanalyzed by Björklund (1994: appendix) and Chu (1995), in reference to "lumbar vertebral parapophyses"; Holtz (1994a: appendix 1, character 3); Holtz (2000 [1998]: appendix I, character 189), Mesozoic taxa from latter assigned to either state "a" or state "b" above; Norell and Clarke (2001: appendix I, character 160), treated similarly by J. A. Clarke (2002: appendix I, character 161), J. A. Clarke and Norell (2002: appendix 2, character 161), and J. A. Clarke (2004: appendix 1, character 161), in terms of "overlap" between alae iliorum preacetabulares and costae; Xu et al. (2002a: supplement, character 181, part); Ji et al. (2005: supplement, part I, character 160). Initial review of literature revealed that one or two pairs of ribs were involved with ilia in a number of basal taxa: *Ceratosaurus*, *Coelophysis*, *Carnotaurus*, Ornithothoraces.

Processes costales are limited in vertebrae synsacrales to those elements bearing costae, which in turn are limited in Neornithes to the cranialmost elements (if any). Character equivalent to status et typus of vertebrae thoracicae synsacrales cum costales (**new term**), here limiting included vertebrae to those firmly synostotic with synsacrum proprius (i.e., no sutura intervertebralia remaining distinct in adults); costae synsacrales including vestigia of costae sternales apparently do not occur, hence the inclusion of the modifier "incompletae" in the character description.

1084. Costae (vertebrales) incompletae synsacrales, corpora costales, forma (**unordered**):

a. slender and well separated;

b. massive and expanded;

c. forming virtually continuous sheet lateroventrally.

Note.—See: Rowe and Gauthier (1990); Rauhut (2003: character 116).

1085. Costae (vertebrales) incompletae synsacrales, corpus costalis, margo cranialis, alae margo costalis pneumaticus (**new term**):

a. absent; **b.** present.

1086. Costae incompletae cervicales, costae vertebrales, modal length of longest (typically caudalmost) element relative to that of associated corpora vertebrae, and (secondarily) breadth of corpora costales:

a. long, former two to four times longer than latter, and corpus costalis comparatively broad;

b. moderate or truncate, former less than twice as long (rarely more) as latter, and corpus costalis typically comparatively slender.

Note.—See: Holtz (2000 [1998]: appendix I, character 201, modified sequence of states); Norell et al. (2001: appendix 1, character 125); J. M. Clark et al. (2002a: appendix 2.2, character 127); Xu (2002: suite II, character 155); Xu et al. (2002a: supplement, character 100); Hwang et al. (2004: supplement, character 124); Xu and Norell (2004: supplement, character 124).

1087. Costae completae interruptae (**new term**):

a. absent; **b.** frequent, if not typical.

Note.—In some cases, these "orphaned" fragmenta of costae sternales are paralleled by dorsal vestigia of respective costae vertebrales; such paired rudimentia, lacking a synchondrosis intercostalis and associated facies articulares, are limited to elements caudal to the costae completae verae.

Gastralia

1088. Gastralia, numerus modalis per latus (**ordered**):

a. 15 or more; **b.** 11–14;

c. eight to ten; **d.** four to eight; **e.** zero.

Note.—Like costae, most gastralia comprise lateral (proximal) and medial (distal) parts—herein referred to as partes lateroproximale et medioventrale, respectively (**new terms**)—contacting at articulationes intragastraliae (**new term**). In one well-preserved dromaeosaurid (Norell and Makovicky 1997), the two cranialmost pairs of gastralia comprise a single pars and articulate along the midline immediately caudal to margo caudalis sterni. In other, more-caudal (posterior, distal) elements, adjacent pairs of the complete (bipartite) gastralia articulate (articulationes intergastraliae medianae; **new term**) along the midline in a "zigzag" or "zipperlike" arrangement—cf. *Tyrannosaurus* (Brochu 2003: fig. 79)—resulting in two articulationes (corresponding to facies articulares intergastraliorum proximalis et terminalis; **new terms**). Gastralia are known for several major subgroups of Reptilia (Romer 1956: fig. 202), the "zigzag" articulationes intergastraliae medianae being characteristic solely of Theropoda.

The latter articulationes synoviales permit sliding of pars laterodorsale along segmenta distalis of the corresponding pars medioventrale and vary from simple, flattened articulationes synoviales ellipsoideae (Sternberg 1933; Norell and Makovicky 1997) to more-refined "saddle-shaped" (heterocoelous) articulationes synoviales sellares (Lambe 1917). These articulationes relate to normal expansion of the abdominal wall during inhalation and movement.

Inductive inferences from gastralia of Crocodylia and *Sphenodon* (Claessens 2004) suggests that series of (plesiomorphic) gastralia of Theropoda were suspended from margo caudalis sterni (craniad) to symphysis pubica (caudad) via a ligmentum gastraliorum medialis and bilaterally paired ligamenta gastraliorum laterales, presumably obviating direct articulationes sternogastralia et pubogastralia (**new terms**). Available specimens suggest an absence of gastralia in Ornithischia and polymorphism in status among Sauropoda.

A possible homology of gastralia with modifed "floating ribs" (i.e., costae completae spuriae sine articulationes vertebrales) in which the articulatio dorsalis with a vertebra and articulatio ventralis with the sternum are lacking is an attractive hypothesis. The derivation of gastralia from costal *Anlagen* is consistent in both topographical and structural aspects, as well as in the serial, predominantly bipartite arrangement of the elements. Finally, a bifucated terminus dorsalis of a gastralium in a dromaeosaurid (Norell and Makovicky 1997) is suggestive of an atavistic aberration in which the bicapitate conformation of the extremitas dorsalis costae of a costa vertebralis, in which the two rami of the bifurcation correspond to the capitulum and tuberculum costae (Baumel and Witmer 1993).

Counter-evidence to the costal origin of gastralia from some fossil Theropoda includes the occurrence of the two series of "costal" structures—gastralia et costae verae—at different subdermal levels, and that cranialmost gastralia overlap immediately dorsal costae sternales in a manner not consistent with typical articulationes (P. J. Currie, pers. comm.). No consensus has been reached on this problem at present.

See: Cracraft (1986: appendix, character 19); Gauthier (1986: 13, synapomorphy of Ornithurae); Cracraft (1988: series IV, character 8); Cracraft and Mindell (1989: table 1, character 8); Benton (1990a: 25), listing absence of gastralia as synapomorphy of Ornithischia; Sanz and Bonaparte (1992: character 11); Sereno and Rao (1992), for *Sinornis*; Chiappe and Calvo (1994: appendix I, character 32); Chiappe (1995b: character 32); Elzanowski (1995: character C5); Hou et al. (1996: character 19); Norell and Makovicky (1997); Chatterjee (1999: appendix II, character 40); Chiappe et al. (1999); Cracraft and Clarke (2001: appendix 2, character 21); Norell and Clarke (2001: appendix I, character 70), treated similarly by J. A. Clarke (2002: appendix I, character 70), J. A. Clarke and Norell (2002: appendix 2, character 70), and J. A. Clarke (2004: appendix 1, character 70); Ji et al. (2001), for dromaeosaurid NGMC 91-A; Zhou and Zhang (2002: appendix III, character 70); Brochu (2003); Ji et al. (2003b); Ji et al. (2005: supplement, part I, character 70).

1089. Gastralia, partes dorsolaterale et ventromediale (i.e., partes associated within each complete or bipartite gastralium), modality for relative lengths:

a. length of dorsolaterale less than that of mediale (ventrale);

b. length of ventromediale less than that of laterale (dorsale);

x. noncomparable in that gastralia absent (Neornithes).

Note.—See: Lambe (1917); Sternberg (1933); Maleev (1974); Madsen (1976); Norell and Makovicky (1997: 3), for dromaeosaurids; Makovicky and Sues (1998: appendix 1, character 57), regarding *Microvenator*; Holtz (2000 [1998]: appendix I, character 203); Norell et al. (2000: appendix 1, character 31); Xu et al. (2002a: supplement, character 103), regarding troödontid *Sinovenator*.

1090. Gastralia, partes ventromediales, forma partorum:

a. dual, plicate elements in close articulation per bilateral pair of respective partes dorsolaterales;

b. single, fully synostotic element per bilateral pair;

x. noncomparable by absence of gastralia (Neornithes).

Note.—See: J. D. Harris (1998: appendix 2, character 83); Brochu (2003).

Juncturae Costarum

Note.—Typically among Archosauromorpha (including Theropoda), juncturae costovertebralia comprise a persistent synchondrosis capitis costae (between capitulum costae and corpus vertebrae) and a synovial articulatio costotransversaria (between tuberculum costae and processus transversus vertebrae). An unusual condition occurs in some Crocodylomorpha, in which costae thoracicae articulate solely with corresponding vertebrae thoracicae via the processes transversariae, i.e., by two articulationes costotransversariae, articulationes tuberculotransversaria et capitulotransversaria (Romer 1956).

1091. Junctura capitis costae cervicales—involving vertebrae costales cervicales, but excluding caudalmost elements or vertebrae cervicothoracicae—typus:

a. articulationes; **b.** synostoses.

Note.—Cursory examination of Theropoda indicated that at least two different transformations (perhaps meriting treatment as a separate, two-state character) led to the replacement of costae incompletae spuriae joined to vertebrae by articulationes capitis costae et costotransversariae, by immobile processes costales united with vertebrae by homologues of synchondroses capitis costae et synostosis costotransversariae. One comparatively simple means (cf. *Alxasaurus*) seems to have involved mere truncation of the processes transverses, which together with the shortening and synostoses of the costae, led to a condition comparable to that of Neornithes. A second means (cf. *Sinraptor*, *Albertosaurus*) evidently included a pronounced ventral redirection of the processes transverses, which combined with the shortening and synostoses of the costae to produce a similar synostotic vestigium costalis as the alternative pathway (in the second case the retention of a foramen transversarium medial to the ventrally canted processus transversus may vary taxonomically).

See: J. D. Harris (1998: appendix 2, character 79).

1092. Junctura intercostalis, synchondrosis between costa incompletae spuriae et costa immediately cranial, status:

a. absent; **b.** present.

1093. Junctura iliocostalis, typus modalis definitivum:

a. absent, or variably developed, *fibrous articulatio*(*nes*) iliocostalis et synsacrocostalis;

b. contact present, as *sutura* iliocostalis;

x. noncomparable where costae synsacrales absent (*Centropus*, Trochilidae, *Megalaima*).

Note.—Costae involved are those of cranialmost vertebrae synsacrales that are truly (generally imperceptably) synostosed with more-caudal (posterior, distal) elements; rarely, costae from more than two such vertebrae are synostotic, with the more-caudal having such short, vestigial costae that the synostotic structures are not readily discernable. See: Norell and Clarke (2001: appendix I, character 160), treated similarly by J. A. Clarke and Norell (2002: appendix 2, character 161).

1094. Articulatio costopubica (**new term**), status *in situ*:

a. absent; **b.** present;

x. noncomparable (Dinornithiformes).

Note.—Discernable only in specimens having elements in position as determined by membranae or as *in vivo*.

1095. Synchondrosis intercostalis, angulus articularis caudalis costarum, as defined by associated pairs of costae vertebrales et sternales (**ordered**; basal polarity "b"):

a. approximately 180°, approaching straight angulus;

b. approximately 90°, perpendicularity or slightly acute angulus;

c. 45° or less, distinctly (sharply) acute angulus.

1096. Sutura costouncinata, typus ligamentosus, status modalis definitivum:

a. present, suturae typically discernable and comparatively weakly unite processes with costae, and in most processes of one costa involved in articulatio intercostalis with one (rarely two) next-caudal costa;

b. absent, suturae typically indiscernable and synostosis complete in adults.

Note.—Junctura characterized by unusually protracted ontogenetic transformation. Condition "a" frequently results in detachment of processus uncinatus from costa during preparation; in some cases, former presence of processus is indicated only by facies juncturae costalis. Even in taxa qualifying for state "b," fossils often manifest detachment of processes uncinates from respective costae vertebrales (e.g., Dromornithiformes, in which evidence for processus based on suturae of costae). See: Marsh (1880: pl. IX), regarding *Hesperornis*.

SKELETON APPENDICULARE

Note.—Elaboration and increased density of os spongiosum within ossa alae et membri pelvici (pachyostosis) apparently characterizes the weight-bearing elements of the most massive avian taxa, regardless of higher-order relationships; e.g., sectioned elements of Dinornithiformes (notably *Dinornis*), modern ratites, and Dromorniformes, and by inference also Diatrymiformes and Phorhusrhacoidea, indicate that this characteristic attains maximal apomorphic condition in gaviportal, flightless taxa.

For general appendicular osteology of birds, see: Barkow (1829); Blanchard (1859); Gegenbaur (1863); W. K. Parker (1868, 1888d, 1889a); Morse (1871, 1872, 1875, 1880); Alix (1874); Baur (1885a); Mehnert (1888); Degen (1894); Baur (1895); Baer (1896); Sieglbauer (1911); Broom (1912); du Toit (1912–1913); Adolphi (1922); Larson (1930); Marples (1930, 1932); Schinz and Zangerl (1937b); Bremer (1940b); Montagna (1945); H. J. Müller (1961a–b, 1963, 1964); Bock (1962, 1968, 1974); Nielsen (1963); Bentz and Zusi (1982); L. D. Martin and Stewart (1985); G. B. Müller (1989); G. B. Müller and Streicher (1989); G. B. Müller and Alberch (1990); Dial et al. (1991); Schummer (1992); Ostrom et al. (1999). Regarding pelvic limb, see: Carlsson (1884), aquatic specializations; R. Schmidt (1898); Schaffer (1903); Prein (1914); Larson (1930), and Engels (1938), cursorial specializations.

1097. Ossa alae et membri pelvici, cellulae pneumaticae (spatia interna enclosed by thin lamina externa), in some containing os spongiosum or (at least seasonally) os medullare, status:

a. absent; **b.** present.

Note.—See: Ojala (1957); Benton (1990a: 21); O'Connor (2004), suggestive that Aves possess supplemental pneumaticity of appendages, treated elementwise herein.

Ossa Cinguli Membri Thoracica

Note.—Phylogenetic origins and the plesiomorphic components of ossa cinguli membri thoracica of Neornithes and allied Theropoda—including possible contributions by corpora suprascapulare et interclavicula, and embryological elements rarely in evidence in adults (anterior and posterior coracoidal elements, procoracoidal element, and cleithrum—are discussed by Romer (1956: figs. 142–146). Of special relevance are exemplary illustrations encompassing evolutionary trends in os coracoideum from subelliptical to subrectangular form and the variations manifested by the clavicular complex.

Sternum

Note.—Ontogeny of the sternum has a substantial history of study, the earliest works predominantly espousing the derivation of the sternum from medioventral synchondroses of cranial costae (e.g., Cuvier 1832; Segond 1864; Lühder 1871; Hoffmann 1879; Lindsay 1885. An early nomenclatural proposal was the subdivision of the element into a cranial "costosternum" and a caudal "xiphosternum" by Fürbringer (1888: vol. I, taf. I–XL; vol. II, taf. I–VII). Subsequent efforts, however, were characterized by minimal efforts to elucidate synonymous terms (e.g., Knöpfli 1918; Hommes 1924; Gladstone and Wakeley 1932; Schinz and Zangerl 1937b; Fell 1939; Hampé (1959); Romanoff 1960; Klima 1962; Jenkins 1993). The early work by W. K. Parker (1868) proposed names for each part of the sternum under the assumption that the structure was evolved independently in ratites and other birds, and seemingly applied names by similarity of position even where this apparently conflicted with homologies indicated by acknowledged ontogeny.

Examination of the literature and of available osteological specimens at key ontogenetic stages revealed that five principal pairs of components of the sternum participate in the definitive sternum of modern Aves. These pairs of primordia or sternal *anlagen* (Romanoff 1960) tend to recapitulate by their developmental changes the broad evolutionary patterns evident among Mesozoic Avialae, despite preservational deficiencies among the latter.

The principal sternal elements are as follows: (**a**) ***anlage* costo-lateralis sterni,** including the definitive processus craniolateralis, pilae costales, and processus lateralis (if present, and herein distinguished nomenclaturally as a complex from superficially similar, typically caudal trabeculae of margo caudalis sterni) and included trabeculae—i.e., "praesternum," "metosteon," "costal process," "costal condyles," and some examples of "intermediate xiphoid" of W. K. Parker (1868), subsequently supported by ontogenetic studies of modern ratites by Glutz von Blotzheim (1958: fig. 26); (**b**) ***anlage* coraco-rostralis sterni,** including the definitive sulcus articularis coracoideus and rostrum sterni—"coracoidal groove," "pro-osteon," and "rostrum" of W. K. Parker (1868); (**c**) ***anlage* corporis sterni,** the paired lamina giving rise to the greater part of the corpus sterni—"lophosteon," "pleurosteon," and "entosteon" of W. K. Parker (1868); (**d**) ***anlage* carina sterni,** giving rise to the medial, initially bilaminate, carina and its caudal extremity the trabecula mediana—"keel" and "middle xiphoid" of W. K. Parker (1868); and provisionally (**e**) ***anlage* caudolateralis,** including the definitive trabeculae caudolateralis et intermedia (if either or both are present) of most taxa—"external xiphoid" and most examples of "intermediate xiphoid" of W. K. Parker (1868). It appears likely that both *anlagen* carina et caudolateralis sterni may contribute to the definitive planum postcarinale, where present, and perhaps other elaborations of the margo caudalis sterni.

Of these proposed partitions, the most troubling are those bearing on: (*i*) the ontogenetic relationship of the typical trabecula caudolateralis of most birds as either a caudolateral extreme of the *anlage* corporis, a late-developing, caudal extension of the *anlage* costo-lateralis, or a separate primordium (issues of ontogenetic variation in nonavian and basal avian Theropoda being especially critical; cf. Elzanowski 1981; Currie and Peng 1993; Dong and Currie 1994 [1993]; and (*ii*) differentiation of some atypical trabeculae caudolaterales (e.g., those in columbiforms and cuculiforms) from true processes laterales (evidently limited to galliforms). Both issues pose potential problems for coding of characters. Typically, incisurae et fenestrae sternales are occluded by membranae incisurarum (fenestrarum) sterni instead of bone.

Although possibly presenting problems of homology, Enantiornithes of Spain (*Iberomesornis*, *Concornis*, and *Eoalulavis*) present a diversity of sternal forms that are both challenging and may provide insights into early evolutionary augmentation of sternal *anlagen*. *Eoalulavis* presents a uniquely simple sternum consisting of a narrow corpus (presumably deriving from metasternal primordium) and a midline zone of synostosis that comprises a rudimentary, largely caudal carina possessing a rostral division and a bi-alar caudal terminus; no lateral or intermediate trabeculae or craniolateral processes are evident. *Concornis* shares some subtle aspects of the sternal *Gestalt* of *Eoalulavis*, but has augmented the element in almost all structural components: (**a**) the carina, although sharing the unusually caudal position of the point of maximal depth and extension to the margo caudalis of the corpus, has broadened and strengthened the rostral sulcus (which accommodates the prominent apophysis furculae) and simplified the trabecula mediana to a simple rounded terminus; (**b**) included a bilateral pair of elongate, terminally bi-alar processes laterales; (**c**) shows rudimentary, irregularly shaped trabeculae intermediae; and (**d**) bounded the cranial limit of the margo costalis with prominent processes craniolaterales, medial to which are dorsoventrally deepened but simply planar facies articulares coracoidei, the latter being robust, strutlike elements. In short, these two fossil taxa reveal outlines of a transformation series deriving a virtually complete neornithine sternum of *Concornis* from a simple, medial, ovoid breast plate (possibly predefinitive) manifested by *Eoalulavis*.

Despite considerable attention, nomenclatural uncertainties and homology of features of the sternum persist. See: Harting (1864); Lühder (1871); Heimerdinger and Ames (1967) and Webster (1992), for incisurae of passerines; and Feduccia (1972), for scansorial birds; Sibley and Ahlquist (1972: table 4); Stegmann (1958); Strauch (1978: characters 36–37), reanalyzed by Björklund (1994: appendix) and Chu (1995); Strauch (1985: character 8), for medial features, reanalyzed by Björklund (1994: appendix) and Chu (1995); and Strauch (1985: character 9), for lateral features; Bledsoe (1988: appendix, character 4), discounted by K. Lee et al. (1997: appendix 2), for ratites; Houde (1988: table 27, character 23); Livezey (1996a: appendix 1, character 21); Dyke and Gulas (2002: appendix 1, character 32). Zhou and Zhang (2003: fig. 2H) concluded that the unique sternum of Mesozoic *Jeholornis* manifests processes laterales, whereas position and form indicate instead a relationship of the structures to the primordia coracorostralis sterni. Another source of ambiguity is characterization by simple tally of incisurae of margo caudalis sterni without concern for identities, e.g., G. Mayr et al. (2003: appendix 1, character 35); G. Mayr (2004d: appendix I, character 15); G. Mayr (2005a: appendix 1, character 15).

Even if the scheme proposed here is correct with respect to broad organizational limits, observed patterns are complicated by the absence of one or more of these components in some taxa (reflecting apomorphic losses of conspicuous parts; e.g., *complete loss* of the definitive carina in ratites, distinct from the variable reductions manifest in flightless neognathous taxa, extreme in purportedly anseriform Dromornithidae) or the limitation of others to a small minority of taxa (reflecting apomorphic gains; e.g., acquisition of an elaborate processus lateralis *sensu stricto* in galliforms). Moreover, the timing of ossification and topographic shifts during ontogeny varies markedly among taxa, both within the sternal elements and between the sternal complex and other skeletal components; unfortunately, available information and specimens only demonstrate the existence of such variation but do not permit detailed assessments and incorporation of these differences as characters *per se*.

Issues of homology not withstanding, herein we adopt the following nomenclature bearing on the ancillary processes, trabeculae, and interposed incisurae and fenestrae of the corpus sterni for purposes of description of characters, a minority of which depart from that recommended by Baumel and Witmer (1993):

CARINA STERNI—*Anlage* I

- Apex carinae
- Margo cranialis carinae
    - Crista lateralis carinae
    - Crista medialis carinae
    - Pila carinae
    - Sulcus carinae
- Margo ventralis carinae

ROSTRUM STERNI—*Anlage* II

- Foramen rostri
- Spina externa rostri
    - Alae spinae sternae
- Spina interna rostri
- Spina communis
- Septum interarticulare
- Spatium intercoracoidale

CORPUS STERNI

- Margo cranialis sterni—*Anlage* III
    - Processus craniolateralis
- Margo costalis sterni—*Anlage* IV
    - Processus lateralis
        - *Basis trabeculae processi*
        - *Trabeculae lateralis*
        - *Spina cranialis*
        - *Angulus lateralis*
        - *Incisura cranialis*
        - *Spina caudalis*
        - *Incisura caudalis*
        - *Spina obliqua*
    - Processus caudolateralis
        - *Basis trabeculae processi*
        - *Trabeculae caudolateralis*
        - *Incisura (fenestra) caudolateralis*
- Margo caudalis sterni—*Anlagen* I et IV
    - *Trabecula intermedia*
    - *Incisura (fenestra) medialis*
    - *Trabecula mediana*
    - *Incisura (fenestra) mediana*
    - *Incisura (fenestra) accessoria*

As is evident from the foregoing scheme, these structures are organized primarily by the appropriate margo sterni, and each processus or group of similarly situated processes is subdivided nomenclaturally to reveal the trabeculae and intervening spatia comprised (listed in topographic sequence under each). No neornithine taxon possesses all of these structures; the complete list encompasses all possible combinations of features found.

Corpus sterni

1098. Corpus sterni definitivum, primordia metasternales osseae (**new term**), status et typus (**ordered**):

a. comprising no derivatives of any sternal *anlagen*, element completely absent as osseus definitive element, or some effectively by symphyses medialis interscapulocoracoides (**new term**);

b. comprising bilaterally paired, typically calcified plates ("metasternales"), variably synchondrotic leading to definitive synostosis medialis without carina;

c. bilaterally paired, medially synostotic, and variably prominent cartilagines carinae (*Microraptor*), also including margo costalis, planum postcarinale (analogous to "xiphial region"), et processus (caudo)lateralis;

d. bilaterally paired cartilagines metasternae, carinae, et comprising rudimentary to intermediate grades of carina, corpus, and trabeculae, and a continuum of medial synostosis of bilateral components (perhaps limited to Enantiornithes);

e. bilaterally paired cartilagines metasternales cum synostosis medialis, as well as interposed, medial, and synostotic carina sterni definitivum ("midline keel");

f. bilaterally paired cartilagines metasternales cum synostosis medialis, as well as interposed, medial, and synostotic carina sterni definitivum ("midline keel"), but secondarily dispossessed of carina in its entirety and (variably) planum postcarinale, ranging from intermediate reductions.

Note.—Refers to primary sternal components and associated substructures. Variations among basal theropods include: a dromaeosaurid with paired, medially articulating (not synostotic) sternal plates having rudimentary sulci coracoidei but lacking a carina (Barsbold 1983; Norell and Makovicky 1997); medially synostotic sternal plates without associated carina in an oviraptorosaur (Barsbold 1983). Diagnosis problematic because of relatively late ossification of the element among archosaurs having indeterminate or protracted growth (hence "definitivum" requires critical assessment of condition of specimens). Ultimately may lead to several, possibly multistate and ordered characters; or, alternatively, require partitioning into several characters, e.g., with respect to carina sterni.

See: Marsh (1880: pl. VI); Thulborn (1984: 126–127, character 14); Cracraft (1986: appendix, character 29); Gauthier (1986: text character 59); Cracraft (1988: series II, character 13); Houde (1988: table 27, character 21); Sanz and Buscalioni (1992: characters 12–13); Sereno and Rao (1992), noting presence of sternal plate(s) in *Sinornis*; Chiappe and Calvo (1994: appendix I, character 33); Russell and Dong (1994b [1993b]: list A, character 7); Holtz (1994a: appendix 1, character 19); Sanz et al. (1995, 1997: character 31); Chiappe et al. (1996: appendix 1, character 30), with respect to carina only; Novas (1996: appendix, character M10); Novas (1996: appendix, character 36), in reference to carina; Novas (1996: appendix, character 68), in reference to shape of "plates"; Novas (1997: appendix, character 38), identically by Novas and Puerta (1997); Chiappe et al. (1998: character 40, expanded); Forster et al. (1998: supplement, character 53, modified); J. D. Harris (1998: appendix 2, character 92); Ji et al. (1998: supplement, character 40, expanded); Makovicky and Sues (1998: appendix 1, character 63); Chatterjee (1999: appendix II, character 48, expanded); J. M. Clark et al. (1999); Ji et al. (1999); Xu et al. (1999b: character 42, modified); Burnham et al. (2000); Currie and Carpenter (2000: appendix 1, character 71); Holtz (2000 [1998]: appendix I, characters 221 [corpus] and 222 [carina]); Xu et al. (2000: supplement, character 29, modified); Zhang and Zhou (2000: fig. 3), regarding *Patagopteryx*; Zhou and Wang (2000); Chiappe (2001a: appendix 1, character 72, expanded); Chiappe (2002: appendix 20.2, character 72, expanded); Norell and Clarke (2001: appendix I, character 71), J. A. Clarke (2002: appendix I, character 71), J. A. Clarke and Norell (2002: appendix 2, character 71), and J. A. Clarke (2004: appendix 1, character 71), regarding "ossified sternal plates"; Norell and Clarke (2001: appendix I, character 74), referred to as "midline ridge from anterior edge," adapted by J. A. Clarke and Norell (2002: appendix 2, character 72), regarding position of rudimentary and typical carinae; Norell et al. (2001: appendix 1, characters 129 [plates] and 130 [processes caudolaterales]); J. M. Clark et al. (2002a: appendix 2.2, characters 131 [plates] and 132 [processes caudolaterales]); Maryanska et al. (2002: appendix 1, character 124); Sereno et al. (2002), regarding *Sinornis*; Xu (2002: suite II, characters 159 [plates] and 160 [processes caudolaterales]); Xu et al. (2002a: supplement, characters 104 [medial synostosis of plates] and 105 [in regard to "distinct lateral xiphoid process posterior to costal margin . . . or with lateral xiphoid process"]); Zhou and Hou (2002: fig. 7.3); Zhou and Zhang (2002: appendix III, characters 71 and 74); Zhou and Zhang (2003); Ji et al. (2003a: 22); Xu et al. (2003); Hwang et al. (2004: characters 128–129); Xu and Norell (2004: supplement, characters 128–129); Ji et al. (2005: supplement, part I, character 71).

1099. Corpus sterni, craniocaudal length relative to that of coracoideum, corpus coracoidei, forma:

a. subequal;

b. former greater, typically substantially so, than latter.

Note.—See: Holtz (2000 [1998]: appendix I, character 224).

1100. Corpus sterni, craniocaudal length relative to lateromedial width (ventral perspective), forma generalis (**unordered**):

a. "trans-rectangular," wider than long;

b. essentially square or subcircular;

c. "longi-rectangular," longer than wide;

d. triangular, longer than wide, isoceles with narrow basis corresponding to margo cranialis sterni.

Note.—See: Sibley and Ahlquist (1972: table 1); Bledsoe (1988: appendix, character 1); Chiappe and Calvo (1994: appendix I, character 31); Chiappe et al. (1996: appendix 1, character 29); K. Lee et al. (1997: appendix 1, character 6); Novas (1997: appendix, character 69); Novas and Puerta (1997), see identical characters in Novas (1997); Chiappe et al. (1998: character 39); Ji et al. (1998: supplement, character 39); Holtz (2000 [1998]: appendix I, character 223); Zhang and Zhou (2000); Chiappe (2001a: appendix 1, character 71); Chiappe (2002: appendix 20.2, character 71).

1101. Corpus sterni, relative width—modal ratio of medial length divided by minimal width of freed, dried elements having typical proportions and preservational integrity (**ordered**):

a. "telesternal"**—**at least 3.0;

b. 'typical"—greater than 2.0 to 3.0;

c. "squarish"—between 1.0 and 2.0;

d. "brachysternal**"**—less than 1.0.

Note.—See: Livezey (1998b: appendix A, character 146); Sereno (2001: table 1, character 2), regarding Alvarezsauridae; Murray and Vickers-Rich (2004: table 9, character 6). Elements of spirit specimens *in situ* may lead to underestimates of caudal widths.

1102. Corpus sterni, facies muscularis sterni exclusive of carina sterni (if present), curvature defined by intersection of axis medianus corporis (lateral perspective) with planum medianum, forma (**ordered**):

a. high, approaching semicircularity;

b. moderate, arc a distinct or modestly curving profile, but less than semicircular;

c. slight, minimal distinctly discernable arc;

d. obsolete, corpus virtually flat.

Note.—Arcus typically most conspicuous near the delimitation between partes cardiaca et hepatica sterni. See: Bledsoe (1988: appendix, character 5), delimiting four states; K. Lee et al. (1997: appendix 1, character 5.

1103. Corpus sternalis, terminus caudalis sterni relative to margo caudalis of corpus proprius at midline of element, forma:

a. extremitas caudalis carinae typically proportioned, i.e., carina closely approaching margo caudalis corporis;

b. extremitas caudalis carinae substantially reduced, i.e., separation at least one-half length of carina;

x. noncomparable (Palaeognathae exclusive of Tinamiformes; Dromornithidae, *Aptornis*).

Note.—See: S. F. Simpson and Cracraft (1981: character 6, part); Cracraft (1985: character 22); Bourdon et al. (2005: appendix 1, character 43).

1104. Corpus sterni, perforata imperfectata (**new term**), status:

a. absent exclusive of pathology;

b. frequent, reflective of thin condition of corpus and limited to primarily or secondarily flightless birds, highly aerial, maneuverable taxa, or some diving birds.

Note.—Also infrequent in flightless anatids (Livezey 1996a) and flightless rallids (Livezey 1998b). See: Fürbringer (1888: pl. V) for some specimens of *Apteryx*, illustrated by McGowan (1982: pl. I–II).

1105. Corpus sterni, facies muscularis aut visceralis sterni, dorsoventral thickness of element as indexed by translucence of light through fully prepared osteological specimens, forma (**ordered**):

a. thick, opaque;

b. moderate, at least regionally semitranslucent;

c. thin, translucent virtually throughout corpus;

d. essentially transparent.

1106. Corpus sterni, facies muscularis sterni, lineae intermusculares (dorsomedialis), status:

a. absent;

b. present, bilateral pair in approximate parallel with axis medianus sterni;

x. noncomparable (*Aptornis*).

Note.—See: Norell and Clarke (2001: appendix I, character 78), treated similarly by J. A. Clarke (2002: appendix I, character 77), J. A. Clarke and Norell (2002: appendix 2, character 77), and J. A. Clarke (2004: appendix 1, character 77); Zhou and Zhang (2002: appendix III, character 78). Based on myology of Neornithes, linea on facies muscularis of corpus sterni demarcates division between mm. supracoracoideus (medial part on corpus and dorsal part on carina) et pectoralis thoracicus (lateral part on corpus and ventral part on carina); Ji et al. (2005: supplement, part I, character 78).

1107. Corpus sterni, facies muscularis sterni, planum postcarinale, status et forma (**unordered**):

a. obsolete, margo caudalis of corpus sterni essentially intersects terminus caudalis of carina sterni;

b. present, moderately small, symmetrical, angularity of which continuous with portion of corpus supporting carina, and of density comparable to remainder of corpus sterni;

c. present, intermediate expanse, regularly shaped, subplanar, and of homogeneous density that is comparable to that of remainder of corpus sterni;

d. present, moderately large, irregularly shaped, subplanar, and of heterogeneous density that is generally less than that of remainder of corpus sterni;

x. noncomparable (ratites, Dromornithidae).

Note.—Assessed relative to carina sterni (neognathous taxa) or corpus sterni (palaeognathous taxa). See: Livezey (1986: appendix 1, characters 83 and 85); Livezey (1989: table 1, character 85); Livezey (1995b: appendix 1, character 9); Livezey (1996a: appendix 1, character 19); Chu (1998: appendix 1, character 69). These and other characters may be treated best as separate. Although exemplars for Anseriformes lack this feature, several other genera manifest it (e.g., *Mergus*, *Cnemiornis*).

1108. Corpus sterni, facies visceralis sterni, sulcus medianus sterni immediately caudal to margo cranialis, foramen pneumaticum, status et forma (**unordered**):

a. absent;

b. present, depressio, undivided, enclosing pori pneumatici aut os spongiosum;

c. present, depressio, divided medially by osseus lamina or trabecula, enclosing (ventrad to facies visceralis sterni) pori pneumatici aut os spongiosum;

d. present, open, divided medially by osseus lamina or trabecula;

e. present, open, entire, and undivided;

x. noncomparable by absence of carina (ratites, Dromornithidae).

Note.—See: Livezey (1986: appendix 1, character 78); Livezey (1989: table 1, character 78); Livezey (1995a: appendix 1, character 2); Livezey (1995b: appendix 1, character 5); Livezey (1996a: appendix 1, character 24); Livezey (1996b: appendix 1, character 10); Livezey (1997a: appendix 1, character 66; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, character 138); Norell and Clarke (2001: appendix I, character 73), treated similarly by J. A. Clarke (2002: appendix I, character 73), J. A. Clarke and Norell (2002: appendix 2, character 73), and J. A. Clarke (2004: appendix 1, character 73); Dyke and Gulas (2002: appendix 1, character 33); Zhou and Zhang (2002: appendix III, character 73); G. Mayr (2003a:

appendix I, character 28); G. Mayr (2004b: appendix 1, character 34); G. Mayr and Ericson (2004: appendix I, character 43); Ji et al. (2005: supplement, part I, character 73).

1109. Corpus sterni, facies visceralis sterni, sulcus medianus sterni et/aut foramen pneumaticum, situs:

a. immediately caudal to pila coracoidea;

b. significantly caudal to pila coracoidea, approximately ventral to basis carinae.

Note.—See: Ji et al. (2005: supplement, part I, character 74).

1110. Corpus sterni, facies visceralis sterni, pori pneumatici, exclusive of those included within foramen pneumaticum, status et situs (**unordered**):

a. absent;

b. present, margo cranialis;

c. present, sulcus medianus sterni;

d. present, margo cranialis et sulcus medianus sterni;

e. present, partes cardiaca et hepatica.

Note.—See: Livezey (1986: appendix 1, character 89); Livezey (1989: table 1, character 89); Livezey (1996a: appendix 1, character 23); Livezey (1997a: appendix 1, characters 64–65; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, characters 137 and 140); G. Mayr (2003: appendix 1, character 28); G. Mayr and Clarke (2003: appendix A, character 72); Dyke and van Tuinen (2004: appendix 1, character 49).

1111. Corpus sterni, facies visceralis sterni, sulcus medianus sterni, status:

a. present, typically distinct through entire length of corpus;

b. absent throughout corpus.

1112. Corpus sterni, facies visceralis sterni, partes cardiaca et hepatica, comparative qualitative differentiation, forma (**unordered**):

a. indistinguishable by aspect or partition;

b. slightly to moderately distinct by lateromedial broadening and dorsal deepening;

c. partitioned structurally by marked, rounded jugum in ventral perspective;

d. pars cardiaca perforated by distinctly more pori pneumatici et/aut other than pars hepatica.

1113. Corpus sterni, facies visceralis sterni, sulcus medianus sterni, partes cardiaca et hepatica, striae osseae transversae (**new term**) et pori pneumatici, status:

a. absent;

b. present, limited to pars cardiaca.

Note.—See: Woolfenden (1961: 36); Livezey (1986: appendix 1, character 89, part); Ericson (1997: table 2, character 28); Chu (1998: appendix 1, character 70).

1114. Corpus sterni, margo costalis sterni, craniocaudal length relative to that of entire corpus sterni on axis mediana (**ordered**):

a. less than one-fourth;

b. between one-fourth and three-fourths;

c. more than three-fourths.

Note.—See: Livezey (1986: appendix 1, character 86); Livezey (1998b: appendix A, character 145).

1115. Corpus sterni, margo costalis, incisurae intercostales, perforatitas et pneumaticitas, status:

a. absent, devoid of pori, fenestrae, or recessi;

b. present, processes costales separated by pori pneumatici or foramina pneumatica within variably distinct, typically rectangular foveae, or by deep recessi conicales.

Note.—See: Livezey (1998b: appendix A, character 147); J. A. Clarke (2002: appendix I, character 74); J. A. Clarke and Norell (2002: appendix 2, character 74); J. A. Clarke (2004: appendix 1, character 74).

1116. Corpus sterni, margo costalis sterni, pila costalis, status:

a. absent, *sensu* lack of structural refinements substantiating ossified articulationes sternocostales;

b. present, *sensu* presence of structural refinements substantiating ossified articulationes sternocostales.

Note.—Note presence of sternal "costal margin" in an oviraptorid (J. M. Clark et al. 1999). Also see: Chiappe (2001a: appendix 1, character 79); Chiappe (2002: appendix 20.2, character 79).

1117. Corpus sterni, margo costalis sterni, pila costalis, lateromedial profile (**ordered**):

a. concave, i.e., invagination within corpus sterni;

b. straight;

c. convex, i.e., invagination extends corpus sterni laterally.

1118. Corpus sterni, margo costalis sterni, pila costalis, terminus caudalis pilae (**new term**), craniocaudal position relative to that of apex incisurae caudolateralis (**ordered**):

a. distinctly cranial, i.e., distance between terminus et apex is at least one to two times the length of the pila;

b. roughly coincident;

c. distinctly caudal;

x. noncomparable (ratites, Dromornithidae, *Aptornis*, Psophiidae, Aramidae, Gruidae).

Note.—See: Houde (1988: table 27, character 22).

1119. Corpus sterni, margo costalis sterni, processus articularis sternocostalis et loculus costalis sterni, numerus modalis per latus (**ordered**):

a. two; **b.** three; **c.** four;
d. five; **e.** six; **f.** seven;
g. eight.

Note.—Counts include prominent and functional examples on processus craniolateralis sterni. See: Sibley and Ahlquist (1972: table 3), in which number of costae in articulation with sternum differs between Cuculidae (four) and Musophagidae (five); Strauch (1978: character 35), reanalyzed by Björklund (1994: appendix) and Chu (1995); Strauch (1985: character 12); Holdaway (1991: appendix 5.1, character 47); Chiappe et al. (1996: appendix 1, character 97); Livezey (1996a: appendix 1, character 25); Livezey (1998b: appendix A, characters 143 and 152), noting intraspecific and limited bilateral variation and challenges of discernment; Chiappe et al. (1999); J. M. Clark et al. (1999: fig. 14); Norell and Clarke (2001: appendix I, character 77), treated similarly by J. A. Clarke (2002: appendix I, character 76), J. A. Clarke and Norell (2002: appendix 2, character 76), and J. A. Clarke (2004: appendix 1, character 76); Zhou and Zhang (2002: appendix III, character 77); G. Mayr and Clarke (2003: appendix A, character 71); J. A. Clarke (2004: appendix 1, character 76); Dyke and van Tuinen (2004: appendix 1, character 48); G. Mayr and Ericson (2004: appendix I, character 45); Murray and Vickers-Rich (2004: table 9, character 5); Ji et al. (2005: supplement, part I, character 77).

1120. Corpus sterni, margo costalis sterni, processus articularis sternocostalis, orientation with respect to facies muscularis sterni (lateral perspective):
a. approximately perpendicular;
b. distinctly angled, terminus dorsalis cranial to terminus ventralis.

1121. Corpus sterni, margo costalis sterni, processus articularis sternocostalis, terminus caudalis pilae, distinct obtuse angulus (approximately 150° with respect to facies muscularis) with margo lateralis of caudal remainder of sternum (lateral perspective):
a. absent; **b.** present.

1122. Corpus sterni, margo costalis sterni, dorsoventral expansion relative to corpus sterni as accommodation of series of processus articularis sternocostalis:
a. absent; **b.** present.

1123. Corpus sterni, margo costalis sterni, processus articularis sternocostalis, facies articularis costalis, forma (**ordered**):
a. unifaceted;
b. bifaceted, two facies connected by narrow septum;
c. bifaceted, two facies of each processus separated by spatium.
Note.—See: Baumel and Witmer (1993: annotation 157); Baumel and Raikow (1993: annotation 83).

1124. Corpus sterni, margo cranialis sterni, depressio (sulcus aut fossa) articularis coracoideus, status et forma (**ordered**):
a. absent, articulatio sternocoracoidea simplex or lacking;
b. present, articulatio rudimentary;
c. present, moderately or well developed;
d. present, extremely truncated sulci or confined fovea or fossa;
e. present, vestigial, sulcus plana, facies articularis, sulcus subplana with craniocaudal broadening laterally, abbreviate sulcus cum fovea lateralis, aut fovea cum articulatio ellipsoidea.
Note.—See: Gauthier (1986: 13, unindexed synapomorphy of Ornithurae); Hou et al. (1996: character 15); K. Lee et al. (1997: appendix 1, character 7); Webster (1992), referred to as a "manubrium," a term properly applicable only to Mammalia; Norell and Makovicky (1997); J. M. Clark et al. (1999); Norell and Clarke (2001: appendix I, character 75); Norell et al. (2001: appendix 1, character 132); J. M. Clark et al. (2002a: appendix 2.2, character 133); Xu (2002: suite II, character 255); Xu et al. (2002a: supplement, character 200); Zhou and Zhang (2002: appendix III, character 75); G. Mayr et al. (2003: appendix 1, character 34), pertaining to comparatively fine-scale differences between sellariform or convex facies articularis coracoideus sterni among "higher" Neornithes; Hwang et al. (2004: supplement, character 130); G. Mayr and Ericson (2004: appendix I, character 42); Xu and Norell (2004: supplement, character 130); Ji et al. (2005: supplement, part I, character 75).

1125. Corpus sterni, margo cranialis sterni, depressio (sulcus) articularis coracoideus, facies articularis coracoideus, forma superficialis:
a. variably deep, elongate sulcus;
b. weakly sellariform or convex, rectangular facies.
Note.—See: G. Mayr (2002a: appendix 1, character 15), with respect to Caprimulgiformes; G. Mayr (2003c: appendix, character 5), with respect to Apodiformes; G. Mayr (2005b: appendix A, character 20).

1126. Corpus sterni, margo cranialis sterni, depressio (sulcus) articularis coracoideus, lateromedial position relative to those of processes craniolaterales (**ordered**):
a. extremitas lateralis sulci (**new term**) extending laterad to at least the midpoint of processus craniolateralis;
b. extremitas lateralis sulci (**new term**) terminating immediately mediad or laterad to margo medialis of processus craniolateralis;
c. extremitas lateralis sulci (**new term**) terminating significantly mediad to margo medialis of processus craniolateralis;
x. noncomparable by absence of processus craniolateralis (*Opisthocomus*).
Note.—See: Fürbringer (1888: pls. V and VII); Livezey (1998b: appendix A, character 139); Xu et al. (1999); Norell et al. (2001: appendix 1, character 131); J. M. Clark et al. (2002a: appendix 2.2, character 134); Xu (2002: suite II, character 238); Hwang et al. (2004: supplement, character 131); Xu and Norell (2004: supplement, character 131).

1127. Corpus sterni, margo cranialis sterni, depressio (sulcus) articularis coracoideus, ventrally distinct, linear jugum extending caudolaterad from margo lateralis of sulcus articularis to continue uninterrupted to merge with margo lateralis et/aut pila ventralis of processus caudolateralis sterni, thereby defining a subtriangular region immediately caudal to basis of processus craniolateralis, status:
a. absent; **b.** present.

1128. Corpus sterni, margo cranialis sterni, pila coracoidea sterni, angulus with respect to margo cranialis sterni, forma (**ordered**):
a. "weakly angled," approximately parallel, angulus approximately 0°;
b. "moderately angled," subdiagonal, angulus between 0° and 45°;
c. "strongly angled," supra-diagonal, angulus greater than 45°.
Note.—See: Mivart (1877: 25, 33); Fürbringer (1888: pls. V and VII); K. Lee et al. (1997: appendix 1, character 4); J. A. Clarke (2004).

1129. Corpus sterni, facies dorsalis, margo cranialis sterni, depressio (sulcus) articularis coracoideus, foramen pneumaticum medianus (**new term**), status et forma (**unordered**):
a. absent;
b. present, exposed within sulcus;
c. present, ventrally enclosed by trianguloid spina externa;
d. present, enclosed by trianguloid spina communis;
e. present, exposed, ventrolateral to sulci, and in spatium intercoracoidale.
Note.—See: Livezey (1986: appendix 1, character 90); Holdaway (1991: appendix 5.1, character 48); Livezey (1996a: appendix 1, character 27); Dyke et al. (2003: appendix 1, character 49), employed again by Dyke (2003: table 1); G. Mayr and Ericson (2004: appendix I, character 41).

1130. Corpus sterni, margo cranialis sterni, depressio (sulcus) articularis coracoideus, orientation or angulus depressionis definitivum with respect to axis rostrocaudalis (**ordered**):
a. laterocranial, i.e., almost cranial;
b. craniolateral, i.e., more lateral than cranial;
c. essentially lateral, i.e. perpendicular;
d. caudolateral, including diagonality.
Note.—In taxa without ossified sternum, may be determined by that of coracoideum, extremitas sternalis. See: Norell and Makovicky (1997); J. M. Clark et al. (1999); Xu et al. (1999b: character 106); G. Mayr (2003c: appendix, character 6); Xu et al. (2000: supplement, character 86); Xu et al. (2002a: supplement, character 183).

1131. Corpus sterni, margo cranialis sterni, depressio (sulcus) articularis coracoideus, marked, subdiagonal caudolateral extent onto facies muscularis sterni, with significant expanse cranial to sulcus et processus craniolateralis, status:
a. absent; **b.** present;
x. noncomparable sulci (Dinornithiformes).

1132. Corpus sterni, margo cranialis sterni, depressio (sulcus) articularis coracoideus, marked medial separation and position on terminus of processes craniolaterales, status:
a. absent; **b.** present.
Note.—See: Livezey (1998b: appendix A, characters 141–142).

1133. Corpus sterni, margo cranialis sterni, depressio (sulcus) articularis coracoideus, labra externa, hiatus labri (**new term**), status:
a. absent; **b.** present.
Note.—Hiatus effects subdivision of bilateral counterparts into respective sectiones medialis et lateralis, the latter with aspect of isolation, continuous with rest of sulcus by sectio vestigialis (**new term**). See: Chu (1998: appendix 1, character 71), regarding labrum internum.

1134. Corpus sterni, margo cranialis sterni, depressio (sulcus) articularis coracoideus, labrum externum, tuberculum labri ventralis, status (**unordered**):
a. absent;
b. present, angulus, essentially incorporated into labrum;
c. present, cranioventrally distinct lamina or torus, departing from curvature of labrum;
d. present, prominent tuberculum.
Note.—See: Livezey (1998b: appendix A, character 144). Tuberculum labri externi typically aligned with linea muscularis ventralis coracoidei (demarcation of mm. pectoralis thoracicus et supracoracoideus), and approximating the terminus lateralis of the labrum.

1135. Corpus sterni, margo cranialis sterni, depressio (sulcus) articularis coracoideus, labrum externum, tuberculum labri ventralis, foramen (a)pneumaticum immediately dorsal to tuberculum, status et typus (**unordered**):
a. absent;
b. present, depressio apneumaticum;
c. present, foramen pneumaticum.
Note.—Foramen may be homologue of fovea for articulationes sternocoracoidei in some ratites (e.g., Dinornithiformes).

1136. Corpus sterni, margo cranialis sterni, sulcus articularis coracoideus et (as continued laterocaudad) linea intermusculares dorsolateralis (mm. pectoralis et supracoracoideus), position of termina lateralis relative to partes of margo costalis sterni:

a. sulcus entirely cranial and medial to terminus cranialis marginis costalis, sulcus neither extending to nor oriented toward margo lateralis sterni;

b. sulcus not entirely cranial to terminus cranialis of marginis costalis, sulcus extending to intersect or oriented toward margo lateralis sterni.

Note.—Character primarily reflects angularity of rostrum sterni relative to margo costalis. See: Archey (1941: fig. 55).

1137. Corpus sterni, margo cranialis sterni, depressiones (sulcus) articulares coracoidei, labrum internum, facies articularis coracoideum, pori pneumatici, status:

a. absent; **b.** present.

1138. Corpus sterni, margo cranialis sterni, depressiones (sulcus) articulares coracoidei, labrum internum, facies articularis coracoideum, basis pilae medianus (**new term**), status et forma (**ordered**):

a. absent;

b. present, moderately distinct;

c. present, conspicuously prominent.

Note.—Feature represents sternal counterpart for mediodorsal "buttress" of extremitas sternalis coracoidei in some taxa.

1139. Corpus sterni, margo cranialis sterni, depressio (sulcus) articularis coracoideus, labrum internum, foramen medialis (**new term**), status:

a. absent; **b.** present.

Note.—A dorsally directed foramen passing from sulcus articularis coracoideus to facies visceralis of margo cranialis of corpus sterni, often in combination with spina communis et foramen rostri.

1140. Corpus sterni, margo cranialis sterni, processus craniolateralis sterni, status:

a. present; **b.** absent.

Note.—See: Norell and Makovicky (1997); J. M. Clark et al. (1999).

1141. Corpus sterni, margo cranialis sterni, processus craniolateralis sterni, forma craniocaudalis (**unordered**):

a. obsolete, rendering vertex craniolateralis mere angularity;

b. moderate or short (comparable to processes caudolaterales), typically subrectangular and including significant dorsal orientational component;

c. elongate (approximating margo cranialis sterni in cranial prominence), robust or laminate, terminus typically acuminate;

d. markedly elongate (approximating rostrum sterni in cranial prominence), lateromedially compressed;

x. noncomparable (Dromaiidae).

Note.—See: Holman (1961, 1964); Strauch (1985: character 11); Bledsoe (1988: appendix, character 2); discounted by K. Lee et al. (1997: appendix 2) for ratites; Livezey (1998b: appendix A, character 141); Dyke et al. (2003: appendix 1, characters 52–53).

1142. Corpus sterni, margo cranialis sterni, processus craniolateralis sterni with respect to axis majoris carinae, angulus (**ordered**):

a. perpendicular, angulus ~ 90°;

b. diagonal, angulus ~ 45°;

c. parallel, angulus ~ 0°.

Note.—See: Holman (1961, 1964); Payne and Risley (1976: character 19), regarding Ardeidae; Dyke et al. (2003: appendix 1, character 51), regarding Galliformes.

1143. Corpus sterni, margo cranialis sterni, processus craniolateralis sterni, pronounced dorsocaudal curvature or orientation, status:

a. absent;

b. present, processus subcolumnar or laminate;

x. noncomparable by truncation of processus (*Aptornis*, *Raphus*, *Pezophaps*).

Note.—See: Andrews (1896: fig. 2) for *Aepyornis*; E. Newton and Clark (1879: pl. XLVIII) regarding *Pezophaps*; Livezey (1998b: appendix A, character 142).

1144. Corpus sterni, margo cranialis sterni, deep, monotonically curved invaginatio between rostrum sterni et processus craniolateralis, status:

a. absent or not marked;

b. present, as described;

x. noncomparable by obsolete rostrum (*Aptornis*).

1145. Corpus sterni, margo cranialis sterni, immediately lateral to basis pilaris carinae and proximal to rostrum sterni, distinctly broad, bilateral, triangular expanses of facies muscularis, status:

a. absent; **b.** present.

1146. Corpus sterni, margo cranialis sterni, facies visceralis, distinct sulcus sellaris medialis (**new term**) at basis of rostrum sterni and between facies articulares coracoidei, status:

a. absent; **b.** present.

1147. Corpus sterni, margines cranialis et costalis sterni, processus craniolateralis sterni et processes costales, significant positioning of processes costales on margo lateralis of processus craniolateralis, status:

a. absent;

b. present, typically majority of processes costales so positioned.

Note.—See: Heimerdinger and Ames (1967: fig. 1), in which virtual totality of processes costales sterni are positioned on margines laterales of processes craniolaterales (i.e., "costal sternum"), whereas few or none extend caudad to latter process (i.e., "metasternum").

1148. Corpus sterni, margines cranialis et costalis sterni, processus craniolateralis sterni immediately medial to sulcus articularis coracoideus, tuberculum

labri externa, depressio enclosing pori pneumatici, status:
a. absent; **b.** present.
Note.—See: Holman (1961: character 4).

1149. Corpus sterni, facies visceralis sterni, basis processi craniolateralis et/aut processus craniolateralis proprius, impressio origii m. sternocoracoidei, status et forma (**ordered**):
a. absent or indiscernable;
b. present, shallow;
c. present, moderately distinct or conspicuous, often pneumatic;
x. noncomparable (Mesitornithidae).
Note.—See: Archey (1941: fig. 55).

1150. Corpus sterni, margo cranialis sterni, sulcus articularis coracoideus (ventral perspective), continuity (caudo)laterad, status et forma (**ordered**):
a. absent;
b. present, laterad to unite with processus craniolateralis, impressio craniolateralis sterni aut basis processi;
c. present, caudolaterad to unite with margo costalis;
x. noncomparable (Mesitornithidae).

1151. Corpus sterni, margo cranialis sterni, sulcus articularis coracoideus, terminus lateralis sulci, deep, subcircular fossa pneumaticus, status:
a. absent; **b.** present.

1152. Corpus sterni, margo cranialis sterni, sulcus articularis coracoideus, terminus lateralis sulci, limited section enclosing pori pneumatici, status:
a. absent; **b.** present.

1153. Corpus sterni, facies muscularis, impressio aut eminentia m. coracobrachialis caudalis, status et forma (**unordered**):
a. absent;
b. present, as impressio ovalis;
c. present, as impressio ovalis within less-deep, more-expansive impressio m. supracoracoideus, together uniquely craniolateral in position;
d. present, as eminentia;
x. noncomparable (Dinornithiformes).
Note.—See: Archey (1941: fig. 55).

1154. Corpus sterni, margo cranialis sterni, processus craniolateralis, basis processi, facies caudalis, recessus pneumaticus, status:
a. absent; **b.** present.
Note.—Evidently vestigium of cranialmost loculus costalis.

1155. Corpus sterni, rostrum sterni (exclusive of processes craniolaterales), forma generalis:
a. narrow and/or transversely sublinear;
b. broad and parabolic.
Note.—See: Chiappe (2002: appendix 20.2, character 77), pertaining to apomorphic "broad and parabolic" rostrum sterni.

1156. Corpus sterni, rostrum sterni aut basis rostrodorsalis carinae sterni, recessus pneumaticus, status et typus (**ordered**):
a. absent;
b. present, small, no wider than basis carina and shallower dorsoventrad than sulcus articularis coracoidei;
c. present, medium, at least as wide as basis carina and at least as deep dorsoventrad as sulcus articularis coracoidei.
Note.—Distinct from recessus dorsalis spinae (characterized elsewhere).

1157. Corpus sterni, rostrum sterni, spina externa rostri, status et forma (**unordered**):
a. absent or obsolete, loss evidently beginning medially;
b. present, short, shallow, medially invaginated, bifurcated spina;
c. present, small tuberculum aut cuneatus;
d. present, prominent, bilaterally compressed, dorsally oriented crista;
e. present, elongate, laminar spina;
f. present, elongate, bipartite spina;
g. present, triangular, prominent, cranially broadening processus;
x. noncomparable by presence of spina communis (Galliformes, Turnicidae, Mesitornithidae, Upupidae, Bucerotidae) or synostosis (Opisthocomidae).
Note.—See: Ligon (1967: table 2); Payne and Risley (1976: character 18), regarding Ardeidae; Strauch (1978: character 38), reanalyzed by Björklund (1994: appendix) and Chu (1995); Livezey (1986: appendix 1, character 79); Siegel-Causey (1988: characters 96–97); Livezey (1989: table 1, character 79); Holdaway (1991: appendix 5.1, character 55); Livezey (1991: appendix 1, character 150); Webster (1992); Livezey (1995b: appendix 1, character 6); Livezey (1995c: appendix II, character 2); Livezey (1996a: appendix 1, character 29); Livezey (1996b: appendix 1, character 10); Livezey (1996c: character 2); Livezey (1997b: appendix 1, character 7); Livezey (1998b: appendix A, character 162); Hughes (2000: appendix 2, characters 96–97), after Seibel (1988: character ST 2); G. Mayr (2002a: legend for fig. 9, node 2, character 1); G. Mayr (2003b: appendix I, character 9); G. Mayr (2003c: appendix, character 4); G. Mayr and Clarke (2003: appendix A, character 70); G. Mayr et al. (2003: appendix 1, character 32); Dyke and van Tuinen (2004: appendix 1, character 47); G. Mayr (2005b: appendix A, character 19).

1158. Corpus sterni, rostrum sterni, spina externa rostri, lateromedially compressed, cranially curvilinear lamina extending from margo ventralis rostri ventrad to apex carinae, status:

a. absent; **b.** present.

Note.—See: G. Mayr (2003b: appendix I, character 9).

1159. Corpus sterni, rostrum sterni, spina externa (or communis) rostri, ala(e) spina(e) sternae, status et forma (**unordered**):

a. absent;

b. present, comprising ala ventralis spina sterni;

c. present, comprising alae laterales spinae sternae;

d. present, comprising both alae ventralis et laterales spinae sternae;

x. noncomparable by absence of carina (Palaeognathae, Dromornithidae).

Note.—See: Sibley and Ahlquist (1972: table 4), who contrasted the "manubrial process" in Tytonidae and Strigidae; Livezey (1997a: appendix 1, character 60; *corrigenda*, Livezey 1998a); also see Hughes (2000: appendix 2, character 96), after Seibel (1988: character ST 2); Livezey (1998b: appendix A, character 165); Dyke (2001b: appendix 1, character 60); Dyke et al. (2003: appendix 1, character 54); G. Mayr (2003b: appendix I, character 9).

1160. Corpus sterni, rostrum sterni, spina externa rostri, prominent dorsocranial elongation and terminal bifurcation, status:

a. absent; **b.** present.

1161. Corpus sterni, rostrum sterni, spina externa rostri, recessus dorsalis spinae (**new term**), status:

a. absent; **b.** present.

Note.—Recessus apneumaticus, typically medial and immediately cranial to labrum internum sulci, and excluding foramina dorsoventrales spinae.

1162. Corpus sterni, rostrum sterni, spina interna rostri, status:

a. absent, typically supplanted by variably broad, deep lacuna marginalis;

b. present, forma as broad, dorsoventrally compressed lamina, thin spina, or variably conformed tuberculum.

Note.—See: Livezey (1986: appendix 1, character 82); Livezey (1991: appendix 1, character 151); Livezey (1995b: appendix 1, character 8); Livezey (1995c: appendix II, character 5); Livezey (1996a: appendix 1, character 28); Livezey (1996b: appendix 1, character 11); Livezey (1996c: character 3); Livezey (1998b: appendix A, character 164); Hughes (2000: appendix 2, characters 96 and 98), after Seibel (1988: character ST 2); G. Mayr et al. (2003: appendix 1, character 33).

1163. Corpus sterni, rostrum sterni, spina communis, status et forma (**unordered**):

a. absent or obsolete;

b. present, a short tuberculum, cuneus, eminentia, or lamina;

c. present, a moderately long processus;

x. noncomparable by absence of carina (most Palaeognathae, *Aptornis*).

Note.—"Spina" *sensu lato* includes septa interarticulares. See: Holman (1961: character 2).

1164. Corpus sterni, rostrum sterni, spina communis et enclosed foramen rostri (if present), status (**ordered**):

a. both spina communis et foramen rostri absent;

b. spina communis present, foramen rostri absent;

c. both spina communis et foramen rostri present;

x. noncomparable by absence of spina communis (Dromornithidae).

Note.—See: Fürbringer (1888: pls. V and VII); Webster (1992); Ericson (1997: table 1, character 36); Livezey (1997a: appendix 1, character 61; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, character 163); Hughes (2000: appendix 2, character 96), after Seibel (1988: character ST 2); Dyke (2001b: appendix 1, character 61). Note that Stercorariidae possess a foramen within the spina externa *sensu stricto*.

1165. Corpus sterni, margo costalis sterni, approximate proportion composed by latter of total craniocaudal length of corpus sterni, magnitudo (**ordered**; polarity uncertain):

a. less than one-fourth;

b. between one-fourth and one-half;

c. between one-half and three-fourths;

d. greater than three-fourths.

1166. Corpus sterni, margo costalis sterni, vertex (ala) postcostalis (**new term**), status et forma (**ordered**):

a. absent;

b. present, subangulus of limited expanse;

c. present, ala of comparatively great, ovate expanse.

1167. Corpus sterni, margo costalis (postcostalis aut lateralis) sterni, deep medial invaginations of corpus immediately caudal to the margo costalis verae aut processus costalis, delimited craniad et caudad (latter including an expanse of substantial bony corpus) by lateral areas of the corpus sterni, effecting a postcostal narrowing, status:

a. absent or only suggested;

b. present, prominent.

Note.—See: Fürbringer (1888).

1168. Corpus sterni, margo costalis (postcostalis aut lateralis) sterni, modest but distinct lateral broadening caudal to margo costalis and commonly adjacent invaginatio, and delimited by narrower sitae marginorum caudal to margo costalis, status:

a. absent; **b.** present.

Note.—See: Jollie (1977: figs. 164, 167, and 168).

1169. Corpus sterni, facies muscularis, regio centralis, ventrally flattened, ovate (ventral) eminentia, status:

a. absent; **b.** present.

Note.—See: Fürbringer (1888: pl. V).

1170. Corpus sterni, facies muscularis, regio medialis, flattened, craniocaudally oriented, sublinear (ventral) eminentia, status:

a. absent; **b.** present.

Note.—See: Fürbringer (1888: pl. V).

1171. Corpus sterni, facies muscularis, impressio aut eminentia m. coracobrachialis caudalis, exceptional caudal extent medial to entire margo costalis, status:

a. absent; **b.** present.

Note.—Caveat to distinguish from pars lateralis of labrum externum of sulcus articularis coracoidei. See: Archey (1941: fig. 55).

1172. Corpus sterni, facies muscularis, facies ventralis, distinct ventral prominentia trabeculares and distinguishable interposed lamina delimiting caudally oriented termina craniales incisorum, status:

a. absent; **b.** present.

Note.—Care to be taken not to confuse with lineae intermusculares (especially those of margines laterales of mm. pectorales thoracicae), e.g., in the similar but provisionally nonhomologous case of Columbiformes.

1173. Corpus sterni, facies muscularis, facies ventralis, prominent jugum subcostalis (**new term**) and distinct sulcus medioventralis costorum (**new term**), typically extending craniocaudad for majority of corpus sterni, margo lateralis (**unordered**):

a. absent, or sufficiently limited in depth and craniocaudal exent;

b. present, moderate; **c.** present, extreme.

Note.—See: Livezey (1998b: appendix A, character 153).

1174. Corpus sterni, facies muscularis, pila caudalis (**new term**), in combination with pilae costales et coracoidea, status:

a. absent;

b. present and typically conjoined, resulting in basinesque aspectus ventralis.

1175. Corpus sterni, margo costalis sterni, processus (trabecula) lateralis, status et forma (**unordered**):

a. absent;

b. present, comprising trabeculae et spina caudalis, with spina cranialis obsolete;

c. present, comprising trabeculae et spinae cranialis et caudalis;

x. noncomparable (*Aepyornis*).

Note.—See: E. Newton and Clark (1879: pl. XLVIII) regarding *Pezophaps*; Andrews (1896: fig. 2) for *Aepyornis*; Chiappe (2001a: appendix 1, characters 74–75); Chiappe (2002: appendix 20.2, characters 74–75).

1176. Corpus sterni, margo costalis sterni, processus (trabecula) caudolateralis, status (**unordered**):

a. absent;

b. present and distinct, evident by incisurae, fenestrae, or both;

c. present but as rudimenta or vestigia, suggested by pila (coalesced trabecula), small or irregular fenestrae or shallow incisurae.

Note.—Rotthowe and Starck (1998: appendix, character 17) proposed that the processus lateralis (and included trabecula obliquum) of galliform birds is derived from an early synostosis of a costa sternalis with a craniolateral *anlage* of the sternum proper, as opposed to a traditional interpretation as neornithine neomorph (Stresemann 1934; D. Starck 1989), an interpretation consistent with retention of both trabeculae laterales et caudolaterales propriae apparent in most or all taxa having the former (e.g., galliforms). Involvement of an actual primordium costalis remains hypothetical, but the summary inference is followed here. Moreover, data indicate that whereas Galliformes and Columbiformes (Boles 1999) both possess processes laterales, the Galliformes alone possess caudolaterales as well (Columbiformes having trabeculae intermediae).

See: E. Newton and Clark (1879: pl. XLVIII) regarding *Pezophaps*; Andrews (1896: fig. 2) for *Aepyornis*; Fürbringer (1888); Cracraft (1974: 503, character 20); S. F. Simpson and Cracraft (1981: character 6, part), in which "trabeculae" are compared by lengths defined by adjacent incisurae; Livezey (1986: appendix 1, character 81); Cracraft (1988: series X, character 3); Livezey (1989: table 1, character 81); Livezey (1995c: appendix II, character 4); Chiappe et al. (1996: appendix 1, character 70); Livezey (1996a: appendix 1, character 20); Livezey (1996b: appendix 1, character 13); K. Lee et al. (1997: appendix 1, character 2); Livezey (1997a: appendix 1, character 62; *corrigenda*, Livezey 1998a); Livezey (1997b: appendix 1, character 6); Chu (1998: appendix 1, character 73); Livezey (1998b: appendix A, character 133); J. M. Clark et al. (1999), regarding oviraptorid (possibly separate) state; Dyke (2001b: appendix 1, character 62); Chiappe (2002: appendix 20.2, characters 74–75); Chiappe and Walker (2002: appendix 11.1, characters 14–15); Dyke and Gulas (2002: appendix 1, character 32), emphasized intervening incisurae; G. Mayr and Clarke (2003: appendix A, character 73); Dyke and van Tuinen (2004: appendix 1, character 50).

1177. Corpus sterni, margo costalis sterni, processes (trabecula) lateralis et caudolateralis, bifurcatio lateral to margo costalis, serving as common pedicel for both processes, and resulting from exceptionally deep incisurae caudolaterales, status:

a. absent; **b.** present.

Note.—See: Holman (1961: character 1).

1178. Corpus sterni, margines cranialis et costalis sterni, processus (trabecula) caudolateralis, continuity of trabecula (ventral perspective) from processus proprius craniad through tuberculum labri ventralis to margo cranialis closely lateral to carina sterni, status:

a. absent; **b.** present.

1179. Corpus sterni, margo costalis sterni, processus caudolateralis (if present), terminus caudalis, distinct lateroventral curvature, status:

a. absent; **b.** present.

1180. Corpus sterni, margo caudalis sterni, processus caudolateralis (if present), facies visceralis, depressio postpilaris (**new term**), status:

a. absent; **b.** present.

1181. Corpus sterni, margo costalis sterni, processus caudolateralis (if present), terminus caudalis, bifurcatio terminalis of common processus comprising terminus modalis of processus caudolateralis et (sub)trabecula medialis, status:

a. absent;

b. present, asymmetrical and/or concave, rare and perhaps pathological.

Fenestra, foramina, et trabeculae marginis caudalis sterni

Note.—These obvious features of margo caudalis sterni of Aves have a long history of study. See: Heimerdinger and Ames (1967: fig 1), in which these various hiata sterni and processes costales essentially comprise the basis for the bipartitioning of the sternum into the rostral "costal sternum" and the caudal "metasternum," the latter encompassing all perforations *sensu lato* of margo caudalis of Passeriformes; G. Mayr and Ericson (2004: appendix I, character 44), for inclusive treatment of diverse trabeculae et fenestrae/incisurae sterni; G. Mayr (2004a: appendix 1, character 38) and G. Mayr (2005a: appendix 1, character 15), for similar tallies of incisurae et/aut fenestrae.

1182. Corpus sterni, margo caudalis sterni, fenestra aut incisura caudolateralis, status et forma modalis (**unordered**):

a. absent; **b.** present, as incisura;

c. present, as fenestra.

Note.—These invaginatae or fenestrae sterni are occluded within the corpus sterni by membranae incisurae (fenestrarum) sterni, extended in some for some distance caudad by cartilagines. Reconstructions for purportedly enantiornithine *Protopteryx fengningensis* indicate a sternum having peculiar and elongate trabeculae "lateralis" directed caudad from the pila costalis (Zhang and Zhou 2000: fig. 3).

See: Fürbringer (1888: pls. V–VII); Cracraft (1974: character 20); Cracraft (1982: series 1, character 5); Elzanowski (1995: 38, character unindexed); G. Mayr (2002a: appendix 1, character 14, part), with respect to Caprimulgiformes; G. Mayr and Clarke (2003: appendix A, character 73); G. Mayr et al. (2003: appendix 1, character 35); G. Mayr (2004d: appendix I, character 15); G. Mayr (2005a: appendix 1, character 15); G. Mayr (2005b: appendix A, character 21).

1183. Corpus sterni, margo caudalis sterni, incisura aut fenestra caudolateralis (if present), cranial extent (**unordered**):

a. absent or obsolete—despite discernable trabecula or pila;

b. rudimentary—incisura appearing as shallow invagination of margo caudalis of corpus sterni;

c. abbreviate—length of incisura aut fenestra less than one-third craniocaudal length of corpus sterni;

d. intermediate—length of incisura aut fenestra between one-third and two-thirds of craniocaudal length of corpus sterni;

e. elongate—length of incisura aut fenestra greater than two-thirds of craniocaudal length of corpus sterni, approaching terminus caudalis of processes costales sterni;

x. noncomparable where incisura (fenestra) et/aut trabecula absent.

Note.—See: Payne and Risley (1976: character 17), regarding Ardeidae; Rotthowe and Starck (1998: appendix, character 32).

1184. Corpus sterni, margo costalis sterni, processus caudolateralis (if present), orientation relative to corpus sterni as reflected (in part) by angulus defined by incisura caudolateralis (**new term**), vertex cranialis angulae (**ordered**):

a. angulus approximately 45°, or vertex approximately diagonal to margo lateralis of trabecula mediana of corpus sterni;

b. angulus between 15° and 45°, vertex is parabolic;

c. angulus essentially undefined, as processus is subparallel to margo costalis and "vertex" is ellipsoidal;

x. noncomparable by absence of processus or incisura, or indeterminate orientation (see character regarding status).

Note.—Strict comparability may be limited to those among taxa either lacking or possessing trabeculae intermediae. Angulus of vertex estimated by intersection of chords of margines cranial to osseus margo incisurae. See: Murray and Vickers-Rich (2004: table 9, character 7), regarding Dromornithidae.

1185. Corpus sterni, margo caudalis sterni, trabecula caudolateralis (if present), margo terminus caudalis, forma (**unordered**):

a. rounded or (sub)rectangular, often obliquely aligned;

b. cruciate, with terminal, transverse pila;

c. (sub)acuminate, variably oriented;

x. noncomparable where presence of trabecula uncertain or known to be absent (e.g., *Confuciusornis*, *Ichthyornis*, and *Lithornis*; see status) or union in case of homologous fenestra (*Aegotheles*).

1186. Corpus sterni, margo caudalis sterni, trabecula intermedia (**new term**), status et forma (**unordered**):

a. absent;

b. present, delimited medially by shallow incisura;

c. present, delimited medially by deep incisura or fenestra.

Note.—See: Fürbringer (1888: pls. V–VII); Cracraft (1971a: fig. 10), in which possession of trabeculae intermediae sterni of nonexemplar, purportedly leptosomatid *Atelornis* differed from *Leptosomus* and resembled *Coracias*; S. F. Simpson and Cracraft (1981: character 6, part), in which "trabeculae" are compared by lengths defined by adjacent incisurae; Livezey (1997a: appendix 1, character 63; *corrigenda*, Livezey 1998a); G. Mayr and Clarke (2003: appendix A, character 73); G. Mayr et al. (2003: appendix 1, character 35); G. Mayr (2004d: appendix I, character 15); G. Mayr (2005a: appendix 1, character 15).

1187. Corpus sterni, margo caudalis sterni, trabecula intermedia (if present), terminus caudalis, forma:

a. rounded, subrectangular, subacuminate, or (rarely) unilaterally hamulate;

b. cruciate, having transverse, bilaterally protrusive (often obliquely slanted) pila transversus terminae, including as extreme case pila caudalis or homologous fenestra;

x. noncomparable by absence of trabecula (see character regarding status).

Note.—See: Livezey (1998b: appendix A, characters 148–150).

1188. Corpus sterni, margo caudalis sterni, incisura aut fenestra intermedia (**new term**), relative cranial extent (**ordered**):

a. rudimentary, incisura appears as minor (perhaps irregular) invaginatio or concavitas;

b. abbreviate, length of incisura aut fenstra less than one-third craniocaudal length of corpus sterni;

c. moderate, length of incisura aut fenstra between one-third and two-thirds of craniocaudal length of corpus sterni;

x. noncomparable by absence of delimiting trabecula intermedia (see character regarding status).

Note.—Contrary to S. L. Olson (1987b), abasal avian polarity of a "four-notched" sternum is unsupported. See: Livezey (1998b: appendix A, characters 148–151); G. Mayr (2002a: appendix 1, character 14, part), with respect to Caprimulgiformes; G. Mayr and Clarke (2003: appendix A, character 73); G. Mayr (2005b: appendix A, character 21). Fenestrae (incisurae) sterni are sealed in life by membrana incisurae (fenestrarum) sterni. Principally reflects caudal extension of trabecula mediana, and may only be strictly comparable among taxa sharing status of trabecula intermediana.

1189. Corpus sterni, trabeculae caudolateralis, intermedia, et mediana, cranialmost relationships at emergence from corpus proprius (i.e., at apices craniales of incisurae), forma:

a. trabeculae caudolateralis, intermedia, et mediana emerge independently and essentially in parallel;

b. trabeculae caudolateralis et intermedia share common cranial nodus separate from trabecula mediana;

x. noncomparable by absence of delimiting trabecula intermedia (see character regarding status).

1190. Corpus sterni, facies muscularis, trabeculae caudolateralis, intermedia, et mediana, respective pilae extending into intersectio in corpus cranial to separation of trabeculae, conspicuous craniocaudal jugum defining a right angulus laterad immediately cranial, status:

a. absent; **b.** present;

x. noncomparable (*Aptornis*).

1191. Corpus sterni, margo caudalis sterni, trabecula mediana, margo aut terminus caudalis, forma definitivum (**unordered**):

a. untapered or weakly tapered, transversely broad, linear or rounded;

b. distinctly tapered, rounded or subrectangular;

c. distinctly tapered, cruciate or shallowly, symmetrically invaginate, including homologous pila incorporated in margines caudales of fenestrae intermediae;

d. distinctly tapered, irregularly invaginated or concave.

Note.—See: S. F. Simpson and Cracraft (1981: character 6, part), in which "trabeculae" and respective lengths are defined by adjacent incisurae; Livezey (1986: appendix 1, character 84); Livezey (1995b: appendix 1, character 10); Chu (1998: appendix 1, character 72); Livezey (1998b: appendix A, characters 148–150, 154); Chiappe (2001a: appendix 1, characters 76 [primarily] and 78); Chiappe (2002: appendix 20.2, characters 76 and 78); Chiappe and Walker (2002: appendix 11.1, character 16).

1192. Corpus sterni, margo caudalis sterni, trabeculae caudolateralis, intermediana, et mediana, relative caudal extents caudal to margo caudalis proprius—sequenced within states from longest to shortest (**unordered**):

a. trabecula intermedia ≥ trabecula mediana ≥ trabecula caudolateralis;

b. trabecula caudolateralis ≥ trabecula mediana ≥ trabecula intermedia;

c. trabecula mediana ≥ trabecula intermedia ≥ trabecula caudolateralis;

d. trabecula caudolateralis ≥ trabecula intermedia ≥ trabecula mediana;

e. trabecula mediana ≥ trabecula caudolateralis ≥ trabecula intermedia;

f. trabecula intermedia ≥ trabecula caudolateralis ≥ trabecula mediana;

x. noncomparable by absence of two or more defining trabeculae (ratites, *Pelecanoides*, *Aptornis*, *Psophia*, *Aramus*, *Grus*, *Cacatua*, Apodiformes).

Note.—Absence was treated as a length of zero. Taxa lacking two or more delimiting trabeculae were considered "noncomparable." See: S. F. Simpson and Cracraft (1981: character 6, part); Livezey (1998b: appendix A, characters 134–135, 151); G. Mayr (2003a: appendix I, character 29); G. Mayr (2004b: appendix 1, character 35).

1193. Corpus sterni, margo caudalis sterni, "aborted development or ossification" in which incisurae et fenestrae are of irregular and variable conformation, and/or corpus is thin and porous, status:

a. absent, margo typically dense, symmetrical, reinforced by pila caudalis;

b. present.

Note.—See: McGowan (1982: pl. II), regarding Apterygidae; Livezey (1996a: appendix 1, character 26), regarding moa-nalos (Anatidae: Thambetochenini).

Carina sterni

1194. Carina sterni, status et forma (**ordered**):

a. absent;

b. present, variably extensive rudimentum or vestigium;

c. present, extending majority of the length of corpus sterni, margo ventralis carinae (lateral perspective) essentially linear, concave, or distinctly convex.

Note.—Length *sensu* margo ventralis carinae relative to margo caudalis of corpus sterni. Truly acarinate sterni among neognathous birds are not affirmed by this study, contrary to the statement by Baumel and Witmer (1993: annotation 161) regarding the flightless psittaciform *Strigops* (Livezey 1992b). However, in this and other profoundly apomorphic, flightless taxa exclusive of wing-propelled diving birds (Livezey 1988, 1989; Raikow et al. 1988), the carina is genuinely vestigial by way of paedomorphosis (Livezey 1990, 1992a–b, 1995d).

See: Friant (1959); Cracraft (1974: 503, character 19); S. L. Olson and Hasegawa (1979, 1985, 1996); Stephan (1979); S. L. Olson (1980); Cracraft (1986: appendix, character 6); Gauthier (1986: 13, unindexed synapomorphy of Ornithurae); Livezey (1986: appendix 1, character 80); Cracraft (1988: series III, character 1); Chiappe and Calvo (1994: appendix I, character 33); Chatterjee (1995: character 10, part); Chiappe (1995a: legend for fig. 1); Chiappe (1995b: characters 31 and 33); Elzanowski (1995: character C1); Livezey (1995b: appendix 1, character 7); Livezey (1995c: appendix II, character 3); Sanz et al. (1995, 1997: character 30); Chiappe (1996b: characters 29–30); Chiappe et al. (1996: appendix 1, character 30); Hou et al. (1996: characters 16–18); Livezey (1996a: appendix 1, character 31); Livezey (1996b: appendix 1, character 12); K. Lee et al. (1997: appendix 1, character 1); Norell and Clarke (2001: appendix I, character 72), J. A. Clarke (2002: appendix I, character 72), J. A. Clarke and Norell (2002: appendix 2, character 72), and J. A. Clarke (2004: appendix 1, character 72), regarding craniocaudal extent; Sereno (2001: table 1, character 3), regarding Alvarezsauridae; Zhou and Zhang (2002: appendix III, character 72); Ji et al. (2005: supplement, part I, character 72).

1195. Carina sterni, margo ventralis carinae (lateral perspective), forma (**unordered**):

a. distinctly convex, including strongly arched profiles;

b. approximately straight;

c. distinctly concave throughout;

x. noncomparable by absence of carina (flightless Palaeognathae).

Note.—See: Livezey (1992b) regarding sternal accommodation of voluminous ingluvies of psittaciform *Strigops* (nonexemplar), which conforms to state "c."

1196. Carina sterni, margo ventralis carinae (lateral perspective), inflection point or shallow concavity approximately one-third of length of carina caudad from apex, status et forma (**ordered**):

a. absent; **b.** present, indistinct;

c. present, marked.

Note.—Fully adult specimens essential for comparisons.

1197. Carina sterni, apex carinae, forma (**unordered**):

a. simple, variably rounded angulus;

b. subhamulate, dorsocranially oriented eminentia;

c. subparabolic, cranially oriented eminentia;

d. acuminate, bilaterally carinate (termina craniales of lineae intermusculares ventromediales), cranially oriented processus;

e. bifurcate, moderately prominent, cranial angulus;

x. noncomparable (flightless Palaeognathae, Dromornithidae, Mesitornithidae, *Aptornis*).

Note.—See: Kuroda (1954: figs. 19–23); Dyke et al. (2003: appendix 1, character 47), employed again by Dyke (2003: table 1).

1198. Carina sterni, apex carinae, craniocaudal position relative to margo cranialis sterni, locus medianus or basis spina interna, if present (**ordered**):
a. well caudal; **b.** moderately caudal;
c. approximately equal;
d. distinctly cranial;
x. noncomparable by absence of element or carina (flightless Palaeognathae, *Sylviornis*, Dromornithidae, Phorhusrhacoidea).
Note.—See: Siegel-Causey (1988: character 95); Ericson (1997: table 1, character 35); Hughes (2000: appendix 2, character 95), after Seibel (1988: character ST 5); Chiappe (2001a: appendix 1, character 73); Chiappe (2002: appendix 20.2, character 73); Chiappe and Walker (2002: appendix 11.1, character 13); G. Mayr (2003a: appendix I, character 27); G. Mayr (2004b: appendix 1, character 33).

1199. Carina sterni, maximal depth ventral and normal to corpus sterni, facies muscularis, relative to minimal width of corpus sterni (exclusive of processes laterales, if present) across points on margo costalis directly lateral to that of maximal depth of carina (**ordered**):
a. obsolete or acarinate, ratio ~ 0;
b. shallow, ratio approximately less than 0.3;
c. moderately deep, ratio approximately 0.2–0.6;
d. deep, ratio approximately 0.6 or greater.
Note.—Constitutes direct index to carina depth, and indirect index to volume of mm. pectoralis et supracoracoideus.

1200. Carina sterni, apex carina, facies articularis clavicularis, status et forma (**unordered**):
a. absent, facies undifferentiated from margo cranialis et apex carina;
b. present, as incisura or concavitas;
c. present, angulus or curva apicalis;
x. noncomparable by acarinate condition (ratites, Dromornithidae) or synostosis sternoclavicularis (*Fregata*, *Pelecanus*, *Balaeniceps*, *Grus*, *Opisthocomus*).

1201. Carina sterni, facies articularis furculae (lateral perspective), forma (**unordered**):
a. rounded or subtly bilobate;
b. distinctly acuminate;
c. angular and craniodorsally oriented, distinctly flattened and distinguishable from rest of margo ventralis aut apex carinae;
x. noncomparable carina sterni or furcula absent (ratites, Dromornithidae) or where synostosis sternoclavicularis present.
Note.—See: Livezey (1998b: appendix A, character 160); Dyke and Gulas (2002: appendix 1, character 31); G. Mayr (2003a: appendix I, character 23). Prominence or lobation in part a reflection of tuberositas ligamenti sternoclavicularis.

1202. Carina sterni, facies lateralis carinae, lacuna carinae (**new term**), status:
a. absent; **b.** present;
x. noncomparable (ratites, Dromornithidae).
Note.—Apomorphic state sometimes accompanied by limited fenestration of corpus sterni. Fenestrae occluded by membranae incisurae (fenestrarum) sterni *in vivo*.

1203. Corpus sterni, facies muscularis sterni, linea intermuscularis dorsolateralis of origii m. supracoracoideus (**new term**), angulus dorsalis relative to axis craniocaudalis or chord of basis carinae (**ordered**):
a. shallow, 30° > angulus, often approximately parallel;
b. moderate, 30° < angulus < 60°;
c. wide, 60° < angulus < 90°;
x. noncomparable by absence of carina et/aut lineae (palaeognathous Neornithes, Dromornithidae).
Note.—Linea in question refers to that typically evident on the corpus sternalis, facies muscularis. See: Livezey (1986: appendix 1, character 88); Livezey (1989: table 1, character 88); Livezey (1995c: appendix II, character 6); Livezey (1996a: appendix 1, character 22); Ericson (1997: table 2, character 27); Livezey (1998b: appendix A, character 136), including aspectus impressionis m. coracobrachialis caudalis; Chu (1998: appendix 1, character 68), in reference to lateromedial position.

1204. Carina sterni, facies lateralis carinae, lineae intermusculares ventromedialis (**new term**) et dorsolateralis, dorsoventral position(s) and craniocaudal orientation(s), a reflection of relative medial depth and shape of m. supracoracoideus (**unordered**):
a. large, extensive—m. supracoracoideus relatively robust, linea ventralis (carinae) typically close to (often parallel with) margo ventralis carinae, and linea dorsolateralis [corporis] obliquely sloping across facies muscularis of corpus sterni, but outline extends essentially to terminus caudalis carinae;
b. caudally truncate, subtriangular—m. supracoracoideus small, linea ventralis [carinae] and linea dorsolateralis [corporis] delimiting a diminutive, trianguloid musculus nestled along the basis or pars cranialis of facies muscularis of corpus sterni and terminating well craniad to terminus caudalis carinae;
x. noncomparable (ratites, Dromornithidae).
Note.—Apomorphic state functionally associated with reduced relative power for elevation of the wing, hence typical of taxa characterized by soaring and gliding flight.

1205. Carina et corpus sterni, facies muscularis, lineae m. pectoralis, limitus mediocaudalis, comparatively laterocranial position such that musculus terminates so as to expose a subtriangular, convex por-

tion of the corpus sterni caudad to the carina (ventral perspective), status:
a. absent; **b.** present.

1206. Carina sterni, basis (dorsalis) et facies lateralis carinae, variably pronounced dorsal depressio origii m. supracoracoideus, status:
a. absent; **b.** present.
Note.—*Fregata* and *Pelecanus* are further distinguished by depressio bounded caudad by pilaris marking terminus caudalis origii m. supracoracoideus.

1207. Carina sterni, margo cranialis carinae, crista lateralis carinae, status:
a. absent or virtually indistinct, margo cranialis carinae rounded;
b. present, distinct, bilateral cristae carinae and typically delimiting interposed sulcus carinae;
x. noncomparable (ratites, Dromornithidae).
Note.—Evidently serves as one of several ancorae for membrana sternocoracoclavicularis.

1208. Carina sterni, margo cranialis carinae, crista mediana carinae, status et forma (**ordered**):
a. absent, margo cranialis carinae rounded;
b. present, a modest cristula;
c. present, a prominent crista, extending significantly craniad to pila carinae;
x. noncomparable (ratites, Dromornithidae).
Note.—True crista diagnosed by pronounced bilateral compression and distinctness from pila carinae. Evidently serves as one of several ancorae for membrana sternocoracoclavicularis. Apparent prominence of crista mediana carinae contingent, in part, upon distinctness of sulcus carinae et cristae laterales carinae, and (state "c") prominence and caudal position of pila carinae.

1209. Carina sterni, margo cranialis carinae, crista medialis carinae, tuberculum cristae medianae (**new term**), status (**unordered**):
a. absent; **b.** present, small, subrectangular;
c. present, large, subtriangular;
x. noncomparable (ratites, Dromornithidae).
Note.—Refers to "flange" on margo cranialis of pila carinae at approximate midpoint between basis carinae et apex carinae. See: Butendieck (1980: fig. 30, feature 40), Butendieck and Wissdorf (1981), Butendieck et al. (1981), suggesting alignment of tuberculum with linea muscularis.

1210. Carina sterni, margo cranialis carinae, pila carinae, orientation relative to margo cranialis carinae, forma:
a. directly ventral;
b. distinctly caudoventral;
x. noncomparable (ratites, Dromornithidae).

1211. Carina sterni, margo cranialis carinae, pila carinae, forma (lateral perspective) *sensu* curvature:
a. concave, i.e., curvilinear; **b.** sublinear;
x. noncomparable (ratites, Dromornithidae, *Aptornis*, *Opisthocomus*).

1212. Carina sterni, margo cranialis carinae, pila carinae, continuation cranioventrally as thin, fenestrated membrana ossificans, status:
a. absent;
b. present, enclosing ansae tracheales;
x. noncomparable (ratites, Dromornithidae).
Note.—See: Livezey (1998b: appendix A, character 159).

1213. Carina sterni, margo cranialis carinae, sulcus carinae, status et depth (**ordered**):
a. absent, margo cranialis convex, planar, or angular;
b. present, sulcus a shallow concavity, not uncommonly partitioned by medial carinula;
c. present, sulcus moderately deep;
d. present, sulcus conspicuously deep, typically sharply emarginated;
x. noncomparable (ratites, Dromornithidae).
Note.—See: Livezey (1998b: appendix A, character 155).

1214. Carina sterni, margo cranialis, sulcus carinae (if present), antrum et cavum trachealis sterni (**new term**), status et forma:
a. absent;
b. present, deep, partially encloses one or more ansae tracheales;
x. noncomparable (ratites, Dromornithidae).
Note.—See: Berndt (1938); Livezey (1998b: appendix A, character 157); Livezey (1998b: appendix A, character 158), regarding "rounded dorsal prominence" enclosed ansae tracheales beyond externum cranialis sterni.

1215. Carina sterni, margo cranialis, pila carinae, basis pilaris (**new term**), fenestrae infraspinalis (**new term**), status:
a. absent; **b.** present;
x. noncomparable (ratites, Dromornithidae).
Note.—Feature refers to typically bilateral fenestrae in the extremitas dorsalis of margo cranialis carinae, separated by crista mediana, and typically permitting only limited access into element (e.g., largely limited to internum of the pila carinae).

1216. Carina sterni, apex and margo ventralis, especially sectio cranialis (**new term**), lateromedial thickness relative to more-dorsal portions of carina:
a. approximately uniform;
b. distinctly thicker (bilaterally expanded);
x. noncomparable (ratites, Dromornithidae).
Note.—See: Livezey (1998b: appendix A, character 161).

1217. Carina sterni, margo ventralis carinae, sulcus marginis carinae (**new term**), status:
a. absent; **b.** present;

x. noncomparable (ratites, Dromornithidae).
Note.—See: Fürbringer (1888: pl. VI).

1218. Carina sterni, margo cranialis carinae, sulcus carinae, foramen pneumaticum, status et forma (**unordered**):
a. absent;
b. present, orbiculate, variably restricted;
c. present, elongate-oblong, occupying much of sulcus carinae, admitting ansae tracheales intrasternales, and largely occluded cranially by torus-shaped membrana ossificans enclosing ansae;
x. noncomparable (ratites, Dromornithidae).
Note.—See: Berndt (1938); Livezey (1986: appendix 1, character 87); Livezey (1989: table 1, character 87); Livezey (1996a: appendix 1, character 30); Livezey (1997a: appendix 1, character 66; *corrigenda*, Livezey 1998a); Chu (1998: appendix 1, character 74); Livezey (1998b: appendix A, character 156); Dyke (2001b: appendix 1, character 66). Note that alternative treatment would allocate *Anseranas* to polymorphic state "a/c/d" to encompass variation in nonexemplar members of Anserinae (e.g., *Cereopsis* and *Olor*).

1219. Carina sterni, margo cranialis, sulcus carinae, foramina pneumatica et/aut pori pneumatici:
a. absent; **b.** present;
x. noncomparable (ratites, Dromornithidae).

Interclavicula

Note.—Relationships are unclear among the processus interclavicularis, episternum (Lühder 1871: 339), and elemental interclavicula or "metaclavicula" (Prum 1988: characters 3–4; Sereno 1991: appendix, ingroup-clades character 23). Reported to be prominent, adjacent to extremitas sternalis coracoideus, and separate from claviculae in prosauropod *Plateosaurus* (Galton 2001), whereas neither claviculae nor interclaviculae known in *Stegosaurus*. In Crocodylia (e.g., *Caiman*), element evidently closely related to primordium homologous with rostrum sterni and perhaps symphysis claviculae.

1220. Os interclavicula, status:
a. present; **b.** absent or indistinguishable.
Note.—State for "absence" necessarily includes any instances in which element exists but is indiscernable, typically incorporated within synostosis interclavicularis et/aut syndesmosis sternoclavicularis. See: Sereno (1991: appendix, p. 52), as apomorphic of Ornithodira.

Clavicula

Note.—Bilateral pair united by **synostosis interclavicularis** composes **furcula** of most neognathous Neornithes. See: Weitzel (1865); Bonsdorf (1871); Fürbringer (1888, 1902).

1221. Claviculae definitivae, status et forma generalis (**unordered**):
a. absent in any form;
b. present, as ossified rudimenta, *not* sufficiently elongated ventrally to effect synostosis with margo lateralis of extremitas sternalis coracoidei;
c. present, ossified and complete, *sensu* having length permitting juncturae omalis et sternalis;
d. present, as ossified rudimentum aut vestigium as separate claviculae, either (*i*) typically attached to scapula et/aut coracoideum by sutura(e), and meeting but asynostotic, or (*ii*) represented by ligamentum aut cartilago corporis claviculae, with variably ossified and synostotic extremitates omales in adult;
e. present, profoundly vestigial and (*i*) synostotic early in ontogeny with margo craniomedialis of os scapulocoracoideum, comprising pars omalis et (sometimes) pars sternalis, further obscured by membrana sternocoracoclavicularis ossificans, and positioned caudad and mediad to cavitas glenoidalis (*Aepyornis*, some Dinornithiformes [cf. *Dinornis*, some *Megalapteryx*, *Pachyornis*], *Rhea*, *Apteryx*, Dromornithidae), or (*ii*) typically attached to scapula et/aut coracoideum by sutura(e), and sufficiently elongated ventrally to effect synostosis with margo lateralis of extremitas sternalis coracoidei, thereby delimiting a complete fenestra claviculocoracoidei (**new term**), and variably invested within membrana sternocoracoclavicularis ossificans.
Note.—Assessment made here (e.g., *Struthio*), in which vestigia of claviculae are inferred, differs from the attribution of the structure in question with a unique "descending process" of the scapula (e.g., Fürbringer 1888, 1902; Broom 1907; Lowe 1928b), a structure positioned and variably conformed as rudimentary claviculae among ratites. The structure in position is taken parsimoniously as homologous ossification of an early cartilaginous rudimentum claviculae. Currently surmised to be plesiomorphic for all Archosauria and apomorphically synostotic for Coelurosauria (Rauhut 2003). Putative "absence" in some cases may include taxa poorly known and referred to "undetermined" status (H. N. Bryant and Russell 1993; Makovicky and Currie 1998).

Vestigia in ratites varies from weakly adherent vestigium in *Casuarius* (Elzanowski 1988) to variation in flighted and flightless carinates (e.g., Psittaciformes), as detailed by Vigors (1830), Fürbringer (1888), Shufeldt (1902b), and Glenny and Friedmann (1954). Best-developed claviculae vestigiales for Dromornithidae (SP 267) are splints approximately (30 mm) synostotic (symphysis acromioclavicularis vestigialis; **new term**) with margines craniomediales partis scapularis ossis scapulocoracoideum. Claviculae vestigiales of Dromornithidae comprise one or two partes—one cranioventral to os scapula (e.g., *Dinornis*, *Megalapteryx*, *Pachyornis*) and a second synostotic to processus procoracoideus.

See: Weitzel (1865); Marsh (1880: pls. VI–VII); Lowe (1928b: fig. 18), treating ratites and differentiating claviculae vestigialia with variable success; Glenny and Friedmann (1954); Glutz von Blotzheim (1958: fig. 25), in which primordia ossium cingulorum membri thoracici differentiated with respect to sectiones marginales showing delayed ossification; Berger (1960b: table 4, character 6), contrasting Cuculidae with Musophagidae; Gauthier (1986: 12, synapomorphy of Avialae); Prum (1988: character 3); Sereno (1991: appendix, ingroup-clade character 24); H. N. Bryant and Russell (1993), treating absence of claviculae as example of larger problem of negative evidence; Chure and Madsen (1998), regarding non-maniraptoran Theropoda; Ericson (1997: table 1, character 44, part); Livezey (1998b: appendix A, character 166); Rauhut (2003: character 131).

1222. Extremitas omalis claviculae (epicleideum), marked craniocaudal increase in breadth relative to pars ventralis of scapus claviculae et extremitas sternalis claviculae, status:

a. absent; **b.** present.

1223. Extremitas omalis claviculae, processus articularis claviculae (**new term**), comprising processes acrocoracoideus et acromialis claviculae, orientation relative to arcus corporis claviculae, forma (**ordered**):

a. virtually identical, essentially a dorsal continuation of scapus;

b. distinct but limited, subangular, ventrocaudal departure;

c. conspicuously angled caudoventrad, typically involving marked angulus acrocoracoideus claviculae (**new term**) at point of maximal deviation;

x. noncomparable (ratites, Dromornithidae, *Fregata*).

Note.—See: G. Mayr (2003c: appendix, character 3); Sereno (2000: table 4, character 1), with respect to “L-shaped” form of “dorsolateral rami” furculae in planum transversus; G. Mayr (2005b: appendix A, character 18).

1224. Extremitas omalis claviculae, processus omalis claviculae, forma *sensu* comparative cranio(dorso)caudal elongation and associated separation of processes et facies articulares acrocoracoideus et acromialis, forma:

a. processus essentially a broadened or truncate terminus corporis, facies articulares closely juxtaposed or narrowly to moderately separated;

b. processus elongate, facies articulares widely separated;

x. noncomparable (ratites, Dromornithidae).

Note.—Relative length of processus acromialis independent of processus acrocoracoideus often reflected as well by distinctness of caudal angling of extremitas omalis claviculae. See: Fürbringer (1888: pls. II–III); Livezey (1986: appendix 1, character 101); Livezey (1989: table 1, character 101); Baumel and Raikow (1993: annotations 95–99), regarding implications for articulationes omales; Baumel and Witmer (1993: annotation 165), with respect to purported absence of processus acrocoracoideus associated with that of processus acromialis scapulae present in some taxa; Ericson (1997: table 1, character 45); Livezey (1996a: appendix 1, characters 36 and 41), in reference to secondary truncation in some flightless anseriforms; Livezey (1996b: appendix 1, character 14); Livezey (1997b: appendix 1, character 8); Chu (1998: appendix 1, character 75); Livezey (1998b: appendix A, character 173); Hughes (2000: appendix 2, characters 105–106), after Seibel (1988: characters FU 1 and FU 2); Sereno (2000: table 4, character 1), with respect to “dorsolateral rami” of furcula; Höfling and Alvarenga (2001), regarding Piciformes; J. A. Clarke (2002: appendix I, character 82); J. A. Clarke and Norell (2002: appendix 2, character 82); G. Mayr (2002a: legend fig. 9, node 4, character 2); J. A. Clarke (2004: appendix 1, character 82); G. Mayr (2004d: appendix I, character 10); G. Mayr (2005a: appendix 1, character 10).

1225. Extremitas omalis claviculae, processus acrocoracoideus claviculae, facies articularis acrocoracoidea, incisura aut fenestra subacrocoracoidea claviculae, status et forma (**unordered**):

a. absent; **b.** present, incisura;

c. present, fenestra.

Note.—Fenestra within lamina medial to synostosis coracoscapularis.

1226. Extremitas omalis claviculae, processus acrocoracoideus claviculae, facies articularis acrocoracoidea, forma as laterally displaced, pedicellate, ovate platform perpendicular to axis majoris claviculae, status:

a. absent; **b.** present;

x. noncomparable (ratites, Dromornithidae, *Aptornis*).

Note.—Feature typically associated with smaller, medial, comparatively caudal facies articularis acrocoracoidea on facies lateralis of dorsocaudal terminus of processus acrocoracoideus claviculae, effecting bipartite pair of mutually perpendicular articulationes acrocoraco-claviculares.

See: G. Mayr (2003b: appendix I, character 22); G. Mayr (2003c: appendix, character 3); G. Mayr and Clarke (2003: appendix A, character 62); G. Mayr et al. (2003: appendix 1, character 27); Dyke and van Tuinen (2004: appendix 1, character 41); G. Mayr (2004b: appendix 1, character 27); G. Mayr (2004d: appendix I, character 9); G. Mayr and Ericson (2004: appendix I, character 36); G. Mayr (2005a: appendix 1, character 9); G. Mayr (2005b: appendix A, character 18).

1227. Extremitas omalis claviculae, facies caudalis, processus acromialis claviculae, recessus pneumaticus acromialis caudomedialis (**new term**), status et forma (**ordered**):

a. absent;

b. present, rudimentary or vestigial, indicated by shallow depressio enclosing pori pneumatici;

c. present, moderately developed, distinctly emarginate and well defined, enclosing foramina pneumatica;

d. present, well developed, deep and well defined, enclosing deep foramen that apparently permits access to internum of element;

x. noncomparable (ratites).

Note.—Recessus, if present, is exposed in caudal perspective, and is positioned immediately ventral to the processus acromialis claviculae, facies articularis acromialis, and medial to processus acromialis claviculae, facies articularis acrocoracoidea, et margo caudalis of scapus claviculae (**new term**). See: G. Mayr and Ericson (2004: appendix I, character 35), in reference to length of processus acromialis.

1228. Extremitas omalis claviculae, processus acromialis claviculae, facies articularis acromialis, forma:

a. nondescript or poorly defined;

b. distinct depressio ovalis or fovea;

x. noncomparable (ratites, Dromornithidae).

1229. Extremitas omalis claviculae, facies caudolateralis, foramina et/aut recessus pneumaticus omalis caudolateralis (**new term**), status (**ordered**):

a. absent;

b. present, foramina without distinct recessus;

c. present, moderately developed recessus, distinctly emarginate and well defined, enclosing foramina pneumatica;

x. noncomparable (ratites, Dromornithidae).

Note.—See: Livezey (1998b: appendix A, character 171). Recessus pneumaticus also present in presynostotic claviculae vestigiales in some *Casuarius*. Recesssus, if present, is exposed in caudal or (in most taxa) lateral perspective, and is positioned immediately ventral to the entire complexus omalis coracoidei (**new term**) comprising processus acromialis claviculae, facies articularis acromialis, et facies articularis acrocoracoidea, and lateral to margo caudalis of scapus claviculae (**new term**). Perhaps better named after ligamenta accommodated by recessus.

1230. Extremitas omalis claviculae, processus articularis claviculae (**new term**), comprising processes acrocoracoideus et acromialis claviculae, forma (**unordered**):

a. unipartite—processus articularis subcylindrical and variably elongate, with terminus rounded, irregularly tubercular, angular, acuminate, or carinate;

b. bipartite and triangular—processus articularis confluent with scapus claviculae but scapus claviculae with terminus subtriangular with broad basis terminal and approximately equally expansive facies articulares at opposite vertices;

c. bipartite and bifurcate—processus articularis confluent with scapus claviculae, but scapus claviculae with terminus bifurcate with subtermina (i.e., facies articularis acrocoracoideus et acromialis) subcarinate;

x. noncomparable (ratites, Dromornithidae).

Note.—See: Livezey (1998b: appendix A, character 172); G. Mayr (2002a: legend fig. 9, node 3, character 3); Höfling and Alvarenga (2001), regarding variation in form among Piciformes; G. Mayr (2003b: appendix I, character 8).

1231. Scapus claviculae (especially pars intermedia), compression or flattening (planum transversus), status:

a. present, craniocaudally or lateromedially compressed, including sublaminate or “strap-shaped”;

b. absent, scapus subcylindrical;

x. noncomparable (ratites, Dromornithidae, Mesitornithidae).

Note.—Two major classes of compression are characterized by oblique torsion adjacent to either extremitates omalis aut sternalis, a feature useful in diagnosis but of dubious utility in distinguishing details.

See: Livezey (1986: appendix 1, character 104); Livezey (1989: table 1, character 104); Livezey (1996a: appendix 1, character 32); Ericson (1997: table 2, character 31), for variation in anseriforms, including flightless species; Höfling and Alvarenga (2001), regarding variation among Piciformes. Among Mesozoic taxa: Enatiornithes (including *Iberomesornis*) are synapomorphic in this feature (Sereno 2000: table 4, character 1); Chiappe (2002: appendix 20.2, character 68) coded relative widths of margines dorsalis et ventralis.

1232. Scapus claviculae (cranial or caudal perspective), margines lateralis et medialis, forma:

a. essentially parabolic or “U-shaped”;

b. essentially chevroniform (“V-shaped”);

x. noncomparable by condition or absence of element (ratites, Dromornithidae, Mesitornithidae).

Note.—See: Höfling and Alvarenga (2001), regarding variation in form among Piciformes; Dyke et al. (2003: appendix 1, character 27), employed again by Dyke (2003: table 1); Ji et al. (2003a: 22).

1233. Scapus (corpus) claviculae, craniocaudal curvature (lateral perspective) exclusive of extremitas omalis, forma (**ordered**):

a. absent or obsolete;

b. present, distinct, but weak to moderate;

c. present, pronounced, often approaching subcircular;

x. noncomparable (ratites, Dromornithidae).

Note.—See: Livezey (1998b: appendix A, character 167); Höfling and Alvarenga (2001), regarding variation in form among Piciformes.

1234. Scapus (corpus) claviculae (exclusive of extremitas omalis), dorsoventral trend in maximal width of scapus, status et forma (**ordered**):

a. present, slight to moderate increase in width ventrad;

b. absent, essentially uniform, dorsal and ventral widths subequal;

c. present, significant decrease in width ventrad;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Mesitornithidae, Dromornithidae).

Note.—See: Höfling and Alvarenga (2001), regarding variation in form among Piciformes; Chiappe (2001a: appendix 1, character 68); Chiappe and Walker (2002: appendix 11.1, character 11); Dyke and Gulas (2002: appendix 1, character 18); G. Mayr (2002a: legend fig. 9, node 5, character 3); Dyke et al. (2003: appendix 1, character 28), employed again by Dyke (2003: table 1).

1235. Scapus claviculae, facies lateralis, distinct depressiones et/aut concavitates, status:

a. absent; **b.** present;

x. noncomparable (ratites, Dromornithidae).

Note.—See: Norell and Clarke (2001: appendix I, character 82), describing a lateral excavation of the elements; treated similarly by J. A. Clarke (2002: appendix I, character 81), J. A. Clarke and Norell (2002: appendix 2, character 81), and J. A. Clarke (2004: appendix 1, character 81).

1236. Extremitas sternalis claviculae, scapus (corpus) claviculae, facies lateralis, recessus pneumaticus lateralis (**new term**), status:

a. absent; **b.** present;

x. noncomparable (ratites, Dromornithidae).

Note.—See: Livezey (1986: appendix 1, character 105); Livezey (1989: table 1, character 105); Sanz et al. (1995, 1997: character 84); Hou et al. (1996: character 9); Livezey (1986: appendix 1, character 103); Livezey (1996a: appendix 1, character 35); Ji et al. (2005: supplement, part I, character 82). In some taxa, status as pori pneumatici aut nutrientes is uncertain.

1237. Extremitas sternalis claviculae, scapus (corpus) claviculae, curvature (lateral perspective):

a. essentially constant in degree from synostosis interclavicularis to extremitas omalis claviculae;

b. characterized by a sharp increase near extremitas omalis claviculae;

x. noncomparable (ratites, Dromornithidae).

Note.—See: Sereno et al. (1994: footnote 12); Chu (1998: appendix 1, character 76). Livezey (1986: appendix 1, character 106) and Livezey (1996a: appendix 1, character 34), in reference to dorsal bowing of the same region that accommodates ansae tracheales intrasternales of some Anserinae; Höfling and Alvarenga (2001), regarding variation in form among Piciformes.

1238. Extremitas sternalis claviculae, facies dorsalis, processus interclavicularis dorsalis (**new term**), status et forma (**unordered**):

a. absent;

b. present, eminentia subspheroidalis;

c. present, tuberculum aut spina;

x. noncomparable (ratites, Dromornithidae).

Note.—See: Fürbringer (1888: pl. IV); Payne and Risley (1976: character 22), regarding "internal spine" of "furculum" [*sic*] among Ardeidae; Livezey (1998b: appendix A, character 170). Relationship is unclear between processus interclavicularis and elemental interclavicula or metaclavicula (Prum 1988: characters 3–4; Sereno 1991: appendix, ingroup-clades character 23). Also see: W. K. Parker (1868), Knopfli (1918), Romanoff (1960), Maillard (1948).

1239. Extremitas sternalis claviculae, symphysis claviculae, facies dorsalis, cisterna symphysialis (**new term**), status:

a. absent; **b.** present;

x. noncomparable (ratites, Dromornithidae).

1240. Extremitas sternalis claviculae, symphysis claviculae, facies ventralis, incisura symphysialis (**new term**), status et forma (**unordered**):

a. absent; **b.** present, as bilobate terminus;

c. present, largely concealed by incorporation within synostosis sternoclavicularis;

x. noncomparable (ratites, Dromornithidae).

Note.—Incisura accommodates apex carina sterni.

1241. Extremitas sternalis claviculae, symphysis claviculae, facies ventralis, incisura symphysialis (**new term**), distinct pair of separate, medially opposing, ovate facies articulares carinae, status:

a. absent; **b.** present;

x. noncomparable (ratites, Dromornithidae).

Note.—See: Stephan (1979: fig. 35); G. Mayr (2004b: 6, character 4).

1242. Extremitas sternalis claviculae, symphysis claviculae, facies cranialis, depressio symphysialis furculae (**new term**), status:

a. absent;

b. present, associated with craniodorsal slope of carina at junctura sternoclavicularis;

x. noncomparable by absence of symphysis claviculae (ratites, Dromornithidae).

1243. Extremitas sternalis claviculae, symphysis claviculae, cavum ansae trachealis (**new term**), status:

a. absent; **b.** present;

x. noncomparable (ratites, Dromornithidae).

Note.—See: Fürbringer (1888: pl. IV, fig. 76). Feature varies among Numididae, likely limited to males; present in nonexemplary Anserinae.

1244. Extremitas sternalis claviculae, facies ventralis aut caudalis, apophysis furculae (hypocleideum), status and depth relative to that of extremitas omalis furculae (**unordered**):

a. absent, including those deeply bifurcated to form incisura;

b. present, short, subcylindrical tuberculum, approximately as deep as extremitas omalis furculae;

c. present, elongate, subcylindrical processus;

d. present, bilaterally compressed, craniocaudally elongated carina;

x. noncomparable by acarinate form (ratites, Dromornithiformes, Mesitornithidae, Gruidae, *Opisthocomus*) or fundamental structural apomorphy (Fregatidae, Pelecanidae, *Balaeniceps*).

Note.—See: Fürbringer (1888: pl. IV); Strauch (1978: character 41); reanalyzed by Björklund (1994: appendix) and Chu (1995); Livezey (1986: appendix 1, character 102); Siegel-Causey (1988: character 101); Livezey (1989: table 1, character 102); Holdaway (1991: appendix 5.1, character 40); Sanz and Buscalioni (1992: character 11, part); Chatterjee (1995: character 9, part); Elzanowski (1995: character O2); Elzanowski (1995: character ?PG5); Kurochkin (1995b: table 1, character 8); Hou et al. (1996: character 10); Livezey (1996a: appendix 1, character 33); Livezey (1996b: appendix 1, character 15); Ericson (1997: table 1, character 46); Livezey (1997a: appendix 1, character 67; *corrigenda*, Livezey 1998a); Siegel-Causey (1997: table I, character 8); Rotthowe and Starck (1998: appendix, characters 10 and 18); Livezey (1998b: appendix A, character 169); Sereno (2000: table 4, character 2); Zhang and Zhou (2000: fig. 3), regarding reconstruction for *Protopteryx*; Chiappe (2001a: appendix 1, character 70); Dyke (2001b: appendix 1, character 67); Norell and Clarke (2001: appendix I, character 81), treated similarly by J. A. Clarke (2002: appendix I, character 80), J. A. Clarke and Norell (2002: appendix 2, character 80), and J. A. Clarke (2004: appendix 1, character 80); Norell et al. (2001: appendix 1, character 133); Chiappe (2002: appendix 20.2, character 70); Chiappe and Walker (2002: appendix 11.1, character 12); J. M. Clark et al. (2002a: appendix 2.2, character 135); Dyke and Gulas (2002: appendix 1, character 19); Xu (2002: suite II, character 161); Xu et al. (2002a: supplement, character 106); Dyke et al. (2003: appendix 1, character 29), identically by Dyke (2003: table 1); G. Mayr and Clarke (2003: appendix A, character 63); Dyke and van Tuinen (2004: appendix 1, character 42); Hwang et al. (2004: supplement, character 132); G. Mayr (2004d: appendix I, character 10); Xu and Norell (2004: supplement, character 132); Ji et al. (2005: supplement, part I, character 81); G. Mayr (2005a: appendix 1, character 10).

Scapula

1245. Extremitas cranialis (caput) scapulae, acromion, extension cranial to facies articularis humeralis et cavitas glenoidalis (**unordered**):

a. well caudal, extremitas cranially diminutive;

b. moderately cranial and straight, not extending craniad to facies articularis coracoideus;

c. well craniad to facies articularis coracoideus, straight and variably elongate;

x. noncomparable, characterized by truncation associated with union of element within os scapulocoracoideum (ratites, Dromornithidae).

Note.—Referred to by some as "processus uncinatus" of scapula, apparently in reference to proximity to costae.

See: Gauthier (1986: 12, unindexed synapomorphy of Avialae); Livezey (1986: appendix 1, character 109); Houde (1988: table 27, character 30); Siegel-Causey (1988: character 104); Livezey (1989: table 1, character 109); Molnar et al. (1990); Novas (1992: character F); Sereno (1994 [1993]: appendix, character 1); Elzanowski (1995: character N'6); Kurochkin (1995b: table 1, character 5); Chiappe et al. (1996: appendix 1, character 86); Hou et al. (1996: character 14, regarding "anterointernal scapular process"); Livezey (1996a: appendix 1, character 38); Ericson (1997: table 1, character 48, part; table 2, character 32); Livezey (1997a: appendix 1, character 68; *corrigenda*, Livezey 1998a); Novas and Puerta (1997: 392, character *i*); Chiappe et al. (1998: character 37); Forster et al. (1998: supplement, character 44); Ji et al. (1998: supplement, character 37); Livezey (1998b: appendix A, character 177); J. A. Wilson and Sereno (1998: appendix, character 72), regarding Sauropoda; Norell and Makovicky (1999); Xu et al. (1999b: character 36); Holtz (2000 [1998]: appendix I, characters 213–214), referring respectively to prominence of acromion *per se* and slope of margo caudalis of processus; Hughes (2000: appendix 2, character 107), for acromion relative to facies articularis clavicularis scapulae; Xu et al. (2000: supplement, character 25); Chiappe (2001a: appendix 1, character 67); J. A. Clarke and Chiappe (2001: character 63); Dyke (2001b: appendix 1, character 68); Norell and Clarke (2001: appendix I, character 103), primarily in reference to taper; Sereno (2001: table 2, character 43), cranial orientation as synapomorphic of Aves; Chiappe (2002: appendix 20.2, character 67); Chiappe and Walker (2002: appendix 11.1, character 9), regarding relative costolateral width of acromion; J. A. Clarke (2002: appendix I, characters 103–104); J. A. Clarke and Norell (2002:

appendix 2, characters 103–104); Zhou and Zhang (2002: appendix III, characters 103–104); Ji et al. (2003a: 22); Rauhut (2003: character 134); J. A. Clarke (2004: appendix 1, characters 103–104); G. Mayr (2004b: appendix I, character 31); Ji et al. (2005: supplement, part I, character 103).

1246. Extremitas cranialis (caput) scapulae, acromion, forma *sensu* cranial lobation:

a. essentially unilobate;

b. distinctly bilobate.

Note.—Biolobate form evidently reflects an elaboration and separation of origiones scapulares mm. subcoracoscapulares (medially) and m. rhomboideus superficialis (laterally). Superficially similar state can occur in which crista ligamenti acrocoraco-acromiali is dorsally laminate.

See: Rich et al. (1985: plate II); Baumel and Witmer (1993: annotation 166); G. Mayr (1998a–b: fig. 16); Höfling and Alvarenga (2001: fig. 8); G. Mayr et al. (2003: appendix 1, character 31); G. Mayr (2004d: appendix I, character 14); G. Mayr (2005a: appendix 1, character 14).

1247. Extremitas cranialis (caput) scapulae, facies articularis clavicularis, truncated but distinctly laterally oriented tuberculum, status:

a. absent; **b.** present.

Note.—See: Holman (1964); Dyke and Gulas (2002: appendix 1, character 12), in reference to “hooked” *vs.* “flat” acromion of galliforms; Dyke (2003: table 1); Dyke et al. (2003: appendix 1, characters 32 and 38); Ji et al. (2005: supplement, part I, character 104).

1248. Extremitas cranialis (caput) scapulae, facies costalis, fossa pneumatica, status:

a. absent; **b.** present.

Note.—See: Holman (1961, 1964), with respect to pneumatic fossa in the ventral base of the glenoid facet; Gauthier (1986: 13, unindexed synapomorphy of Ornithurae); Livezey (1986: appendix 1, character 111); Livezey (1989: table 1, character 111); Chatterjee (1995: character 7); Livezey (1996a: appendix 1, character 37). Perhaps related to apparently apneumatic depressio or recessus in similar position. See: Chiappe and Calvo (1994: appendix II, character 5), with respect to “deep fossa on the cranial end”; Livezey (1998b: appendix A, character 176); Livezey (1998b: appendix A, character 178), incorrectly attributed to the collum scapulae; Hughes (2000: appendix 2, character 107). Possible that fossa or depressio is homologous with impressiones insertiorum mm. subscapularis, capita laterale et mediale. See: Archey (1941: fig. 54).

1249. Extremitas cranialis scapulae, margo cranialis ventral to acromion and dorsal to facies articularis humeralis, porus aut foramen pneumaticum, status:

a. absent; **b.** present.

Note.—May represent cranially shifted homologue of preceding apomorphy. See: Dyke et al. (2003: appendix 1, character 36).

1250. Extremitas cranialis (caput) scapulae, facies lateralis, fossa pneumatica, status:

a. absent; **b.** present.

Note.—See: Gauthier (1986: 13, unindexed synapomorphy of Ornithurae); Livezey (1986: appendix 1, character 111); Livezey (1989: table 1, character 111); Chatterjee (1995: character 7); Livezey (1996a: appendix 1, character 37).

1251. Extremitas cranialis (caput) scapulae, crista ligamentum acrocoraco-acromiali, status et forma (**unordered**):

a. present, a laterally “everted” cristula;

b. absent or indiscernable from terminus acromialis *per se*;

c. present, a distinct, subacuminate or variably spatulate processus, laterally emarginate crista, or quasi-bilobate eminentia;

x. noncomparable (ratites, Dromornithidae).

Note.—See: Fürbringer (1888: pl. III), figured *Eurystomus* as bifurcated; Baumel and Witmer (1993: annotation 166), listed *Cathartes*, *Ardea*, *Branta*, *Phoenicopterus*, and *Columba* having prominent processes; Dyke and Gulas (2002: appendix 1, characters 15 and 49), regarding acromion, spatium between facies articularis clavicularis et facies articularis humeralis; Maryanska et al. (2002: appendix 1, character 126).

1252. Extremitas cranialis (caput) scapulae, facies lateralis, sulcus supracoracoideus, status et forma (**ordered**):

a. absent or indiscernable;

b. present, distinct but of only moderate depth;

c. present, exceptionally deep, often accentuated by curved acromion;

x. noncomparable (ratites, Dromornithidae).

Note.—Apomorphic states most readily diagnosed by variably concave facies lateralis of extremitas cranialis scapulae in region between acromion and facies articularis humeralis (depth exceeding aspect deriving solely from these two delimiting landmarks), cranial to collum scapulae (i.e., aspect of scapula forming caudodorsal part of canalis triosseus).

1253. Extremitas cranialis (caput) scapulae, processus glenoidalis coracoidei, facies articularis humeralis, size relative to maximal width of other parts of extremitas cranialis, forma:

a. unremarkable, former no larger than latter;

b. disproportionately expanded (in part effected by indistinguishability of facies articularis coracoideus), facet at least as large as complement of extremitas cranialis, and sessile (*Aptornis*) or pedicellate.

Note.—See: Makovicky and Norell (2004: character 220) and Xu and Norell (2004: supplement, character 220), regarding "supraglenoid buttress."

1254. Extremitas cranialis (caput) scapulae, processus glenoidalis scapulae, facies articularis humeri, facies dorsalis, typus:

a. fossa, subplanar to concave;

b. cotyla, convex;

x. noncomparable (ratites, Dromornithidae).

Note.—See: Dyke and Gulas (2002: appendix 1, character 16).

1255. Extremitas cranialis (caput) scapulae, processus glenoidalis scapulae, labrum et facies articularis humeri, margines juncturae coracoscapularis, status et forma (**ordered**):

a. absent, smoothly surfaced cavitas involving refined synostosis coracoscapularis;

b. present, indistinct, typically indicated only by shallow incisurae in labrum ventralis of cavitas glenoidalis;

c. present, moderately distinct, represented by sulcus suturalis glenoidalis (**new term**) within less-firmly synostotic ossa coracoscapulares;

d. present, conspicuous, a variably broad fissura articularis (**new term**).

Note.—See: Bledsoe (1988: appendix, character 8), discounted by K. Lee et al. (1997: appendix 2) for ratites, "medial groove of cavitas glenoidalis"; J. D. Harris (1998: appendix 2, character 84), with respect to "pronounced notch separating acromial process of scapula and coracoid"; Azuma and Currie (2000: appendix 1, character 68); Dyke et al. (2003: appendix 1, character 35). BMNH *Archaeopteryx* left doubt as to apparent sutura.

1256. Corpus scapulae, facies lateralis et/aut pars intermedia of margo dorsalis corporis, cristae (tuberculum) insertiorum mm. latissimus dorsi cranialis et dorsalis, status:

a. absent or obsolete;

b. present, prominent.

Note.—See: Baumel and Witmer (1993: annotation 168).

1257. Corpus scapulae, facies lateralis, concavitas longitudinalis, status:

a. absent, essentially planar throughout or shallow concavitas limited to pars cranialis et medius;

b. present, distinctly concave throughout, accentuated by lateral displacement of margo dorsalis of scapus;

x. noncomparable (Dromornithidae).

1258. Corpus scapulae, (*i*) relative length (e.g., relative to vertebrae thoracicae) and (*ii*) relative breadth (ratio of length to breadth at midpoint typically exceeds four), forma:

a. element short and broad, ratio of length to minimal height of scapus less than nine;

b. element long and slender, ratio of length to minimal height of scapus greater than ten;

x. noncomparable (Dromornithidae).

Note.—See: Gauthier (1986: text character 41); Pérez-Moreno et al. (1993); Elzanowski (1995: character O4); Holtz (2000 [1998]: appendix I, character 211); Rauhut (2003: character 132).

Tuberculae et impressiones musculorum scapulae

Note.—One or more small tuberculae corresponding to insertiones aut origiones musculares are discernable on the scapulae of some birds. Unfortunately, many taxa appear to lack them and when discernable they often cannot be differentiated with respect to associated musculi. These, and the confusing citations of them within the literature, follow:

Tuberculum m. scapulotricipitis—on margo ventralis scapus, caudolateral to processus glenoidalis, serves as situs origii m. scapulotricipitis, caput scapulae;

Tuberculum retinaculi—comparatively caudomedial, serving as ancora retinaculum m. scapulotricipitis;

Tuberculum (impressio) tendinis proximalis m. expansor secundariorum—variably distinct, typically on facies medioventralis of collum scapulae;

Tuberculum scapulae—feature of uncertain relevance, comparatively caudal, lateral, probably represents tuberculum origii m. deltoideus major.

See: Archey (1941: fig. 55); Maryanska et al. (2002: appendix 1, character 11); Livezey (1986: appendix 1, character 110); Livezey (1995c: appendix II, character 8); Chiappe and Walker (2002: appendix 11.1, character 10), in relation to depressiones on facies medialis of collum scapulae, likely impressio origo m. subscapularis caput mediale; Dyke and Gulas (2002: appendix 1, character 10), in reference to "distinct tubercle" (tuberculum scapulae, likely tuberculum origii m. serratus superficialis cranialis) in galliforms; Livezey (1986: appendix 1, character 112); Livezey (1989: table 1, character 112); Kurochkin (1995b: table 1, character 6); Livezey (1996a: appendix 1, character 39), regarding impressio(nes) insertiorum mm. rhomboideus superficialis et/aut profundus marginis dorsalis corporis scapulae.

1259. Corpus scapulae, margo ventralis, tuberculum m. scapulotricipitis, status et forma:

a. absent or obsolete;

b. present, impressio or cristula.

Corpus (scapus) scapulae—forma generalis

Note.—Characterization of general shape of the corpus scapulae, as well as overlying departures from these general contours in the extremitas caudalis (spina) scapulae, is challenging both from the standpoint of mere description and (perhaps more difficult) with respect to integration with characters and variation encoded by previous investigators in different, often paleontological contexts. The following distillations represent an attempt to extract the essentials of elementwise form and elaborations thereof pertaining to specific subparts of the element. Literature citations only indicate previously published characters—numerous, diverse, and variably interrelated—having some bearing on the features noted.

Partitions and conventions employed herein for characterization of postcolumnar form of scapula *sensu* curvature, comprise: (*i*) deviation from linearity and parallelism with respect to columna vertebralis of axis (curvi)linearis majoris or standard axis of element *per se*; (*ii*) dorsoventral deviations of either or both margines dorsales aut ventrales relative to standard axis, including generalized tapering (herein treated as widely distributed and provisionally plesiomorphic, e.g., Holman 1964: 10), broadening or other departures from uniform width; (*iii*) sagittal (lateromedial) curvature relative to axis majoris; (*iv*) craniocaudal positions of either of the foregoing classes of curvature with respect to axis majoris; (*vi*) dorsoventral directions, craniocaudal positions, margines involved, and magnitudes of comparative angularities or other abrupt departures from monotonicity of axis majoris; and (*vii*) forma (especially dorsoventralis) of extremitas caudalis (spina) scapulae.

1260. Corpus (scapus) scapulae, monotonic ventral curvature general to scapus (i.e., that described by [curvi]linear axis majoris scapulae), status et forma (**unordered**):

a. absent, corpus scapulae essentially straight;

b. present, moderate, corpus et margo dorsalis scapulae slightly to moderately convex;

c. present, pronounced, corpus et margo dorsalis scapulae conspicuously convex.

Note.—See: Fürbringer (1888: pl. III); Chiappe and Calvo (1994: appendix I, character 30); Chiappe (1995b: character 30); Sanz et al. (1995, 1997: character 29); Chiappe (1996b: character 28); Chiappe et al. (1996: appendix 1, character 28); Forster et al. (1998: supplement, character 50); Livezey (1998b: appendix A, character 174); Hughes (2000: appendix 2, character 108), after Seibel (1988: character SC 15); Norell and Clarke (2001: appendix I, character 101); J. A. Clarke (2002: appendix I, character 101); J. A. Clarke and Norell (2002: appendix 2, character 101); Zhou and Zhang (2002: appendix III, character 102); J. A. Clarke (2004: appendix 1, character 101); Ji et al. (2005: supplement, part I, characters 101–102).

1261. Corpus scapulae, lateromedial (sagittal) curvature, status:

a. absent or obsolete, corpus straight;

b. present, curvature mediad but of variable magnitude, facies medialis et margines dorsalis et ventralis (dorsoventral perspective) variably concave.

Note.—See: Fürbringer (1888: pl. III); Bledsoe (1988: appendix, character 10), with respect to os(sa) scapulocoracoideum of ratites, discounted by K. Lee et al. (1997: appendix 2); Chiappe (2001a: appendix 1, character 66); Chiappe (2002: appendix 20.2, character 66), with respect to sagittal curvature.

1262. Corpus scapulae, margo dorsalis scapulae, angulus subterminalis (**new term**), provisionally identified with spatium interinsertiones mm. rhomboideus superficialis et profundus, status:

a. absent or indiscernable;

b. present, distinct;

x. noncomparable (*Aptornis*).

Note.—See Fürbringer (1888: pl. III, part); Andrews (1896: fig. A). Problematic character both with respect to diagnosis and intermediacy, but also partial redundancy with shape of terminus corporis scapulae.

1263. Extremitas caudalis (spina) scapulae, pars caudalis, modal failure to ossify to similar degree as cranial segment, status:

a. absent; **b.** present.

Note.—See: Fürbringer (1888: pl. III).

1264. Extremitas caudalis (spina) scapulae, pars caudalis, significant departure of terminal shapes from that of collum et scapus scapulae in general, status et forma (**unordered**):

a. absent, terminus blunt or tapered;

b. moderately spatulate;

c. broadly spatulate;

d. conspicuously hamulate, forming a rounded, ventrally oriented hook.

Note.—See: Fürbringer (1888: pl. III); Ostrom (1976a); Holman (1961, 1964); Stephan (1979); Gauthier (1986: 12); Livezey (1986: appendix 1, character 108); Bakker et al. (1988); Livezey (1989: table 1, character 108); Novas (1992: character G); Sereno et al. (1993: legend for fig. 3a); Chiappe and Calvo (1994: appendix I, character 29); Chiappe (1995a: legend for fig. 1); Holtz (1994a: appendix 1, character 113), with respect to a "narrow, straplike blade"; Chiappe (1995b: character 29); Livezey (1995c: appendix II, character 7); Sanz et al. (1995, 1997: character 28); Chiappe (1996b: character 27); Chiappe et al. (1996: appendix 1, character 27); Livezey (1996a: appendix 1, character 40); Novas (1996: appendix, character A4); Ericson (1997: table 1, characters 49–50); Chiappe et al. (1998: character 36); Forster et al. (1998: supplement, character 43); J. D. Harris (1998: appendix 2, characters 85–87); Höfling and Alvarenga (2001), regarding modern Piciformes; J. D. Harris (1998: appendix 2, character 88); Ji et al. (1998: supplement, character 36); Livezey (1998b: appendix A, character 179); Makovicky and Sues (1998: appendix 1, character 59); Chatterjee (1999: appendix II, character 43); Azuma and Currie (2000: appendix 1, character 29, part); Currie and Carpenter (2000: appendix 1, character 69); Holtz (2000 [1998]: appendix I, character 212); Zhou et al. (2000); Chiappe (2001a: appendix 1, character 65); Ji et al. (2001), regarding dromaeosaurid NGMC 91-A; Norell and Clarke (2001: appendix I, character 100), treated similarly by J. A. Clarke (2002: appendix I, character 100), J. A. Clarke and Norell (2002: appendix 2, character 100), and J. A. Clarke (2004: appendix 1, character 100); Norell et al. (2001: appendix 1, character 134); Chiappe (2002: appendix 20.2, character 65); J. M. Clark et al. (2002a: appendix 2.2, character 136); Dyke and Gulas (2002: appendix 1, character 11); Xu (2002: suite II, character 162); Xu et al. (2002a: supplement, characters 107 and 111); Zhou and Zhang (2002: appendix III, characters 100–101); Dyke et al. (2003: appendix 1, character 31), employed again by Dyke (2003: table 1); Rauhut (2003: character 133); Hwang et al. (2004: supplement, character 133); G. Mayr (2004b: appendix 1, character 32); Xu and Norell (2004: supplement, character 133); Ji et al. (2005: supplement, part I, character 100).

Coracoideum (Os Coracoideum)

Note.—It is generally considered that the coracoideum avium represents a homologous composite of the coracoideum-precoracoideum complex of lepidosaurian Reptilia, a derivation shared with Crocodylia and perhaps synapomorphic of Archosauria (Howell 1937). Basalmost Reptilia (e.g., seymouriamorphs) indicate that a more-basal condition was tripartite by discernment of plesio-primordia as follows: anterior coracoid (including procoracoid), glenoid, and posterior (true) coracoid (Romer 1956: fig. 142). Practically speaking, however, processus procoracoideus of Neornithes is indistinguishably united with other primordia, and among Aves the element is treated as a single element. Beddard (1898a) interpreted the unique medial expanse of *Struthio*, here inferred to include a clavicular primordium within apparent os coracoideum, to represent an exceptionally large homologue of the "os procoracoideum" of distantly related Tetrapoda.

1265. Extremitas omalis coracoidei, forma *sensu* (*i*) craniocaudal length (i.e., craniocaudal expanse between processes acrocoracoideus et procoracoideus) relative to that of corpus et extremitas sternalis coracoidei, et (*ii*) prominence of both processes acrocoracoideus et procoracoideus:

a. substantial, interprocessural distance at least one-third length of corpus, both processes well developed;

b. truncated, interprocessural distance less than one-quarter length of corpus, both processes abbreviate and respective bases mutually juxtaposed;

x. noncomparable (ratites).

Note.—Mesoenas has no processus procoracoideus, instead a bifacetate scapula joins with coracoid and articulates with humerus, with acrocoracoid joining with tiny vestigium of extremitas omalis claviculae which in turn joins with processus acrocoracoideus.

1266. Extremitas omalis coracoidei, processus acrocoracoideus, status (**unordered**):

a. absent;

b. rudimentary or vestigial within ossa coracoscapulares;

c. present;

d. present but distinctly (apparently secondarily) truncate, processus essentially limited to width accommodating facies articularis clavicularis.

Note.—See: Gauthier (1986: 12, unindexed synapomorphy of Avialae; 13, unindexed synapomorphy of Ornithurae); Chatterjee (1995: character 8, part); Elzanowski (1995: character C8); G. Mayr (2002a: appendix 1, character 17), with respect to Caprimulgiformes; Dyke et al. (2003: appendix 1, character 40), employed again by Dyke (2003: table 1); G. Mayr (2004c: appendix, character 2); G. Mayr and Ericson (2004: appendix I, character 38).

1267. Extremitas omalis coracoidei, processus acrocoracoideus, principal dorsoventral orientation relative to axis majoris craniocaudalis coracoidei:

a. essentially coplanar;

b. distinctly ventral;

x. noncomparable (Dromornithidae).

Note.—See: Livezey (1986: appendix 1, character 98); Kurochkin (1995b: table 1, character 2), partitioning forms as crescentiform, subquadragular, and longitudinal; Livezey (1995c: appendix II, character 9); Hughes (2000: appendix 2, character 102), after Seibel (1988: character CO 20); Livezey (1998b: appendix A, character 180); Sereno (2001: table 2, character 44), as synapomorphic of Aves.

1268. Extremitas omalis coracoidei, processus acrocoracoideus (tuberculum brachiale), dorsomedial curvature with respect to axis majoris coracoidei, status et forma (**ordered**):

a. absent, angling or curvature obsolete, processus cranially aligned;

b. present, moderate medioventral inflection or angling (may be exaggerated by deep sulcus m. supracoracoideus);

c. present, pronounced ventral angling, distinctly hamulate;

x. noncomparable (Dromornithidae, *Aptornis*).

Note.—See: Holman (1961, 1964); Strauch (1978: character 40), and reanalyzed by Björkland (1994) and Chu (1995); Hughes (2000: appendix 2, character 103), after Seibel (1988: character CO 20); Dyke (2001a: appendix 1, character 22); Norell and Clarke (2001: appendix I, character 95), J. A. Clarke (2002: appendix I, character 95), J. A. Clarke and Norell (2002: appendix 2, character 95), and J. A. Clarke (2004: appendix 1, character 95), with respect to apomorphy of "hooked medially"; G. Mayr (2002a: appendix 1, character 16), with respect to Caprimulgiformes; Zhou and Zhang (2002: appendix III, character 95); G. Mayr and Clarke (2003: appendix A, character 64), in reference to facies articularis clavicularis to sulcus supracoracoideus; G. Mayr (2005b: appendix A, character 13); Ji et al. (2005: supplement, part I, character 95).

1269. Extremitas omalis coracoidei, processus acrocoracoideus, margo cranialis et corpus coracoidei, facies ventralis, ventral to cavitas glenoidalis, forma superficialis (**unordered**):

a. unexpanded, ventrally cylindrical;

b. expanded, ventrally triangular, and *laterally* bounded by jugum or "tuber";

c. expanded, ventrally triangular (apex or jugum ventralis aligned with linea intermuscularis ventralis), not *laterally* bounded by jugum;

x. noncomparable (*Aptornis*).

Note.—See: Livezey (1998b: appendix A, character 185); Norell et al. (2001: appendix 1, character 136); J. M. Clark et al. (2002a: appendix 2.2, character 137); Xu (2002: suite II, character 163); Hwang et al. (2004: supplement, character 134); Xu and Norell (2004: supplement, character 134).

1270. Extremitas omalis coracoidei, processus acrocoracoideus, facies articularis clavicularis (medial perspective), margo caudalis, concavitas caudomedialis marginis (**new term**), status:

a. absent; **b.** present;

x. noncomparable (*Fregata*, *Pelecanus*).

Note.—Apomorphic state may be preceded by bilobate condition observed in many related taxa. See: Livezey (1986: appendix 1, character 97); Dyke and Gulas (2002: appendix 1, character 6); Dyke et al. (2003: appendix 1, character 42), employed again by Dyke (2003: table 1).

1271. Extremitas omalis coracoidei, processus acrocoracoideus, facies articularis clavicularis (medial perspective), moderately deep lateromedially, broad dorsoventrally, and ovate, spatulate aspectus, status:

a. absent; **b.** present.

1272. Extremitas omalis coracoidei, processus acrocoracoideus, facies articularis clavicularis (medial perspective), comparatively expanded, planar, elliptical lamina elliptica articularis (**new term**), status et orientation (**unordered**):

a. absent;

b. present, principally dorsal;

c. present, principally lateral;

x. noncomparable (*Fregata*, *Pelecanus*).

Note.—See: Cottam (1957); G. Mayr (2003a: appendix 1, character 22); Bourdon et al. (2005: appendix 1, character 45).

1273. Extremitas omalis coracoidei, processus acrocoracoideus, facies medialis, sulcus m. supracoracoideus, comparative lateromedial compression in planum transversus (**ordered**):

a. weakly or not compressed, essentially circular, facies medialis inflated, cylindrical;

b. moderately compressed, subelliptical, with limited medial flattening;

c. strongly compressed, flattened-elliptical or sublaminate, with deeply recessed facies medialis sulci;

x. noncomparable (Dromornithidae).

Note.—See: Fürbringer (1888); Strauch (1978: character 40), reanalyzed by Björklund (1994: appendix) and Chu (1995); Ericson (1997: table 1, character 43); Livezey (1998b: appendix A, character 187); Chiappe and Walker (2002: appendix 11.1, character 4), in reference to lateral compression of extremitas omalis; Dyke and Gulas (2002: appendix 1, character 2), with respect to being "hooked sternally" in some galliforms; G. Mayr (2004a: appendix 1, character 33); G. Mayr and Ericson (2004: appendix I, character 40).

1274. Extremitas omalis coracoidei, processus acrocoracoideus, facies medialis, margo caudalis, recessus infra-acrocoracoideus (**new term**), status et forma (**ordered**):

a. absent;

b. present, single, either typus dorsalis or typus ventralis;

c. present, double by jugum or oriented lamina craniocaudally within sulcus m. supracoracoideus;

x. noncomparable (Dromornithidae).

Note.—Lamina medialis of facies articularis clavicularis provides variable medial concealment for recessus; also critical to discriminate *bona fide* recessus from simple cranial coverage by variably hamulate processes acrocoracoidea.

1275. Extremitas omalis coracoidei, processus acrocoracoideus, tuberculum brachialis, facies medialis, sulcus m. supracoracoideus (especially adjacent to facies articularis clavicularis or tuberculum brachiale), recesses, pori, et/aut foramina pneumatica, status et situs (**unordered**):

a. absent, sulcus apneumatic;

b. present, pori pneumatici limited to margo cranialis sulci, proximate or extending to facies articularis clavicularis;

c. present, pori pneumatici within one or two mediocaudally exposed, cranially occluded recessus to facies articularis clavicularis;

d. present, pori et/aut foramina pneumatica distributed widely in sulcus (*Balaeniceps*), or in both sulcus et facies articularis clavicularis;

x. noncomparable (Dromornithidae).

Note.—Where prominence cranial to sulcus, tuberculum brachialis serves as ancora ligamentosa acrocoraco-acromialis (Baumel and Witmer 1993: annotation 171b). See: Livezey (1986: appendix 1, character 95); Siegel-Causey (1988: characters 60–61); Livezey (1989: table 1, character 95); Livezey (1991: appendix 1, character 154); Livezey (1996a: appendix 1, character 42); Livezey (1996b: appendix 1, character 17), in reference to "brachial tuberosity"; Chu (1998: appendix 1, character 78), regarding foramen pneumaticum in "triosseal face"; Livezey (1998b: appendix A, character 186); J. A. Clarke (2002: appendix I, characters 90–91), J. A. Clarke and Norell (2002: appendix 2, characters 90 [general pneumatization] and 91 [proximodistal position of foramen pneumaticum]), and J. A. Clarke (2004: appendix 1, characters 90–91); Zhou and Zhang (2002: appendix III, characters 90–91); G. Mayr (2004b: appendix 1, character 29); G. Mayr and Ericson (2004: appendix I, character 39); Ji et al. (2005: supplement, part I, characters 90–91).

1276. Extremitas omalis coracoidei, processus acrocoracoideus, impressio ligamenti acrocoracohumeralis, status et forma (**ordered**):

a. absent, terminus cranialis acrocoracoideus (or homologous tuberculum) globular or laminar, lacking obliquely oriented sulcus, depressio, or fossa;

b. rudimentary or vestigial, represented by variously vague indications of limita;

c. present, shallow and (often) broad;

d. present, distinct, but truncate and (often) narrow, terminated craniad by comparatively enlarged impressio ligamentum acrocoraco-acromiale and arcuate form of processus acrocoracoideus;

x. noncomparable (Dromornithidae, *Aptornis*).

Note.—See: Kurochkin (1995b: table 1, character 1); J. A. Clarke (2004: fig. 47).

1277. Extremitas omalis coracoidei, processus acrocoracoideus, impressio ligamenti acrocoracohumeralis, foramina aut pori pneumatica, status:

a. absent; **b.** present;

x. noncomparable (Dromornithidae).

1278. Extremitas omalis coracoidei, processus acrocoracoideus, tuberculum brachiale, status and length relative to diameter of cavitas glenoidalis (**unordered**):

a. present, former less than twice latter;

b. present, former approximately twice latter;

c. absent;

x. noncomparable (Dromornithidae, *Aptornis*).

Note.—Originally described as "bicipital tubercle" or "acrocoracoidal process," both terms having nomenclatural shortcomings and traditions of questionable application (Baumel and Witmer 1993: annotation 171b), a complex synonymy pertains, in which tuberculum brachiale has been replaced variously with "tuber brachialis" (Ballmann 1969a), "tuberculum brachialis" (Lambrecht 1933), and "tuberositas humeralis." This uncertainty and imprecision related to variation in form render this assessment diffficult in many Neornithes.

See: A. D. Walker (1977); Ostrom (1976a: fig. 14); Perle et al. (1993, 1994); Chiappe and Calvo (1994: appendix II, character 4), regarding "process above the humeral articular facet of the coracoid" (either processus glenoidalis aut acrocoracoideus) in Enantiornithes; Pérez-Moreno et al. (1994: legend for fig. 3, character 13); Novas (1996: appendix, character 6); Novas (1996: appendix, character 40), with reference to "bicipital tubercle"; Novas (1997: appendix, characters 6 and 42), identically coded by Novas and Puerta (1997); Chiappe et al. (1998: character 34); Forster et al. (1998: supplement, character 46); J. D. Harris (1998: appendix 2, character 89); Ji et al. (1998: supplement, character 34); Makovicky and Sues (1998: appendix 1, character 61); Chatterjee (1999: appendix II, character 46), in reference to anterior and dorsal orientation of the "acrocoracoid process"; Azuma and Currie (2000: appendix 1, character 29); Xu et al. (1999b: character 38); Holtz (2000 [1998]: appendix I, characters 218–219); Zhou et al. (2000); Chiappe (2001: appendix 1, character 60); Chiappe (2002: appendix 20.2, character 60), explicitly synonymizing with the "acrocoracoidal process"; Maryanska et al. (2002: appendix 1, character 128), in reference to Oviraptorosauria; Xu et al. (2002a: supplement, character 108), perhaps related to anterior surface of coracoid and delimitation of "subglenoid fossa"; Zhou and Zhang (2002: appendix III, character 94).

1279. Extremitas omalis coracoidei, processus glenoidalis coracoidei, forma:

a. obsolete, approximately level with rima cranialis of cavitas;

b. present, ventrally prominent, forming processus caudoventralis preglenoidalis (**new term**), with tapering, angular terminus extending ventrad beyond rima cranialis of cavitas.

Note.—See: Gauthier (1986); Rauhut (2003: character 136), with respect to ventral eminentia of coracoideum delimiting rima cranialis of cavitas glenoidalis.

1280. Extremitas omalis coracoidei, processus glenoidalis coracoidei, facies (sulcus) articularis humeralis (labrum glenoidale), primary position (dorsoventral and lateromedial dimensions) relative to processus acrocoracoideus (**unordered or stepmatrix**):

a. dorsal; **b.** laterodorsal;
c. dorsolateral; **d.** ventrolateral;
x. noncomparable (Dromornithidae).

Note.—Shift in cavitas glenoidalis and associated parts of proximate pectoral girdle inferred neuroanatomically to have entailed one from ventral orientation in Mammalia and plesiomorphic Reptilia (Howell 1937).

See: Kurochkin (1995b: table 1, character 3); Novas (1996: appendix, character P3); Chu (1998: appendix 1, character 79); Norell and Clarke (2001: appendix I, character 94); J. A. Clarke (2002: appendix I, character 94); J. A. Clarke and Norell (2002: appendix 2, character 94); Dyke and Gulas (2002: appendix 1, character 5); Dyke et al. (2003: appendix 1, character 41); J. A. Clarke (2004: appendix 1, character 94); Ji et al. (2005: supplement, part I, character 94).

1281. Extremitas omalis coracoidei, processus glenoidalis coracoidei, facies articularis scapularis, typus et forma (**unordered**):

a. cotyla aut fovea, subsessile with adjacent facies dorsalis of processus glenoidalis, small, variably deep, variably differentiated from adjacent surfaces;
b. cotyla aut fovea, distinctly pedicellate;
c. fossa, wide and deep;
d. subcondylar, convex or subplanar;
e. articulatio linea, semisutural jugum;
x. noncomparable (Dromornithidae, *Aptornis*).

Note.—See: Fürbringer (1888: pls. II–III); Elzanowski (1995: character N1, part); Hou et al. (1996: characters 11 and 13); Novas (1996: appendix, character 38); Ericson (1997: table 1, character 40); Hughes (2000: appendix 2, character 104); Dyke and Gulas (2002: appendix 1, character 1); Dyke et al. (2003: appendix 1, character 37); G. Mayr et al. (2003: appendix 1, character 28); G. Mayr and Ericson (2004: appendix I, character 37).

1282. Extremitas omalis coracoidei, processus acrocoracoideus et processus procoracoideus, synostosis omalis, articulatio transversus scapulae dividing delimited foramen approximately equally, status:

a. absent; **b.** present.

Note.—Union evidently in part a result of medially hamulate processus acrocoracoideus and cranially elongate processus procoracoideus.

1283. Extremitas omalis coracoidei, processus procoracoideus (dorsal perspective), status and comparative prominence (**ordered**):

a. absent;
b. present, rudimentary, an angulus, shallow cotyla, or cristula;
c. present, moderately prominent, a (typically curved) tuberculum, terminus proprius (exclusive of ancillary tuberculae) approximating margo medialis corporis;
d. present, an elongate processus verae, terminus proprius distinctly extending mediad et/aut dorsad to corpus, some manifesting former condition curving mediodorsad around margo medialis corporis;
x. noncomparable (Dromornithidae, *Aptornis*).

Note.—In ratites, processus procoracoideus is a vestigial, variable angulus on margo medialis coracoidei of os coracoideum aut scapulocoracoideum, typically opposite cavitas glenoidalis. Sinclair and Farr (1932) illustrated Phorusrhacoidea as having simple strutlike bone lacking one or possibly both processes. See: Cracraft (1974: 505, character 24), regarding "coracoidal process" of some ratites; A. D. Walker (1980); Thulborn (1984: 126–127, character 11); Cracraft (1986: appendix, character 70); Cracraft (1988: series III, character 11); G. Mayr (1998); Mourer-Chauviré (1983); Chiappe and Calvo (1994: appendix I, character 24); Pérez-Moreno et al. (1994: legend for fig. 3, character 14); Chatterjee (1995: character 8, part); Chiappe (1995a: legend for fig. 1); Chiappe (1995b: character 24); Elzanowski (1995: character N1, part); Sanz et al. (1995, 1997: character 23); Chiappe (1996b: character 22); Chiappe et al. (1996: appendix 1, character 22); Hou et al. (1996: character 12); Ericson (1997: table 1, character 41); Chu (1998: appendix 1, character 80); Höfling and Alvarenga (2001); Livezey (1998b: appendix A, characters 181–182); Chatterjee (1999: appendix II, character 49); Hughes (2000: appendix 2, character 101); Chiappe (2001a: appendix 1, character 57); Norell and Clarke (2001: appendix I, character 85); Chiappe (2002: appendix 20.2, character 57); J. A. Clarke (2002: appendix I, character 85); J. A. Clarke and Norell (2002: appendix 2, character 85); Dyke and Gulas (2002: appendix 1, character 4); Maryanska et al. (2002: appendix 1, character 127); Zhou and Zhang (2002: appendix III, characters 85 and 96); J. A. Clarke (2004: appendix 1, character 85); G. Mayr (2004d: appendix I, character 11); G. Mayr (2005a: appendix 1, character 11); Ji et al. (2005: supplement, part I, character 85).

1284. Extremitas omalis coracoidei, processus procoracoideus, extension caudad along margo medialis coracoidei by medially expansive crista procoracoidei (**new term**), status:

a. absent or obsolete; **b.** distinctly present;
x. noncomparable (Dromornithidae).

Note.—See: Livezey (1998b: appendix A, character 189). New feature refers to variably prominent and extensive crista marginis medialis.

1285. Extremitas omalis coracoidei, processus procoracoideus, caudoventral extension and concavitas by elongate sulcus m. supracoracoideus, status et forma (**ordered**):

a. absent or obsolete;

b. present, moderate; **c.** present, deep;

x. noncomparable by absence of comparable processus (Dromornithidae, *Aptornis*).

Note.—See: Archey (1941: fig. 54); Siegel-Causey (1988: characters 58–59), who emphasized concavity proximal to tuberculum brachiale of processus acrocoracoideus; Chiappe and Calvo (1994: appendix II, character 3); Holtz (2000 [1998]: appendix I, character 215); J. A. Clarke (2002: appendix I, characters 97–98); J. A. Clarke and Norell (2002: appendix 2, characters 97–98); Zhou and Zhang (2002: appendix III, characters 90–91, 96, and 98).

1286. Extremitas omalis aut corpus coracoidei, processus procoracoideus, facies ventralis, foramen (incisura) nervi supracoracoidei et/aut pneumaticum, status et forma (**unordered**):

a. absent, nervus centrally positioned and not intersecting element;

b. foramen (incisura) nervi supracoracoidei present, resulting from lateral displacement of nervus toward margo medialis coracoidei, but foramen pneumaticum absent and not providing access to internum ossis, some taxa possess foramen delimited medially only by ligamentum ossificans;

c. foramen nervi supracoracoidei et pneumaticum procoracoidei present, positioned comparatively craniad in base of processus procoracoideus, admitting access of diverticulum pneumaticum to internum ossis.

Note.—Absence of foramina typically the result of lateral or cranial position of processus procoracoideus such that nervus passes mediad to element. See: Berger (1960b: table 4, character 7); Cracraft (1974: 505, character 23), regarding ratites; Harrison and Walker (1976a: fig. 5a); Ostrom (1976a: fig. 14; 1987); Strauch (1978: character 39), reanalyzed by Björklund (1994: appendix) and Chu (1995); Strauch (1985: character 13); Livezey (1986: appendix 1, character 92); Siegel-Causey (1988: character 63); Livezey (1989: table 1, character 92); Holdaway (1991: appendix 5.1, character 63); Andors (1992: table 2, character 28); Chiappe and Calvo (1994: appendix I, character 27); Chiappe (1995b: character 27); Sanz et al. (1995, 1997: characters 26 and 75); Chiappe (1996b: character 25); Chiappe et al. (1996: appendix 1, character 25); Livezey (1996a: appendix 1, character 43); Ericson (1997: table 1, character 37, part; table 2, character 30); Livezey (1997a: appendix 1, character 69; *corrigenda*, Livezey 1998a); Chu (1998: appendix 1, character 81); Chiappe et al. (1998: character 35); Ji et al. (1998: supplement, character 35); Forster et al. (1998: supplement, character 51, modified); Livezey (1998b: appendix A, character 184); Zhou et al. (2000); Chiappe (2001a: appendix 1, characters 61–62); J. A. Clarke and Chiappe (2001: character 66); Dyke (2001a: appendix 1, character 19), opposing G. Mayr (2001f: 2) regarding state(s) of apodiforms; Dyke (2001b: appendix 1, character 69); Norell and Clarke (2001: appendix I, characters 96–98, based on previous version of character enumerated PV 97); Chiappe (2002: appendix 20.2, characters 61–62); J. A. Clarke (2002: appendix I, characters 96–98); J. A. Clarke and Norell (2002: appendix 2, characters 96–98); Chiappe and Walker (2002: appendix 11.1, characters 6 and 8); G. Mayr (2002a: appendix 1, character 18), with respect to Caprimulgiformes; Zhou and Zhang (2002: appendix III, characters 91 and 96); G. Mayr (2003a: appendix I, character 24); G. Mayr and Clarke (2003: appendix A, characters 65–66), treating foramina (a)pneumatica separately; G. Mayr et al. (2003: appendix 1, character 29); Xu et al. (2003); J. A. Clarke (2004: appendix 1, characters 96–98); Dyke and van Tuinen (2004: appendix 1, character 38); G. Mayr (2004a: appendix 1, characters 43–44), regarding foramina nervi supracoracoidei aut pneumatica procoracoidei, respectively; Bourdon et al. (2005: appendix 1, character 46); G. Mayr (2005b: appendix A, character 14); Ji et al. (2005: supplement, part I, characters 96–98).

1287. Extremitas omalis coracoidei, processus procoracoideus, dorsoventral orientation with respect to plana transversa corporis (**ordered**):

a. dorsal to corpus coracoidei;

b. subequal to that of corpus coracoidei;

c. ventral to corpus coracoidei;

x. noncomparable (ratites).

Note.—See: Livezey (1998b: appendix A, character 183).

1288. Extremitas omalis coracoidei, processus procoracoideus, craniocaudal orientation relative to axis majoris et margo medialis of corpus (**ordered**):

a. craniomedial, oblique to margo medialis, angulus cranialis acute;

b. medial, approximately perpendicular to margo medialis;

c. caudomedial, oblique to margo medialis, angulus cranialis obtuse;

x. noncomparable (ratites).

1289. Extremitas omalis coracoidei, processus procoracoideus, prominent extension significantly craniomediad to cotyla scapularis by variably flattened tuberculum apicalis procoracoidei (**new term**), status:

a. absent; **b.** present.

Note.—See: G. Mayr (2003a: appendix I, character 25); G. Mayr (2004a: appendix 1, character 34).

1290. Corpus coracoidei (dorsoventral perspective), forma generalis (**unordered**):

a. short-subrectangular, clipeate;

b. truncate-trapezoidal;
c. elongate-triangular.

Note.—See: Ostrom (1976a: fig. 14); Thulborn (1984: 126–127, character 10); Cracraft (1986: appendix, character 17); Gauthier (1986: text characters 42 and 72); Cracraft (1988: series III, character 5); Houde (1988: table 27, characters 27–28); Andors (1992: table 2, character 26); Sanz and Bonaparte (1992: character 12); Sanz and Buscalioni (1992: character 10); Russell and Dong (1994a [1993a]: table 2, character 34); Russell and Dong (1994b [1993b]: list B, character 5); Chiappe and Calvo (1994: appendix I, character 25); Holtz (1994a: appendix 1, character 46); Chatterjee (1995: character 8, part); Chiappe (1995a: legend for fig. 1); Chiappe (1995b: character 25); Elzanowski (1995: character O5); Sanz et al. (1995, 1997: character 24); Chiappe (1996b: character 23); Chiappe et al. (1996: appendix 1, character 23); Novas (1996: appendix, character M8); Novas (1996: appendix, character 37); Novas (1997: appendix, character 39); Novas and Puerta (1997), see identical characters in Novas (1997); Sues (1997: appendix 1, character 29); J. D. Harris (1998: appendix 2, character 90); Azuma and Currie (2000: appendix 1, character 30); Chiappe et al. (1998: character 33); Ji et al. (1998: supplement, character 33); Forster et al. (1998: supplement, character 49); Makovicky and Sues (1998: appendix 1, character 60); Chatterjee (1999: appendix II, character 45, modified); Xu et al. (1999a: character 40); Xu et al. (1999b: character 40); Currie and Carpenter (2000: appendix 1, character 70); Holtz (2000 [1998]: appendix I, character 217); Xu et al. (2000: supplement, character 27); Chiappe (2001a: appendix 1, character 58); Norell and Clarke (2001: appendix I, character 86), treated similarly by J. A. Clarke (2002: appendix I, character 86), J. A. Clarke and Norell (2002: appendix 2, character 86), and J. A. Clarke (2004: appendix 1, character 86); Norell et al. (2001: appendix 1, character 138); Chiappe (2002: appendix 20.2, character 58); J. M. Clark et al. (2002a: appendix 2.2, character 139); Zhou and Zhang (2002: appendix III, character 86); Rauhut (2003: character 138); Hwang et al. (2004: supplement, character 136); Xu and Norell (2004: supplement, character 136); Ji et al. (2005: supplement, part I, character 86).

1291. Corpus coracoidei, forma generalis *sensu* height (exclusive of "anterior ventral process") relative to length:
a. element higher than long;
b. element longer than high.

Note.—See: Rauhut (2003: character 137).

1292. Corpus coracoidei, forma generalis *sensu* length relative to width of facies articularis sternalis (**ordered**):
a. "exceptionally elongate"—length approximately four times width or more;
b. "moderately elongate"—length between three and four times width;
c. "typically proportioned"—length between two and three times latter width;
d. "truncate"—former length no more than two times latter width.

Note.—See: Holtz (1994a: appendix 1, character 102, referring only to taper); Livezey (1998b: appendix A, character 192); G. Mayr (2002a: legend fig. 9, node 3, character 2).

1293. Corpus coracoidei, facies dorsalis (exclusive of fossae pneumaticae), concavitas superficialis (**ordered**):
a. planar or only weakly concave;
b. moderately concave; **c.** deeply concave.

Note.—See: Chiappe and Calvo (1994: appendix II, character 2); Novas (1996: appendix, character M9); Sereno et al. (1996: footnote 45, character 28) and Sereno et al. (1998: footnote 22, character 29) characterized the "crescentic" form of the sternal end of the element; Novas (1997: appendix, characters 40–41) and Novas and Puerta (1997), with identical characters in Novas (1997); Sanz et al. (1997: footnote 29, character *vii*); Livezey (1998b: appendix A, character 193); Sereno (2000: table 4, character 3); Chiappe (2001a: appendix 1, character 63); Norell and Clarke (2001: appendix I, character 88, after character PV 89 limited to impressio m. sternocoracoidei); J. A. Clarke (2002: appendix I, characters 88–89); J. A. Clarke and Norell (2002: appendix 2, characters 88–89); Chiappe (2002: appendix 20.2, character 63); Chiappe and Walker (2002: appendix 11.1, character 7); Xu et al. (2002a: supplement, character 110); Zhou and Zhang (2002: appendix III, characters 88–89); J. A. Clarke (2004: appendix 1, characters 88–89); Ji et al. (2005: supplement, part I, characters 88–89).

1294. Corpus coracoidei, facies dorsalis, impressiones (tuberculae) insertii m. sternocoracoidei, status et forma (**ordered**):
a. absent or not discernable with certainty;
b. present, shallow, striae musculares slightly developed, typically indicated only by depressio and jugum cranial to facies articularis sternalis;
c. present, moderately deep, typically with linea rugositae or striae musculares moderately developed;
d. present, very deep, often with striae musculares well developed, margo cranialis augmented by tuberculum marginalis et/aut recessus caudomedialis dorsale.

Note.—See: Holman (1961, 1964); Ericson (1997: table 1, character 38); Rotthowe and Starck (1998: appendix, character 34); Livezey (1998b: appendix A, character 195); Norell and Clarke (2001: appendix I, character 93), regarding both impressio et linea intermuscularis; Zhou and Zhang (2002: appendix III, character 93); G. Mayr and Clarke (2003: appendix A, character 67); Dyke and van Tuinen (2004: appendix 1, character 45); Ji et al. (2005: supplement, part I, character 93).

1295. Corpus coracoidei, facies dorsalis, pori pneumatici aut foramen pneumaticum, status et forma (**ordered**):

a. absent; **b.** present, pori pneumatici;

c. present, pori pneumatici within recessus or large foramen;

x. noncomparable (Dromornithidae).

Note.—See: Holman (1961, 1964); Livezey (1986: appendix 1, character 93); Livezey (1989: table 1, character 93); Livezey (1996a: appendix 1, character 44); Novas (1996: appendix, character 39), with respect to "dorsal fossa"; Ericson (1997: table 1, character 39), who referred in turn to A. D. Walker (1980: fig. 2) and Chiappe and Calvo (1994: 232); Livezey (1997a: appendix 1, character 70; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, character 191); Rotthowe and Starck (1998: appendix, character 35), in reference to "pneumatization" of element; Sereno (2000: table 4, character 3), in reference to "posterior fossa"; Dyke (2001b: appendix 1, character 70); Norell and Clarke (2001: appendix I, character 91); Dyke and Gulas (2002: appendix 1, character 3); Zhou and Zhang (2002: appendix III, characters 90–91); G. Mayr and Clarke (2003: appendix A, character 67); Dyke et al. (2003: appendix 1, character 39); G. Mayr (2004a: appendix 1, character 36).

1296. Corpus coracoidei, facies ventralis, depressio including single foramen neurovascularia, status:

a. absent; **b.** present;

x. noncomparable (Dromornithidae, *Aptornis*).

1297. Corpus coracoidei, facies ventralis, linea intermuscularis ventralis (dividing origiones m. supracoracoideus medially from m. coracobrachialis caudalis laterally, latter not to be confused with depressio m. coracobrachialis caudalis), et associated aspectus superficialis ventralis, status et forma:

a. absent or indistinct (linea incompleta without apparent superficial effect), facies ventralis essentially laminate or semicylindrical;

b. present, distinct, facies ventralis bilaminate.

Note.—See: Fisher (1945); Livezey (1986: appendix 1, character 96); Siegel-Causey (1988: characters 55–56); Livezey (1989: table 1, character 96); Livezey (1996a: appendix 1, character 45); Livezey (1996b: appendix 1, character 18); Ericson (1997: table 2, character 29); Livezey (1998b: appendix A, character 190); J. A. Clarke (2002: appendix I, character 93); J. A. Clarke and Norell (2002: appendix 2, character 93); Zhou and Zhang (2002: appendix III, character 93); J. A. Clarke (2004: appendix 1, character 93).

1298. Corpus coracoidei, facies ventralis, margo lateralis, area of corpus lateral to linea intermuscularis, ossification of regio, typus:

a. os typica; **b.** membrana ossificans.

Note.—Fürbringer (1888: pl. IV, 27).

1299. Corpus coracoidei (lateral perspective), facies ventralis, margo lateralis, convexity, status:

a. absent, margo linear or slightly concave;

b. present; **x.** noncomparable (*Aptornis*).

Note.—See: Chiappe and Calvo (1994: appendix II, character 1); Sanz et al. (1995, 1997: character 74); Chiappe (2001a: appendix 1, character 59); Norell and Clarke (2001: appendix I, character 87), treated similarly by J. A. Clarke (2002: appendix I, character 87), J. A. Clarke and Norell (2002: appendix 2, character 87), and J. A. Clarke (2004: appendix 1, character 87); Chiappe (2002: appendix 20.2, character 59); Chiappe and Walker (2002: appendix 11.1, character 5); J. A. Clarke and Norell (2002: appendix 2, character 87); Zhou and Zhang (2002: appendix III, character 87); Ji et al. (2005: supplement, part I, character 87).

1300. Corpus coracoidei, sectio proximal to extremitas sternalis, margo medialis, incisura cristae medialis (**new term**), status:

a. absent; **b.** present.

Note.—Character subject to intrafamilial and interfamilial variation, related to structural weakness of apomorphic state being a deficiency of a fragile crista medialis coracoidei. Best scored using series of specimens.

See: G. Mayr (1998a–b: pl. 7, fig. 23); G. Mayr et al. (2003: appendix 1, character 30, fig. 4); G. Mayr (2004c: appendix I, character 12); G. Mayr (2005: appendix 1, character 12).

1301. Corpus coracoidei, margo medialis, sulcus marginis m. sternocoracoideus (**new term**), status:

a. absent; **b.** present.

Note.—Sulcus marginis is ellipsoidal, and muscular homology tentative.

1302. Extremitas sternalis coracoidei, angulus medialis, tuberculum ancorae ligamentosa, status:

a. absent; **b.** present;

x. noncomparable (*Aptornis*).

1303. Extremitas sternalis coracoidei, processus lateralis, status et forma (**unordered**):

a. absent;

b. present, shallow, obtuse angulus (including rudimentary or vestigial), margo supraangularis linear;

c. present, tuberculum (variably oriented), width approximating length, margo supraangularis typically linear;

d. processus linearis, width markedly less than length, margo supraangularis linear;

e. processus hamularis, margo supraangularis curvilinear;

x. noncomparable (*Aptornis*).

Note.—See: Holman (1961, 1964); Harrison and Walker (1976a: figs. 5a and 5d); Livezey (1986: appendix 1, character 99); Livezey (1989: table 1, character 99); Andors (1992: table 2, character 27); Livezey (1995c: appendix II, character 10); Livezey (1996a: appendix 1, character 46); Höfling and Alvarenga (2001), regarding modern Piciformes; Chiappe (2001a: appendix 1, character 64); Norell and Clarke (2001: appendix I, character 92), regarding simple status; Chiappe (2002: appendix 20.2, character 64); J. A. Clarke (2002: appendix I, character 92); J. A. Clarke and Norell (2002: appendix 2, character 92); Dyke and Gulas (2002: appendix 1, characters 7–8); Xu (2002: suite I, character 165); G. Mayr (2002a: appendix 1, character 19), with respect to Caprimulgiformes; Zhou and Zhang (2002: appendix III, character 92); Dyke et al. (2003: appendix 1, characters 43–44, and 46), employed again by Dyke (2003: table 1); G. Mayr (2003a: appendix I, character 26); J. A. Clarke (2004: appendix 1, character 92); Bourdon et al. (2005: appendix 1, character 47); Ji et al. (2005: supplement, part I, character 92); G. Mayr (2005b: appendix A, character 15).

1304. Extremitas sternalis coracoidei, processus lateralis, width relative to facies articularis sterni and translucence and uncommon fenestration (i.e., exceptionally thin regio) of processus, status et forma:

a. former not wider than latter, and regio not translucent;

b. former wider than latter, and regio translucent and at times fenestrated;

x. noncomparable (*Aptornis*).

1305. Extremitas sternalis coracoidei, processus lateralis, minimal craniocaudal width relative to lateromedial width of facies articularis sternalis:

a. former distinctly less than latter;

b. former subequal to latter;

x. noncomparable (*Aptornis*).

1306. Extremitas sternalis coracoidei, processus lateralis, terminus processi, facies ancorae ligamentosa, status:

a. absent or indiscernable; **b.** present;

x. noncomparable (*Aptornis*).

1307. Extremitas sternalis coracoidei, processus lateralis, angulus lateralis, modest depressio including one or more foramina neurovascularia (oriented mediad) in or slightly cranial to facies articularis sterni, labrum internum, status:

a. absent; **b.** present;

x. noncomparable (*Aptornis*).

1308. Extremitas sternalis coracoidei, processus lateralis, angulus lateralis, incisura labri lateralis (**new term**), status:

a. absent; **b.** present;

x. noncomparable (*Aptornis*).

1309. Extremitas sternalis coracoidei, processus lateralis, angulus lateralis, aspectus produced in combination with angulus lateralis et margo supraangularis lateralis, in which laterocranially oblique margo is distinguished by rounded eminentia at midpoint, status:

a. absent; **b.** present;

x. noncomparable (*Aptornis*).

Note.—See: G. Mayr (2004b: appendix 1, character 30).

1310. Extremitas sternalis coracoidei, crista articularis sternalis, dorsoventral differentiation and lateromedial division (and sectiones defined thereby) of labri externa et interna by hiatus articularis (**new term**), forma:

a. extent comparable for much of facies;

b. margo sternalis rounded and lacking jugum interfacialis (**new term**) and irregular, subtubercular eminentia replacing sectiones propriae;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—Baumel and Raikow (1993: annotation 89) pointed out that lateromedial subdivision results in the sulcus articularis being “concavo-convex,” i.e., concave in axis dorsoventralis with short radius of curvature, and convex in axis mediolateralis with long radius of curvature. See: Dyke and Gulas (2002: appendix 1, character 9), regarding variation in “excavation” of facies articularis sternalis in galliforms; G. Mayr (2004d: appendix I, character 13), in related treatment of comparative dorsoventral depth of crista articularis; G. Mayr (2005a: appendix 1, character 13).

1311. Extremitas sternalis coracoidei, crista articularis sternalis (sectiones medialis et lateralis), labrum interna, forma (**unordered**):

a. smoothly curving;

b. interrupted by central fossa rugosa;

c. characterized by prominent circular fossa medialis.

Note.—Evidently, the apomorphic “interruptae” cited above coincide with the hiatus between sectiones medialis et lateralis of facies articularis. See: Livezey (1986: appendix 1, character 94), in reference to “dorsal sternal facet”; Hughes (2000: appendix 2, character 99), in reference to “ventralis prominent, centered, rounded, and facing sternally”; Zhou and Zhang (2002: appendix III, characters 88–89).

1312. Extremitas sternalis coracoidei, facies ventralis, crista articularis sternalis (sectio lateralis), labrum externa, loculus pilae costalis, status (**new term**):

a. absent; **b.** present.

Note.—Indentation in *Aptornis* that accommodates articulation of vertex craniolateralis sterni into facies ventralis coracoidei.

1313. Extremitas sternalis coracoidei, facies ventralis, crista articularis sternalis, sectio medialis (**new term**), pila articularis columnaris externa (**new term**), status et labri (**unordered**):

a. absent;

b. present, involving labrum externum only, but including both sectiones medialis et lateralis;

c. present, involving labrum externum, sectio medialis only;

d. present, involving labrum internum only;

e. present, involving both labri internum et externum;

f. present, involving both labri internum et externum, section "intermedius" or coincident with hiatus intersectionalis;

x. noncomparable (*Aptornis*).

Note.—New feature refers to "buttress" (hemicylindrical dorsoventral expansion of margo cranialis of facies articularis sternalis coracoidei), which must depart from general curvature of facies articularis and possess distinct prominence to be distinguished from merely prominent labrum. Where confined to sectio lateralis, terminus typically coincides with hiatus between sectiones medialis et lateralis of facies articularis.

See: Livezey (1986: appendix 1, character 100); Livezey (1989: table 1, character 100); Kurochkin (1995b: table 1, character 4); Livezey (1995c: appendix II, character 11); Livezey (1996b: appendix 1, character 19), in reference to "ventral (external) sternal facet." Dyke and Gulas (2002: appendix 1, character 9) described variation in "excavation" of facies articularis sternalis in galliforms.

1314. Extremitas sternalis coracoidei, facies articularis sternalis, labrum externa, cranial extent of margo cranialis labri (and correlated cranial expanse) relative to those of labrum interna (**ordered**):

a. former significantly cranial to latter, producing externally (ventrally) angled facies articularis;

b. former approximately equal to latter, producing facies articularis of dorsoventrally equal expanse;

c. former distinctly caudal to latter, producing internally (dorsally) angled facies articularis;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Opisthocomus*).

Note.—See: Payne and Risley (1976: character 20), regarding craniocaudal position of margo cranialis of facies articularis internum among Ardeidae; Livezey (1998b: appendix A, character 198); Hughes (2000: appendix 2, character 100), after Seibel (1988: character CO 19).

1315. Extremitas sternalis coracoidei, crista articularis sternalis (sectiones medialis et lateralis), crista intermedia (dorsoventral perspective), concavitas cristae, status et forma:

a. absent to minor;

b. present, conspicuously curved;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromornithidae).

Note.—See: Chu (1998: appendix 1, character 82).

1316. Extremitas sternalis coracoidei, crista articularis sternalis (sectiones medialis et lateralis), crista intermedia (caudal perspective), concavitas dorsalis cristae, status et comparative depth (**ordered**):

a. present, deep;

b. present, shallow;

c. absent or obsolete, crista sublinear;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—See: G. Mayr (2003c: appendix, character 1); G. Mayr (2005b: appendix A, character 16).

1317. Extremitas sternalis coracoidei, facies articularis sternalis, distinct fovea enclosing foramina neurovascularia aut pneumatica, status:

a. absent; **b.** present.

Note.—See: Livezey (1998b: appendix A, character 197).

Juncturae Cinguli Membri Thoracici

Note.—The traditionally narrow view of Aves independent of other groups of Tetrapoda (especially Reptilia), understandably gave rise to the notion that synostosis among ossa clavicula, scapula, et coracoideum was a comparatively rare condition largely limited to the flightless palaeognathous taxa (i.e., ratites). Recognition that Aves are included among Theropoda and (more inclusively) Reptilia, revealed that rigid juncturae cinguli membri thoracici is taxonomically widespread among reptiles (Romer 1956).

1318. Junctura sternoclavicularis, involving extremitas sternalis claviculae and carina sterni, apex carina, status et typus (**unordered**):

a. present, articulatio synovialis, facies articularis variably conformed;

b. present, elongate syndesmosis, attachment by comparatively elongate and ligamentum elasticus sternoclaviculare;

c. present, abbreviate syndesmosis, attachment by comparatively truncate and semikinetic ligamentum sternoclaviculare;

d. present, synchondrosis, deriving ontogenetically from junctura cartilaginis, typically retaining sutura vestigialis following ossification;

e. present, synostosis, sutura definitivum indiscernable;

f. absent, typically by absence of (conjoined) extremitas sternalis claviculae.

Note.—See: Allis (1835); W. C. L. Martin (1835); Mivart (1878: pls. *lix–lxi*); Fürbringer (1888: pl. IV); Shufeldt (1902a: figs. 42, 50, and 51); Harrison and Walker (1976a: fig. 6a–b); Cracraft (1985: character 23); Ericson (1997: table 1, character 47); Livezey (1998b: appendix A, character 168); G. Mayr (2003a), G. Mayr and Clarke (2003: appendix A, character 63), who dismissed homology of synostotic and asynostotic apophysis furculae; G. Mayr (2004b: appendix 1, character 28). Sibley and Ahlquist (1972: table 4) contrasted Tytonidae as having a synchondrosis, but Strigidae as having an articulatio simplex; difference not confirmable with prepared skeletons; Bourdon et al. (2005: appendix 1, character 44).

1319. Junctura sternoclavicularis, situs proximodistalis carinae sternalis:

a. distal, approximately at apex carina;

b. proximal, distinctly proximal to apex carina;

x. noncomparable (ratites, Dromornithidae).

Note.—See: Fürbringer (1888: pl. IV, fig. 57).

1320. Junctura (symphysis) interclavicularis, i.e., medial conjoining of claviculae to form definitive furcula, status et typus (**unordered**):

a. absent, claviculae (degree of ossification notwithstanding) are present but fail to join medially;

b. present, but claviculae and junctura (if present) remain cartilaginous or ligamentous;

c. present, claviculae are osseous, but junctura remains cartilaginous or ligamentous;

d. present, claviculae are osseous and medially synostotic;

x. noncomparable (most ratites, Dromornithidae, *Aptornis*).

Note.—Sibley and Ahlquist (1972: table 3) contrasted the typical furculae of Cuculidae with the “absence” of furcula in Musophagidae. Current reviews of medially unified claviculae among Mesozoic taxa include those by H. N. Bryant and Russell (1993), Chure and Madsen (1996), and Makovicky and Currie (1998). See: Ostrom (1976a); Berger (1960b: table 4, character 6); Thulborn (1984: 126–127, character 9); Cracraft (1986: appendix, character 20); Gauthier (1986: text character 58); Cracraft (1988: series I, character 2); Houde (1988: table 27, character 29); Prum (1988: characters 3–4); Chiappe (1991a–b); Sanz and Bonaparte (1992: character 13, part); Sanz and Buscalioni (1992: character 11); Sereno and Rao (1992); Russell and Dong (1994b [1993b]: list A, character 6); Holtz (1994a: appendix 1, character 41); Sereno et al. (1994: footnote 12); Chatterjee (1995: character 9, part); Chiappe (1995b: character 34); Sanz et al. (1995, 1997: character 32); Kurochkin (1995b: table 1, character 9); Chiappe (1996b: character 31); Hou et al. (1996: character 8); Norell et al. (1997); Sereno et al. (1996: footnote 45, character 27); Sues (1997); Chiappe et al. (1998: character 38); Forster et al. (1998: supplement, character 52); J. D. Harris (1998: appendix 2, character 91); Ji et al. (1998: supplement, character 38); Makovicky and Sues (1998: appendix 1, character 62); Chatterjee (1999: appendix II, character 47); Norell and Makovicky (1999: 29); Xu et al. (1999a: character 39, modified); Xu et al. (1999b: character 41); Burnham et al. (2000); Holtz (2000 [1998]: appendix I, character 225); Xu et al. (2000: supplement, character 28); Zhang and Zhou (2000: fig. 3); Ji et al. (2001), regarding dromaeosaurid NGMC 91-A; Norell and Clarke (2001: appendix I, character 79), treated similarly by J. A. Clarke (2002: appendix I, character 78), J. A. Clarke and Norell (2002: appendix 2, character 78), and J. A. Clarke (2004: appendix 1, character 78); Sereno et al. (2002), regarding *Sinornis*; Zhou and Zhang (2002: appendix III, character 79); Ji et al. (2005: supplement, part I, character 79).

1321. Angulus (synostosis) interclavicularis (cranial or caudal perspective):

a. angulus approximating or exceeding 90°, element shallowly curved or “boomerang-shaped”;

b. angulus less than 70°, element parabolic (“U-shaped”) or chevroniform (“V-shaped”);

x. noncomparable in taxa lacking synostosis interclavicularis.

Note.—In parabolic furculae, angulus defined as that of intersection of tangent lines to facies lateralis claviculae. See: Chure and Madsen (1996); Norell et al. (1997); and Makovicky and Currie (1998). See: Barsbold (1974, 1983); Ostrom (1976a); Sanz and Bonaparte (1992: character 13, part); Sanz and Buscalioni (1992: character 11) proposed intervals of 90° and 60°; Sues (1997: appendix 1, character 30); Chiappe (1991a–b); Chiappe and Calvo (1994: appendix I, character 34); Chatterjee (1995: character 9, part); Chiappe (1995b: character 34); Sanz et al. (1995, 1997: character 32); Chiappe (1996b: character 31); Hou et al. (1996: character 8) in reference to “laterally flexible” condition; Ericson (1997: table 1, character 44, part); Chiappe et al. (1998: character 38); Ji et al. (1998: supplement, character 38); Forster et al. (1998: supplement, character 52); Chatterjee (1999: appendix II, character 47, modified); Norell and Makovicky (1999); Xu et al. (1999a: character 39, modified); Xu et al. (1999b: character 41); Xu et al. (2000: supplement, character 28); Norell and Clarke (2001: appendix I, character 80), treated similarly by J. A. Clarke (2002: appendix I, character 79), J. A. Clarke and Norell (2002: appendix 2, character 79), and J. A. Clarke (2004: appendix 1, character 79); Chiappe (2001a: appendix 1, character 69); Chiappe (2002: appendix 20.2, character 69); Dyke and Gulas (2002: appendix 1, character 17); Zhou and Zhang (2002: appendix III, character 80); Ji et al. (2005: supplement, part I, character 80). Some flightless anseriforms show apomorphic divergence of (synostotic) claviculae (Livezey 1996a: character 32, part).

1322. Junctura interclavicularis (cranial or caudal perspective), marked diverticulum symphysialis (**new term**), which accommodates penetration of carina sterni by ansae tracheales, status:

a. absent; **b.** present;

x. noncomparable (ratites, Dromornithidae).

Note.—See: Livezey (1986: appendix 1, character 106); Livezey (1996a: appendix 1, character 34).

1323. Membrana sternocoracoclavicularis ossificans, status (**ordered**):

a. absent;

b. present, moderately extensive, partially ossified (residua including spinae procoracoideae et spiculae mediocaudales coracoideae), spanning variably extensive regio medial to ossa coracoideum et scapula and investing to variable degree the claviculae, if present;

c. present, very extensive, largely ossified, assuming some of structural and functional properties of diminutive processus procoracoideus;

x. noncomparable (Dromornithidae).

Note.—See: Fürbringer (1888: pls. III–IV); Baumel and Raikow (1993: annotation 87).

Articulatio Coracoscapularis (Scapulocoracoidei)

1324. Angulus juncturae (articularis) coracoscapularis, typus et modus (**ordered**):

a. sublinear, approximating 180°;

b. obtuse, 90°–180°, typically approximating 135° with respect to planum facies articularis sternocoracoideus;

c. right, approximating 90°;

d. acute, less than 90°.

Note.—See: Fürbringer (1888: pls. II–III); Nauck (1930a–b); Friant (1945a, 1946); Ostrom (1976a); Feduccia (1980, 1986); Tarsitano and Hecht (1980); Gauthier (1986: 13); Chiappe and Calvo (1994: appendix I, character 28); Chiappe (1995b: character 28); Sanz et al. (1995, 1997: character 27); Chiappe (1996b: character 26); Chiappe et al. (1996: appendix 1, character 26); Chiappe et al. (1998: character 32); Ji et al. (1998: supplement, character 32); Forster et al. (1998: supplement, characters 47–48); Chatterjee (1999: appendix II, character 42, modified); Xu et al. (1999b: character 39); Holtz (2000 [1998]: appendix I, character 220); Xu et al. (2000: supplement, character 26); Chiappe (2001a: appendix 1, character 56); Norell and Clarke (2001: appendix I, character 99), Chiappe (2002: appendix 20.2, character 56); J. A. Clarke (2002: appendix I, character 99); J. A. Clarke and Norell (2002: appendix 2, character 99); Zhou and Zhang (2002: appendix III, character 99); J. A. Clarke (2004: appendix 1, character 99); Xu et al. (2003); Ji et al. (2005: supplement, part I, character 99).

Reversed in some flightless birds—e.g., ratites and the extinct moa-nalos—considered by Livezey (1996a: appendix 1, character 47) and Livezey (1998b). Early notion that synostosis scapulocoracoidei and other apomorphies of the membri thoracici were evidence of the plesiomorphy of flightlessness in ratites was espoused by Broom (1907) and Lowe (1928b).

1325. Articulatio(nes) coracoscapularis, omus, situs craniocaudalis:

a. cranial, at processus acrocoracoideus, "at the shoulder (proximal) end of coracoid";

b. caudal, at facies articularis scapularis, "well below the shoulder (proximal) end of coracoid";

x. noncomparable (Dromornithidae).

Note.—Requires improved description to include modern forms, refers to relative importance or presence of articulationes omales. See: Chiappe (1995b: character 26); Cracraft (1986: appendix, character 69); Cracraft (1988: series III, character 10); Chiappe and Calvo (1994: appendix I, character 26); Sanz et al. (1995, 1997: character 25); Chiappe et al. (1996: appendix 1, character 24); Chiappe et al. (1996: appendix 1, character 26), in reference to coplanarity or angularity of junctura coracoscapularis; Chiappe et al. (1998: character 31); Ji et al. (1998: supplement, character 31); Norell and Makovicky (1999); Chiappe (2001a: appendix 1, character 55); Chiappe (2002: appendix 20.2, character 55); Zhou and Zhang (2002: appendix III, character 94).

1326. Junctura (syndesmosis) coracoscapularis (scapulocoracoidei), typus:

a. essentially immobile (akinentic)—junctura a synostosis, syndesmosis, or sutura—some manifesting ontogenetic variation;

b. variably mobile (kinetic)—junctura an articulatio synovialis, comprising variously ligamentous combinations of articulatio acrocoraco-acromiale (between processus acrocoracoideum coracoidei and acromion scapularis) cranially and articulationes coracoscapulares dorsalis et ventralis (between facies articularis scapularis coracoidei and cotyla articularis scapularis coracoidei) caudoventrally.

Note.—Among nonavialian Theropoda, there is an increasing tendency for ankylosis of ossa scapula et coracoideum with age, with a sutura coracoscapularis discernable in *Tyrannosaurus* (P. J. Currie, pers. comm.). Of Dinornithiformes, only *Euryapteryx* and *Emeus* not confirmed to have possessed ossa scapulocoracoidea; fovea sterni suggested element occurred at least in former genus.

See: W. K. Parker (1868); Fürbringer (1888: pls. II–III); Lowe (1928b: fig. 18) regarding ratites; Glutz von Blotzheim (1958); Cracraft (1974: 503, character 22); Rich (1980b: fig. 1N); Thulborn (1984: 126–127, character 12); Feduccia (1985); Cracraft (1986: appendix, character 36); Gauthier (1986: 13, unindexed synapomorphy of Ornithurae); Cracraft (1988: series I, character 7); Houde (1988: table 27, characters 25–26); D. Starck (1989); Chiappe and Calvo (1994: appendix I, character 23); Chiappe (1995b: character 23); Elzanowski (1995: character O3); Sanz et al. (1995, 1997: character 22); Chiappe (1996b: character 21); Chiappe et al. (1996: appendix 1, character 21); Livezey (1996a: appendix 1, character 48), regarding irregularly frequent, convergent condition in some flightless anseriforms (Thambetochenini); K. Lee et al. (1997: appendix 1, character 8), especially concerning ratites; Chiappe et al. (1998: character 30); Ji et al. (1998: supplement, character 30); Forster et al. (1998: supplement, character 45); Chatterjee (1999: appendix II, character 41, modified); Xu et al. (1999b: character 37); Chiappe (2001a: appendix 1, character 54); Norell and Clarke (2001: appendix I, character 83), treated similarly by J. A. Clarke (2002: appendix I, character 83), J. A. Clarke and Norell (2002: appendix 2, character 83), and J. A. Clarke (2004: appendix 1, character 83); Norell et al. (2001: appendix 1, character 137); Chiappe (2002: appendix 20.2, character 54); J. M. Clark et al. (2002a: appendix 2.2, character 138); Xu (2002: suite II, character 164); Xu et al. (2002a: supplement, character 109); Zhou and Zhang (2002: appendix III, character 83); G. Mayr and Clarke (2003: appendix A, character 68); Hwang et al. (2004: supplement, character 135); Xu and Norell (2004: supplement, character 135); Ji et al. (2005: supplement, part I, characters 83–84).

1327. Articulatio coracoscapularis, typus (**unordered**):

a. concave cotyla scapularis coracoidei in combination with tuberculum coracoideus scapulae, effecting a moderately formed gomphosis or “ball-and-socket” joint;

b. facies articulares essentially laminar or sublinear, effecting an articulatio ellipsoidea aut plana;

x. noncomparable, junctura not articulatio (ratites, Dromornithidae).

Note.—See: Norell and Clarke (2001: appendix I, character 84), treated similarly by J. A. Clarke (2002: appendix I, character 84), J. A. Clarke and Norell (2002: appendix 2, character 84), and J. A. Clarke (2004: appendix 1, character 84); Ji et al. (2005: supplement, part I, character 84).

1328. Ossa scapula et coracoideum—if synostostic, producing os scapulocoracoideum)—margo medialis, enclosure of small foramina or large fenestra within membrana sternocoracoclavicularis ossificans, status (**unordered**):

a. absent;

b. present, including one or more comparatively small foramina;

c. present, including a single comparatively large fenestra, in part delimited by included clavicula vestigialis;

x. noncomparable in absence of synostosis coracoscapularis et/aut membrana ossificans.

Note.—Occurs infrequently also in some anseriforms (Thambetochenini; Livezey 1996a) and raphids (Livezey 1993).

1329. Junctura (articulatio) sternocoracoidea, status et typus (**unordered**):

a. articulatio plana aut squamata;

b. articulatio synovialis sellaris;

c. synostosis sternocoracoideus, in which margo cranialis, sulcus articularis coracoideus, is braced mediodorsally by narrow osseus, laminate pons, typically with open canalis ventralis;

d. synostosis sternocoracoideus, effected directly by lateromedial series of spiculae osseae between facies articulares.

Note.—See: Livezey (1996a: appendix 1, character 48); Livezey (1998b: appendix A, character 199). State “c” also found in some moa-nalos, flightless rallids, perhaps limited to older adults.

1330. Articulatio sternocoracoidea, ligamentum sternocoracoideum laterale, status:

a. absent; **b.** present.

Note.—See: Fürbringer (1888); Baumel and Raikow (1993: annotation 92).

1331. Junctura intercoracoidea et spatium intercoracoidale, status modalis et typus definitivum (**ordered**):

a. absent—wide, symmetrical **spatium intercoracoidale**;

b. absent—close symmetrical, medial juxtaposition or virtually undifferentiable, extremely limited **articulatio simplex**;

c. present—an **articulatio synovialis** between extremitates sternales coracoidei, angulae (vertices) caudomediales, that of os coracoideum dexter ventral to that of os coracoideum sinister;

d. present—**syndesmosis** intercoracoideus or **symphysis** sternocoracoidea.

Note.—See: Fürbringer (1888: pl. IV); Beddard (1901a), on *Anastomus*; Ligon (1967: table 2); Sibley and Ahlquist (1972: table 3); Cracraft (1974: 503, character 21); Gauthier (1986: 12–13); Bledsoe (1988: appendix, character 6); Houde (1988: table 27, character 24); Chatterjee (1995: character 8, part); Ericson (1997: table 1, character 34; table 2, character 26); K. Lee et al. (1997: appendix 1, character 3); Chiappe (2001a: appendix 1, character 77); J. A. Clarke and Chiappe (2001: character 65); Norell and Clarke (2001: appendix I, character 76); J. A. Clarke (2002: appendix I, character 75), in which rudimentary overlap in anseriform *Anatalavis* inferred by S. L. Olson (1999) was disputed; J. A. Clarke and Norell (2002: appendix 2, character 75); Zhou and

Zhang (2002: appendix III, character 76); G. Mayr (2003c: appendix, character 2); G. Mayr and Clarke (2003: appendix A, character 69); J. A. Clarke (2004: appendix 1, character 75); Dyke and van Tuinen (2004: appendix 1, character 46); G. Mayr (2004a: appendix 1, character 37); G. Mayr (2005b: appendix A, character 18); Ji et al. (2005: supplement, part I, character 76).

1332. Junctura omalis, os coracoideum lateral to impressio ligamenti acrocoracohumeralis and immediately ventrocaudal to cavitas glenoidalis (vestigium), i.e., eminentia articularis humeralis (**new term**), status et forma (**unordered**):

a. present, prominent, and embedded within the membrana sternocoracoclavicularis ossificans in some taxa possessing os scapulocoracoideum;

b. present, mediolaterally compressed jugum;

c. absent or indistinguishable;

x. noncomparable where junctura acrocoracoclavicularis an articulatio.

Note.—See: Cracraft (1974: character 24); Bledsoe (1988: appendix, character 9); K. Lee et al. (1997: appendix 1, character 9), in reference to “coracoidal process” of scapulocoracoideum.

Juncturae Regionis Omalis

Note.—Juncturae regionis omalis, including composite articulationes, syndesmoses, et synostoses—various combinations of which compose a variably kinetic complex of juncturae, involving subtle combinations of these arthrological classes, and supportive of the extremitas proximalis of membri thoracici (precluding diagnosis of many syndesmoses, synchondroses, or kinetic suturae from articulationes). I.e., syndesmoses supported by ligamenta, articulatio synoviales aut syndesmoses, and infrequently synostoses—collectively form facies medialis of the **cavitas glenoidalis** (Fürbringer 1888: pls. II–III; Stegmann 1964; Baumel and Raikow 1993: annotation 93). There is marginal evidence of a shift from coplanarity (180º) between processi glenoidalis scapulae et coracoidei in Mesozoic taxa (e.g., *Archaeopteryx*, *Confuciusornis*, Alvarezsauridae, “nonavian theropods”) through obtuse (90º–180º) in ratites, to perpendicular (90º) in other Ornithothoraces, including most Neornithes. Passing mediad to the cavitas glenoidalis is the **canalis triosseus**, which serves musculi critical for movement of the wing.

See: Andrews (1896: fig. A); Romer (1956: figs. 143–145); Chiappe (1996b); Chiappe et al. (1996: appendix 1, character 26); Chure and Madsen (1996: fig. 1); Chiappe et al. (1999); Norell et al. (2001: appendix 1, character 139); J. M. Clark et al. (2002a: appendix 2.2, character 140); Xu (2002: suite II, character 160); Hwang et al. (2004: supplement, character 137); Xu and Norell (2004: supplement, character 137).

The essential pairwise juncturae in question are:

(*i*) junctura (syndesmosis) procoraco-scapularis (involving facies articularis scapulae), perhaps limited to junctura ligamentosa—via ligamentum coracoscapulare interosseum;

(*ii*) junctura (syndesmosis) procoraco-clavicularis;

(*iii*) junctura (syndesmosis, articulatio, aut synostosis) acrocoraco-clavicularis;

(*iv*) junctura (syndesmosis aut articulatio) acrocoraco-acromialis, provisionally homologous precursor of synostosis coracoscapularis;

(*v*) junctura (syndesmosis) acromio-clavicularis;

(*vi*) junctura (syndesmosis aut synostosis) acrocoraco-procoracoidea.

The last of these—variously robust conjoining of the processes acrocoracoideus et procoracoideus within a single element (os coracoideum), perhaps involving ligamentum ossificans in some cases, is considered to be variation secondary to the fundamental structure of the cinguli omalis and treated last. Ancillary variation within single features of single elements—e.g., terminal bifurcation of the clavicula et scapula—were treated under respective elements. Juncturae interclaviculae, sternocoracoidea, et coracoscapulares were treated earlier in this section.

The basic analytical approach to be used here is to treat each of the five “primary” juncturae omales as separate characters, principally as binary or presence-absence status characters. These assessments were based initially on Fürbringer (1888: pls. II–III), augmented by additional references (e.g., Mitchell 1915: fig. 5), and direct examination of specimens of taxa.

1333. Junctura procoraco-scapularis (**new term**), status et typus (**unordered**):

a. absent;

b. present, gomphosis involving condylus scapularis et cotyla coracoidea;

c. present, articulatio (synovialis) cotylaris;

d. present, articulatio (synovialis) plana aut syndesmosis;

e. present, synostosis.

Note.—Primarily based on Fürbringer (1888: pls. II–III) and Mitchell (1915: fig. 5), as refined by examination of skeletons, i.e., codings primarily derive from confamilials of exemplars. Portion of scapula involved typically is the variably differentiated facies articularis clavicularis, with less-frequent contact by the acromion scapulae. Portion of scapula involved typically is the variably differentiated facies articularis clavicularis of the acromion scapulae.

1334. Junctura procoraco-clavicularis, status:

a. absent;

b. present, typically syndesmosis;

x. noncomparable by absence or vestigial status of claviculae (ratites).

Note.—See: Fürbringer (1888: pls. II–III), Mitchell (1915: fig. 5), codings primarily derive from confamilials of exemplars; Baumel and Raikow (1993: annotations 86 and 97). Clavicula involved may be extremitas omalis or adjacent scapus.

1335. Junctura acrocoraco-clavicularis, typus:

a. articulatio plana aut syndesmosis;

b. synostosis;

x. noncomparable by absence of claviculae or junctura (basal Avialae, basal Ornithurae, ratites, Dromornithidae).

Note.—Primarily based on Fürbringer (1888: pls. II–III), Mitchell (1915: fig. 5), as refined by examination of confamilials of exemplars and confamilials; Cottam (1957); G. Mayr (2003a: appendix 1, character 22); Ericson (1997: table 1, character 42); Bourdon et al. (2005: appendix 1, character 45). Closely related character of coracoideum involves status et forma of processus acromialis claviculae.

1336. Junctura acrocoraco-acromialis, status et typus (**ordered**):

a. absent;

b. present, articulatio plana aut syndesmosis;

c. present, broad synostosis;

x. noncomparable (*Aepyornis*).

Note.—Primarily based on Fürbringer (1888: pls. II–III), as refined by direct study of exemplars.

1337. Junctura acromio-clavicularis, status et typus (**ordered**):

a. absent;

b. present, articulatio synovialis aut syndesmosis;

c. present, synostosis.

Note.—Primarily based on Fürbringer (1888: pls. II–III), as refined by direct study of skeletons; some codings derive from confamilials of exemplars; Mitchell (1915: fig. 5). See also: Payne and Risley (1976: character 21), regarding status of "posterior furcular process" among Ardeidae; Thulborn (1984: 126–127, character 13); L. D. Martin (1992) regarding state(s) in Gastornithiformes; Baumel and Raikow (1993: annotations 98–99); Ericson (1997: table 1, character 42).

1338. Synostosis acrocoraco-procoracoideus (**new term**), producing arcus acrocoraco-procoracoideus (**new term**), status modalis:

a. absent, hiatus of variable width;

b. present, forming (within coracoideum) an arcus supracoracoideus, involving to variable degree interposed ligamentum ossificans or fragmentum claviculae.

Note.—Primarily based on Fürbringer (1888: pls. II–III), as refined by dissections, i.e., codings primarily derive from confamilials of exemplars. Depiction of *Chunga* by Fürbringer (1888: pl. II–44, as *Dicholophus*) failed to depict the apomorphic arcus present in Cariamidae. See: Stegmann (1958); Berger (1960b: table 4, character 7), regarding absence of circumosseus canalis "formed by the dorsal processes of the coracoid" in Cuculidae, and presence in Musophagidae; Sibley and Ahlquist (1972: table 3), contrasting absence of "bony canal formed by coracoid" in Cuculidae with presence of "bony canal formed by dorsal processes of coracoid" in Musophagidae; Livezey (1998b: appendix A, character 188), regarding Gruiformes. Charadriiformes especially challenging, in which variably cranial extension of processus procoracoideus by laminate ligamentum ossificans toward tuberculum brachiale of the sulcus supracoracoideus is discussed by Strauch (1978: character 40), and reanalyzed by Björkland (1994) and Chu (1995). This character is a secondary component of the complexus juncturae omalis.

1339. Juncturae claviculo-acrocoracoidea, acromio-clavicularis, acromio-acrocoracoidea, et scapulo–procoracoidea, mutual conjoinment to form a compound junctura claviculo-procoraco-scapularis (**new term**) delimiting either a *fenestra* or (by tight suturae or articulationes) an occluded *focus*—status modalis:

a. absent, at least one of the juncturae delimiting margo lacking;

b. present, delimiting a central fenestra or focus, a triosseous junctura with suturae completely occluding fenestra immediately cranial to processus procoracoideus;

x. noncomparable (ratites, Dromornithidae, *Aptornis*).

Note.—See: Fürbringer (1888: pls. II–III), especially figure 41 (*Psophia*) for "occluded" version of state "b"; Mitchell (1915: fig. 5). Fenestrae and foci in apomorphic junctura were not partitioned as separate states as this resulted as much from width of elements as arthrological geometry. Fenestra unique to extremitas omalis claviculae in *Fregata* not homologous.

Canalis (Foramen) Triosseus (Omalis)

1340. Canalis (foramen) omalis (triosseus), cranial composition, status, numerus et nomina ossae (**unordered**):

a. absent;

b. present, biosseous, incomplete, involving ossa scapula et coracoideum;

c. present, triosseous, incomplete, involving ossa clavicula, scapula, et coracoideum;

d. present, triosseous, vestigial, involving limited margo claviculae vestigium;

e. present, uniosseous, involving only os coracoideum, restricted to taxa having arcus acrocoraco-procoracoideus.

Note.—Given variation in numbers of ossa involved, traditional name clearly misleading, hence alternative name of "canalis omalis" is proposed. See: McGowan (1982: 183), who concluded that " . . . some ratites possess the remnants, or the makings of a triosseal canal"; Baumel and Witmer (1993: annotation 177), who included *Columba* among taxa in state "c," whereas specimens indicate arcus verae lacking or exceptionally variable, instead suggested by rudimentum of ligamentum acrocoraco-acromiale ossificans.

Cavitas Glenoidalis

1341. Cavitas glenoidalis completas, status modalis (**ordered**):
a. present; **b.** vestigial; **c.** absent.

1342. Cavitas glenoidalis, cavitas relative to axes anatomica, forma (**unordered**):
a. caudoventral or caudolateral;
b. lateral;
c. subperpendicular, facies oriented almost ventrally, sometimes diminutive and poorly defined;
d. obliquely ventrolateral to approximately parallel;
x. noncomparable (ratites).

Note.—Shift in cavitas glenoidalis and associated parts of proximate pectoral girdle inferred neuroanatomically to have entailed one from ventral orientation in Mammalia and plesiomorphic Reptilia (Howell 1937). Multi-elemental character often described in terms of processus glenoidalis scapulae (e.g., Rauhut 2003: character 135). See: Fürbringer (1888: pls. II–III); Gauthier (1986: 13–14, unindexed synapomorphy of Aves and Ornithurae); Bledsoe (1988: appendix, character 7); Sereno and Rao (1992); Chiappe and Calvo (1994: appendix I, character 28); Elzanowski (1995: character N'1); Chiappe (1996b: character 24); Novas and Puerta (1997: 392, character *ii*); Chu (1998: appendix 1, character 77); Xu et al. (1999b: character 105); K. Lee et al. (1997: appendix 1, character 10); Chatterjee (1999: appendix II, character 44); Norell and Makovicky (1999); Holtz (2000 [1998]: appendix I, character 216); Norell et al. (2001: appendix 1, character 140); J. M. Clark et al. (2002a: appendix 2.2, character 141); Dyke and Gulas (2002: appendix 1, characters 13–14), regarding facies articularis humeri; Sereno et al. (2002), regarding *Sinornis*; Xu (2002: suite II, character 167); Xu et al. (2002a: supplement, characters 85 and 112); Dyke et al. (2003: appendix 1, character 34), employed again by Dyke (2003: table 1); Xu et al. (2003); Rauhut (2003: character 135); Hwang et al. (2004: supplement, character 138); Xu and Norell (2004: supplement, character 138).

1343. Fibrocartilago (os) humeroscapularis, status:
a. absent or indiscernable; **b.** present;
x. noncomparable (*Aepyornis*, Dinornithiformes).

Note.—Synonymous with "os humeroscapulare" (G. Jäger 1857; Fürbringer 1888), this variably ossified fibrocartilago occurs in the dorsal part of the capsula articularis omalis in a minority of taxa (Baumel and Raikow 1993: annotation 100). Absent a comprehensive survey of taxonomic distribution of this diminutive element, presence probably will be underestimated. Where present, this element typically serves as situs origii m. deltoideus major, typically caput craniale (Pycraft 1907b–c; Berger 1956a–b; Hoff 1966: 29; Vanden Berge and Zweers 1993: annotation 79).

Ossa Alae

Longitudines relativum

Note.—Many ratios and proportions relating diverse combinations of pectoral and pelvic elements are described in the literature (Anderson et al. 1985; Christiansen and Bonde 2000). Necessarily redundant, at least in part, and in some cases without general applicability, a number of these were not employed herein, including: **pectoral to pelvic appendage**—Gauthier (1986: characters 60 and 73); Russell and Dong (1994b [1993b]: list A, character 8; list B, character 6); Azuma and Currie (2000: appendix 1, character 52); Holtz (2000 [1998]: appendix I, character 226); Ji et al. (2003a: 22); **pectoral limb to columna vertebralis "presacralis"**—Ostrom (1976a); Gauthier (1986: character 60); Forster et al. (1998: supplement, character 65); J. D. Harris (1998: appendix 2, character 101); Xu et al. (1999b: character 48); Currie and Carpenter (2000: appendix 1, character 80); Holtz (2000 [1998]: appendix I, character 227); Xu et al. (2000: supplement, character 35); **pectoral truncation related to secondary flightlessness**—Cracraft (1974: 505, character 25); Cracraft (1982: series 3, character 1); Houde (1988: table 27, character 37); Chiappe and Calvo (1994: appendix I, character 36); Pérez-Moreno et al. (1994: legend for fig. 3, character 16); Novas (1994 [1993]: appendix, character 45); **humerus to scapula**—Azuma and Currie (2000: appendix 1, character 58); Holtz (2000 [1998]: appendix I, character 229), credited originally to Pérez-Moreno et al. (1993); Norell et al. (2001: appendix 1, character 135); J. M. Clark et al. (2002a: appendix 2.2, character 142); J. A. Clarke (2002: appendix I, character 102); J. A. Clarke and Norell (2002: appendix 2, character 102); Maryanska et al. (2002: appendix 1, character 125); Xu (2002: suite I, character 54; suite II, character 245); Xu et al. (2002a: supplement, character 190); Xu et al. (2003). Similarly, ulna compared with scapula by: Xu et al. (1999b: character 103); Xu et al. (2000: supplement, character 83); J. A. Clarke (2004: appendix 1, character 102); Hwang et al. (2004: supplement, character 139); Xu and Norell (2004: supplement, character

139); **humerus to ulna**—Ji et al. (2005: supplement, part I, character 105); **humerus to manus**—Maryanska et al. (2002: appendix 1, character 147); **humerus to tarsometatarsus**—G. Mayr (2004d: appendix I, character 34); G. Mayr (2005a: appendix 1, character 35); **brachium and antebrachium to manus**—Gauthier (1986: text character 43); Holtz (2000 [1998]: appendix I, character 233); Maryanska et al. (2002: appendix 1, character 146); **ulna to manus**—Forster et al. (1998: supplement, character 66); Xu et al. (1999a: character 61); Xu et al. (1999b: character 49); Holtz (2000 [1998]: appendix I, character 262); Xu et al. (2000: supplement, character 36); **carpometacarpus to coracoid**—G. Mayr (2003c: appendix, character 21); **femur to manus**—Maryanska et al. (2002: appendix 1, character 148); **humerus to os metacarpale II**—Maryanska et al. (2002: appendix 1, character 143); **digitus alulae, phalanx proximalis to radius,** diameters—Xu and Norell (2004: supplement, character 207); Hwang et al. (2004: character 207); **humerus to femur**—Novas (1994 [1993]: appendix, character 35); Novas (1996: appendix, characters 7, 41–42); Novas (1997: appendix, characters 7, 43–44), identically treated by Novas (1997); Rauhut (2003: character 139); **ulna to femur**—Sereno et al. (1996: footnote 45, character 37); Azuma and Currie (2000: appendix 1, character 110); Holtz (2000 [1998]: appendix I, character 231); Maryanska et al. (2002: appendix 1, character 149); **ulna to os metatarsale III**—Xu et al. (1999b: character 104); Xu et al. (2000: supplement, character 84); **manus to pes**—Chu (1998: appendix 1, characters 84 and 97); Sereno et al. (1998: footnote 22, character 4); Xu et al. (1999a: character 63); Holtz (2000 [1998]: appendix I, character 228); **indices relating antebrachium and manus**—J. D. Harris (1998: appendix 2, character 95), Azuma and Currie (2000: appendix 1, character 77) and Currie and Carpenter (2000: appendix 1, character 74) used a ratio of lengths of manus divided by that of brachium and antebrachium as index of "relative manus length"; De Klerk et al. (2000: 330, character 5), who cited in turn Holtz (2000 [1998]); Norell and Clarke (2001: appendix I, character 105), citing in turn Sereno et al. (1996); Maryanska et al. (2002: appendix 1, character 135); Zhou and Zhang (2002: appendix III, character 105).

1344. Humerus (brachium), total length relative to that of ulna et/aut radius (antebrachium), forma (**ordered**):

a. four-thirds or more;

b. between one-half and four-thirds;

c. between one-quarter and one-half;

x. noncomparable by absence of ossa alae (Dinornithiformes).

Note.—See: Cracraft (1974: character 26); K. E. Campbell and Tonni (1980), regarding Teratornithidae; Bledsoe (1988: appendix, characters 11 and 29); Sanz and Bonaparte (1992: character 14); Perle et al. (1993); Chiappe (1995b: character 36); Sanz et al. (1995, 1997: character 34); Chiappe (1996b: character 33); Chiappe et al. (1996: appendix 1, character 32); Novas (1996: appendix, character 44); K. Lee et al. (1997: appendix 1, character 11); Novas (1997: appendix, character 46), using inverse ratio for radius and humerus, repeated by Novas and Puerta (1997); Chiappe et al. (1998: character 48); Ji et al. (1998: supplement, character 48); Forster et al. (1998: supplement, character 57, modified); Chatterjee (1999: appendix II, character 53); Azuma and Currie (2000: appendix 1, character 53); Holtz (2000 [1998]: appendix I, characters 230 and 232); Chiappe (2001a: appendix 1, character 94); Ji et al. (2001), regarding unnamed dromaeosaurid NGMC 91-A; Norell and Clarke (2001: appendix I, character 105), comparing lengths of humerus and ulna, treated similarly by J. A. Clarke (2002: appendix I, character 105), J. A. Clarke and Norell (2002: appendix 2, character 105), and J. A. Clarke (2004: appendix 1, character 105); Chiappe (2002: appendix 20.2, character 94); Dyke and Gulas (2002: appendix 1, character 23); Maryanska et al. (2002: appendix 1, character 135); Zhou and Zhang (2002: appendix III, character 105); Dyke et al. (2003: appendix 1, character 62), employed again by Dyke (2003: table 1); G. Mayr and Clarke (2003: appendix A, character 82); G. Mayr et al. (2003: appendix 1, character 40); Rauhut (2003: character 145), compared closely related ratios for humerus with radius; Dyke and van Tuinen (2004: appendix 1, character 58); G. Mayr (2004a: appendix 1, character 43); G. Mayr and Ericson (2004: appendix I, character 56); G. Mayr (2004d: appendix I, character 17), regarding relative lengths of humerus and ulna; G. Mayr (2005a: appendix 1, character 17).

Humerus

1345. Os humerus, status ossis:

a. present;

b. absent, or represented in minority of individuals in various taxa by vestigium manifested as eminentia angularis at situs homologous to cavitas glenoidalis of some ossa coracoscapulares, strictly homologous to caput humeri vestigialis.

Note.—Empirical basis for possible presence of humerus in Dinornithiformes is: (*i*) variably positioned, reduced cavitas glenoidalis in os scapulocoracoideum (single candidate element at BMNH), and (*ii*) infrequent microvestigium synostotic with os scapulocoracoideum.

1346. Os humerus, proportion of total proximodistal length relative to the transverse width of extremitas proximalis humeri, forma (**ordered**):

a. former at least three times latter;
b. former two to three times latter;
c. former less than two times latter;
x. noncomparable by absence of ossa alae (Dinornithiformes).

Note.—See: Zusi and Bentz (1984); G. Mayr (2003c: appendix, character 10); G. Mayr et al. (2003: appendix 1, character 39); G. Mayr (2005b: appendix A, character 25). Extraordinary variation within Trochilidae makes suitability of states "b" and "c" vary conditionally with the taxon considered.

1347. Os humerus, virtual linearity independent of relative elongation, status et forma (**unordered**):
a. absent, curved;
b. present, linear, elongate;
c. present, linear, truncate;
x. noncomparable by absence of ossa alae (Dinornithiformes).

Note.—See: G. Mayr (2003a: appendix I, character 30); Bourdon (2006: supplement, character 58).

1348. Os humerus, especially extremitas proximalis humeri, exceptional reduction in size (length and/or robustness of corpus), disproportionate proximoventral prominence, and apparent general torsion, in addition to several qualitative changes—(*i*) virtual loss of caput, fossa pneumotricipitalis, et (epi)condylae; (*ii*) disproportionate robustness of eminentia m. latissimi dorsi, incisura capitis, et tuberculum dorsale; and (*iii*) torsion-related positional changes of the fossa m. brachialis et incisura capitis—most or all related to profound, evidently secondary flightlessness, status:
a. absent; **b.** present;
x. noncomparable by absence of ossa alae (Dinornithiformes).

Note.—Virtually all aspects of character critically comparative for diagnosis.

Extremitas proximalis humeri

1349. Extremitas proximalis humeri, caput humeri, dorsoventral width relative to that of extremitas proximalis humeri, forma:
a. former distinctly less than latter;
b. former subequal to latter;
x. noncomparable by absence of ossa alae (Dinornithiformes).

Note.—Alternative conceptualizations of character is intertubercular or maximal proximal width of humerus. See: G. Mayr (2002a: appendix 1, character 20), with respect to Caprimulgiformes and Apodiformes; G. Mayr (2005b: appendix A, character 15).

1350. Extremitas proximalis humeri, caput humeri, facies (margo) caudalis, tuberculum capitis origo m. humerotricipitis (**new term**), forma:
a. indiscernable or low impressio;
b. prominent tuberculum;
x. noncomparable by absence of ossa alae (Dinornithiformes).

Note.—See: Zusi and Bentz (1982); Bannasch (1986a–b: fig. 38); Bannasch (1987); G. Mayr (2003c: appendix, character 13); G. Mayr (2005b: appendix A, character 28).

1351. Extremitas proximalis humeri, caput humeri, relative craniocaudal and transverse breadths (proximal perspective):
a. broadly oval, at least twice as broad transversely than craniocaudad;
b. distinctly orbiculate, less than twice as broad transversely than craniocaudad;
x. noncomparable by absence of ossa alae (Dinornithiformes).

Note.—See: Rauhut (2003: character 140), in terms of "proximal articular facet of humerus" in relation to cavitas glenoidalis.

1352. Extremitas proximalis humeri, caput humeri, forma generalis (**unordered**):
a. cranially concave and caudally convex;
b. subspheroidal, margo proximalis centrally concave;
c. globular or spheroidal;
x. noncomparable by absence of ossa alae (Dinornithiformes).

Note.—See: Houde (1988: table 27, character 35); Chiappe and Calvo (1994: appendix I, character 37); Chiappe and Calvo (1994: appendix II, characters 6–7), listed subtle synapomorphies of caput humeri in Enantiornithes; Chiappe (1995a: legend for fig. 1); Chiappe (1995b: character 37); Sanz et al. (1995, 1997: character 35); Chiappe (1996b: character 34); Chiappe et al. (1996: appendix 1, character 33); Chatterjee (1995: character 11, part); Sanz et al. (1995, 1997: character 35); Chatterjee (1999: appendix II, character 55); Chiappe (2001a: appendix 1, characters 81–82); Norell and Clarke (2001: appendix I, character 106), similarly by J. A. Clarke (2002: appendix I, character 106), J. A. Clarke and Norell (2002: appendix 2, character 106), and J. A. Clarke (2004: appendix 1, character 106); Chiappe (2002: appendix 20.2, characters 81 [general] and 82 [central depressio]); Chiappe and Walker (2002: appendix 11.1, character 17 [central depressio]; fig. 11.8); Sereno et al. (2002), regarding *Sinornis*; Vickers-Rich et al. (2002), concerning *Avimimus*; Zhou and Zhang (2002: appendix III, character 106); Ji et al. (2005: supplement, part I, character 106).

1353. Extremitas proximalis humeri, caput humeri, focus capitis humeri (**new term**) relative to axis proximodistalis humeri, forma dorsoventralis (**ordered**):
a. slightly to moderately dorsal;
b. slightly or moderately ventral;

c. conspicuously ventral, beyond margo ventralis humeri;

x. noncomparable by absence of ossa alae (Dinornithiformes).

Note.—See: Bledsoe (1988: appendix, character 15), disparaged by K. Lee et al. (1997: appendix 2) for ratites; Novas (1996: appendix, character 8, part); Novas (1997: appendix, character 8); Novas and Puerta (1997), see identical characters in Novas (1997); G. Mayr (2004b: appendix 1, character 36).

1354. Extremitas proximalis humeri, caput humeri, separation from crista deltopectoralis and tuberculum dorsale ("externus"), status:

a. diminished, caput low and poorly distinguished adjacent features;

b. pronounced, caput offset and well distinguished from tuberculum dorsale;

x. noncomparable by absence of ossa alae (Dinornithiformes).

Note.—See: Bannasch (1986a–b: fig. 38); Bannasch (1987); Gauthier (1986: 14, unindexed synapomorphy of Aves); Elzanowski (1995: character N2); Kurochkin (1995b: table 1, character 11); Makovicky and Sues (1998: appendix 1, character 65); Holtz (2000 [1998]: appendix I, character 236).

1355. Extremitas proximalis humeri, facies caudalis, incisura capitis humeri, laterodistal extension and orientation as sulcus incisurae transversus (**new term**), status et forma (**unordered**):

a. absent (Dromaeosauridae [Velociraptorinae, *Deinonychus*], *Enantiornis*, *Archaeopteryx*, *Confuciusornis*) or obsolete by expansion of facies caudalis immediately distal to incisura;

b. absent, by obstruction related to fundamental alteration of underlying structure of extremitas proximalis humeri;

c. obsolete, by proximal continuity of caput et ventrally expanded crista deltopectoralis, associated with obsolescence and cranial shift of tuberculum dorsale;

d. present, separating caput humeri et tuberculum ventrale, terminating approximately at margo distalis capitus or persisting as broad sulcus to margo dorsalis fossae pneumotricipitalis without discernable curvature;

e. present, separating caput humeri et tuberculum ventrale ("internus"), extending significantly toward or passing distad to tuberculum dorsale (**other** Neornithes, including in *Galbula*–"*Passer*" [comparatively indistinct dorsal to margo caudalis corporis]) or continuing to margo dorsalis humeri, passing proximad to tuberculum dorsale;

x. noncomparable by absence of ossa alae (Dinornithiformes, *Aptornis*).

Note.—Deep sulci or depressiones related to incisura capitis on facies caudalis humeri, especially sulcus parallel to facies ventralis of margo caudalis typically pertain to origo m. humerotriceps. Superficially similar condition approached in *Puffinus*.

See: Ligon (1967: table 4); Gauthier (1986: 13, unindexed synapomorphy of Ornithurae; character 67); Livezey (1986: appendix 1, characters 23–24); Cracraft (1988: series III, characters 7–8); Cracraft (1988: series VIII, character 8; series XVI, character 2) pertaining to caprimulgiforms and apodiforms; Cracraft (1988: series XVI, character 3), with respect to sulcus in caprimulgiforms and apodiforms; Siegel-Causey (1988: characters 74–75); Livezey (1989: table 1, character 23); Chiappe and Calvo (1994: appendix I, characters 38–39); Chiappe (1995b: character 38); Elzanowski (1995: 38, character unindexed); Livezey (1995a: appendix 1, character 4); Sanz et al. (1995, 1997: character 36); Chiappe (1996b: characters 35–36); Chiappe et al. (1996: appendix 1, character 34); Livezey (1996b: appendix 1, character 20); Ericson (1997: table 1, character 51, part); Holtz (2000 [1998]: appendix I, character 239, part); Norell and Clarke (2001: appendix I, character 108); Chiappe and Walker (2002: fig. 11.8), regarding *Enantiornis*; J. A. Clarke (2002: appendix I, character 108); J. A. Clarke and Norell (2002: appendix 2, character 108); Zhou and Zhang (2002: appendix III, character 108); G. Mayr (2003a: appendix I, character 31); J. A. Clarke (2004: appendix 1, character 108); G. Mayr (2004b: appendix 1, character 38); G. Mayr and Ericson (2004: appendix I, character 48); Ji et al. (2005: supplement, part I, character 108).

1356. Extremitas proximalis humeri, facies (perspective) proximalis, incisura capitis humeri, forma *sensu* depth relative to caput humeri, facies cranialis:

a. cranial depth less than planum capitis cranialis;

b. cranial depth equal to or greater than planum capitis cranialis, typically coplanar with sulcus ligamentosa transversus;

x. noncomparable (Dinornithiformes, Sphenisciformes).

1357. Extremitas proximalis humeri, facies (perspective) proximalis, incisura capitis humeri, forma *sensu* comparative breadth of incisura and angulus of orientation of tuberculum ventrale relative to caput humeri:

a. approximating a sulcus with parallel laminae ventrales et dorsales;

b. laminae ventrales et dorsales distinctly diverging craniad, incisura comparatively broad and (often) shallow, vertex cranialis typically broadly rounded;

x. noncomparable by absence or unique apomorphy of ossa alae (Dinornithiformes, Sphenisciformes).

1358. Extremitas proximalis humeri, facies (perspective) caudalis, incisura capitis humeri, forma generalis (**unordered**):

a. absent or obsolete;
b. variably shallow, broad sulcus;
c. extremely narrow, constricted sulcus;
d. comparatively deep, subelliptical fossa;
x. noncomparable by absence of ossa alae (Dinornithiformes).

Note.—Mere status encoded elsewhere, and state "d" enhanced by presence of either or both cristae incisurae capitis but may qualify in the absence of either or both, or be excluded in the presence of same; condition less apparent in those taxa characterized by "double" fossae pneumotricipitalia.

1359. Extremitas proximalis humeri, caput humeri, crista incisurae capitis distalis (**emended term**), status:
a. absent;
b. present, variably slanted and robust;
x. noncomparable by absence of ossa alae (Dinornithiformes).

Note.—Prominence of cylindrical foveae or depressiones delimited in part by these cristae is one of the more obvious manifestations. Specification of two cristae necessitated by variation in cranial (proximal) and caudal (distal) delimitation of the incisura.

See: Strauch (1978: character 42), reanalyzed by Björklund (1994: appendix) and Chu (1995), regarding "ridge in capital groove of humerus"; Siegel-Causey (1988: characters 74–75); Ericson (1997: table 1, characters 52–53), with respect (in part) to a distinct crista between tuberculum ventrale et caput humeri at caudal (anconal) terminus of incisura capitis; Livezey (1998b: appendix A, character 203), who interpreted this feature as tuberculum m. scapulohumeralis cranialis; J. A. Clarke and Chiappe (2001: character 2), regarding the distal closure and pitlike aspect of the incisura capitis; Norell and Clarke (2001: appendix I, character 109), in reference to incisura being an open sulcus or "closed by a muscular tubercle," treated similarly by J. A. Clarke (2002: appendix I, character 109), J. A. Clarke and Norell (2002: appendix 2, character 109), and J. A. Clarke (2004: appendix 1, character 109); Chiappe and Walker (2002: fig. 11.8), regarding *Enantiornis*; Dyke and Gulas (2002: appendix 1, character 50); Zhou and Zhang (2002: appendix III, character 109); Dyke et al. (2003: appendix 1, character 61); Dyke (2003: table 1); Ji et al. (2005: supplement, part I, character 109).

1360. Extremitas proximalis humeri, facies caudalis, caput humeri, incisura capitis—delimited cranially by crista incisurae capitis proximalis (**emended term**), caudally by crista incisurae capitis distalis, ventrally by tuberculum ventrale, and dorsally by caput humeri—pori pneumatici marginales, status:
a. absent; **b.** present;
x. noncomparable by absence of crista (Dinornithiformes).

Note.—Incisura accommodates labrum scapulae of cavitas glenoidalis during adduction alae; presence of foramina aut pori considered with or without presence of cristae incisurae capiti.

1361. Extremitas proximalis humeri, facies caudalis, caput humeri, incisura capitis, crista incisurae capitis distalis, depressio (tuberculum) insertii m. coracobrachialis caudalis (**new term**), status et forma (**unordered**):
a. absent or indiscernable;
b. present, depressio aut fovea, within crista incisurae;
c. present, tuberculum, in absence of crista;
x. noncomparable (Dinornithiformes).

Note.—Situs insertii m. coracobrachialis caudalis typically positioned comparatively ventrad, on crus dorsalis of fossa pneumotricipitalis. See: Bannasch (1986a–b: fig. 38); Bannasch (1987); G. Mayr and Ericson (2004: appendix I, character 53), synonymized with "medial knob of humerus" of Bock and McEvey (1969a: fig. 19).

1362. Extremitas proximalis humeri, facies caudalis, caput humeri, incisura capitis, crista incisurae capitis distalis, orientation dorsad from tuberculum ventrale, broad, elevated, and flat caudal aspect, and caudal closure of incisura capitis, status:
a. absent;
b. present, unique forma characteristic;
x. noncomparable (Dinornithiformes).

Note.—See: Chiappe and Walker (2002: fig. 11.8) regarding *Enantiornis*.

1363. Extremitas proximalis humeri, facies caudalis, caput humeri, incisura capitis, crista incisurae capitis distalis, comparatively low and sloping forma, enclosing fenestrae or entire fossa pneumatica within incisura capitis, status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes).

1364. Extremitas proximalis humeri, tuberculum ventrale ("internus"), forma generalis (**unordered**):
a. triangular, often rounded;
b. rectangular, craniocaudally compressed and proximodistally elongate;
c. tubercular, great medial, subangular prominence, parallel or proximal to caput;
d. obsolete, associated with uniquely conformed and ventrally directed caput humeri;
x. noncomparable, ossa alae absent (Dinornithiformes).

Note.—See: Stephan (1979); S. L. Olson (1980); Bledsoe (1988: appendix, character 14, three states); Houde (1988: table 27, character 34); Russell and Dong (1994a [1993a]: table 2, character 35); Sereno (1994 [1993]: appendix, character 2); Livezey (1996a:

appendix 1, character 50); Novas (1996: appendix, characters 8 and P4); Novas (1996: appendix, character 43), distinguishing "conical" from "craniocaudally compressed and longitudinally elongated"; Ericson (1997: table 1, character 54); K. Lee et al. (1997: appendix 1, character 12); Novas (1997: appendix, character 45); Novas and Puerta (1997), see identical characters in Novas (1997); Sereno et al. (1998: footnote 22, character 32); Xu et al. (1999a: character 55); Holtz (2000 [1998]: appendix I, characters 237–239); J. A. Clarke and Chiappe (2001: character 5); Norell and Clarke (2001: appendix I, character 111), treated the presence of "ventral tubercle"; Maryanska et al. (2002: appendix 1, character 130); Zhou and Zhang (2002: appendix III, character 111), regarding mere presence; Rauhut (2003: character 141); Ji et al. (2005: supplement, part I, character 111).

1365. Extremitas proximalis humeri, tuberculum ventrale ("internus"), forma *sensu* caudal prominence relative to caput humeri, status et forma:

a. former less than or equal to latter;

b. former distinctly greater than latter;

x. noncomparable (Dinornithiformes).

1366. Extremitas proximalis humeri (caudal or "anconal" perspective), tuberculum ventrale ("internus"), proximodistal position relative to fossa pneumotricipitalis or homologous situs:

a. comparatively cranioproximal, exposing completely fossa pneumotricipitalis;

b. comparatively caudodistal, largely or completely concealing fossa pneumotricipitalis;

x. noncomparable (Dinornithiformes).

Note.—See: Livezey (1986: appendix 1, character 27); Livezey (1989: table 1, character 27); Livezey (1995a: appendix 1, character 5); Livezey (1996b: appendix 1, character 22).

1367. Extremitas proximalis humeri, tuberculum ventrale ("internus"), tuberculum proprius (facies muscularum treated separately), orientation (**unordered**):

a. ventral; **b.** proximal; **c.** caudal;

x. noncomparable (Dromornithidae).

Note.—See: Cracraft (1986: appendix, character 65); Sanz et al. (1995, 1997: character 36); Chiappe et al. (1998: character 42); Ji et al. (1998: supplement, character 42); Forster et al. (1998: supplement, character 55, modified); Xu et al. (1999a: character 57, modified); Chatterjee (1999: appendix II, character 58, modified); Chiappe (2001a: appendix 1, character 83); Chiappe (2002: appendix 20.2, character 83).

1368. Extremitas proximalis humeri, tuberculum ventrale ("internus"), facies ancorae insertii muscularum (**new term**), principal orientation (**unordered**):

a. caudal; **b.** dorsal; **c.** distal;

x. noncomparable (ratites, Dromornithidae).

Note.—Serves as ancora insertii m. subscapularis (capita laterale et mediale) et (in taxa lacking separate tuberculum or crista incisurae capitis) m. coracobrachialis caudalis.

1369. Extremitas proximalis humeri, tuberculum ventrale ("internus"), crista tuberculae (**new term**), status:

a. absent; **b.** present;

x. noncomparable (Dinornithiformes).

Note.—New feature is caudally directed, semicircular crista directed essentially perpendicular from facies caudalis humeri.

1370. Extremitas proximalis humeri, caput humeri, tuberculum dorsale ("externus"), forma (**unordered**):

a. absent or indistinct;

b. present—impressio aut jugum, not elevated or buttressed, typically sloping distally with facies caudalis of corpus humeri;

c. present—tuberculum, prominent, buttressed, typically with facies articularis elevated, planar, and distinctly caudal to facies caudalis of corpus humeri;

d. present—tuberculum, diminutive, distinctly delimited by elevated rimae with central fovea, on facies *cranialis* of basis cristae;

e. present—facet, subelliptical, sloping with facies caudalis of crista deltopectoralis, distinctly outlined but caudal elevation obsolete (especially distally) and sometimes obscured in part by impressiones musculares;

f. diminished—small, proximal, indistinct, marginal facet;

g. obsolescent—minute irregularity approaching indiscernability;

x. noncomparable by absence, variable, unique form, or situs of element (ratites, Dromornithidae).

Note.—Assessed relative to basis proximalis cristae deltopectoralis. See: Zusi and Bentz (1984: fig. 15); Livezey (1986: appendix 1, character 32); Bledsoe (1988: appendix, character 18); Siegel-Causey (1988: character 78); Livezey (1989: table 1, character 32); Baumel and Witmer (1993: annotation 183); Livezey (1995a: appendix 1, character 7); Livezey (1995c: appendix II, character 16); Livezey (1996b: appendix 1, character 24); K. Lee et al. (1997: appendix 1, character 13); Chu (1998: appendix 1, character 85); Livezey (1998b: appendix A, characters 207 and 213); J. A. Clarke and Chiappe (2001: character 4); G. Mayr and Clarke (2003: appendix A, character 76), limited to elongation in modern Psittaciformes; Dyke and van Tuinen (2004: appendix 1, character 54); G. Mayr and Ericson (2004: appendix I, character 47); Novas et al. (2004: appendix, characters 35 and 47).

1371. Extremitas proximalis humeri, caput humeri, tuberculum dorsale ("externus"), position relative to that of caput humeri (**unordered**):

a. vertex of margines proximalis et dorsalis humeri, closely proximate with caput et crista deltopectoralis;

b. terminus proximalis of crista deltopectoralis, but well distal to caput and directly dorsal to approximate midpoint of fossa pneumotricipitalis;

c. margo caudalis corporis, immediately dorsal to fossa pneumotricipitalis and directly distal to caput humeri;

x. noncomparable (Dinornithiformes).

Note.—Tuberculum dorsale serves as situs ancorae insertii mm. supracoracoideus et deltoideus minor.

1372. Extremitas proximalis humeri, caput humeri (*sensu* midpoint), position proximodistalis relative to tuberculum dorsale ("externus"), situs:

a. caput distal to tuberculum;

b. caput proximal to tuberculum;

x. noncomparable (Dinornithiformes, Dromornithidae).

Note.—See: Norell and Clarke (2001: appendix I, character 107); J. A. Clarke (2002: appendix I, character 107); J. A. Clarke and Norell (2002: appendix 2, character 107); Zhou and Zhang (2002: appendix III, character 107); J. A. Clarke (2004: appendix 1, character 107); Ji et al. (2005: supplement, part I, character 107), by comparison of maximal proximality of midpoint *vs.* distal terminus.

1373. Extremitas proximalis humeri, caput humeri, facies cranialis, immediately proximal to sulcus ligamentosa transversus, depressio et foramen pneumatica aut neurovascularia, status:

a. absent; **b.** present;

x. noncomparable (Dinornithiformes).

Crista deltopectoralis

Note.—This prominent, diagnostically important feature of the humerus comprises several different aspects of form, optimally treated as separate characters. Previous analyses, which treated narrow samples of taxa or confounded multiple, evidently independent features of the crista deltopectoralis, are numerous. Differences in approach, however, necessitate caution in comparison of these earlier works and the present characterizations, especially those combining aspects of form into single characters. Accordingly, references ascribed to the following characters are unavoidably ambiguous or redundant in some instances.

See also: Ballmann (1969a: fig. 57); Sereno (1991a: appendix, ingroup character 25); Azuma and Currie (2000: appendix 1, character 55); Chiappe (2001a: appendix 1, character 86); Norell et al. (2001: appendix 1, character 141); Chiappe (2002: appendix 20.2, character 86); J. M. Clark et al. (2002a: appendix 2.2, character 143); Xu (2002: suite I, character 15; suite II, character 168); Xu et al. (2002a: supplement, character 113); Hwang et al. (2004: supplement, character 140); Xu and Norell (2004: supplement, character 140).

1374. Extremitas proximalis humeri, crista deltopectoralis (oblique caudal perspective), status et forma (profile) marginalis (**unordered**):

a. absent or obsolete;

b. present, subarcuate (rounded-convex) and comparatively elongate, crista lacking distinct angulae;

c. present, essentially triangular, crista propria possessing one distinct angulus;

d. present, bi-tubercularly or bi-angularly concave, rudimenta evidently largely comprising two tuberculae separated by deep, arcuate concavity—processus insertii m. pectoralis subcutanea thoracica;

e. secondarily diminutive, element practically acristate, often precluding reliable characterization of form;

x. noncomparable (Dinornithiformes).

Note.—States assessed exclusive of overlying features characterized separately. See: Payne and Risley (1976: character 23), regarding Ardeidae; Gauthier (1986: 14, unindexed synapomorphy of Aves); Livezey (1986: appendix 1, character 25); Livezey (1989: table 1, character 25); Andors (1992: table 2, character 29); Novas (1992: character 1); Sereno et al. (1993: legend for fig. 3a); Novas (1994 [1993]: appendix, character 2); Elzanowski (1995: character N'5); Livezey (1996b: appendix 1, character 21); Livezey (1998b: appendix A, character 204); Makovicky and Sues (1998: appendix 1, character 64); Sereno et al. (1998: footnote 22, character 3); Azuma and Currie (2000: appendix 1, character 55); Holtz (2000 [1998]: appendix I, character 241); G. Mayr (2003c: appendix, character 7); Xu et al. (2002a: supplement, character 113), from which provisional states of Mesozoic taxa were taken; Zhou and Zhang (2002: appendix III, character 113); G. Mayr (2003a: appendix I, characters 32–33); G. Mayr and Clarke (2003: appendix A, character 75); Dyke and van Tuinen (2004: appendix 1, character 51); G. Mayr (2004b: appendix 1, character 39); G. Mayr and Ericson (2004: appendix I, character 46); G. Mayr (2005b: appendix A, character 22).

1375. Extremitas proximalis humeri, crista deltopectoralis (oblique caudal perspective), distal displacement and variably conspicuous dorsocranial elongation and hamulation, status et forma (**ordered**):

a. absent or indistinct;

b. present, crista essentially acuminate;

c. present, crista extremely elongated, deeply hamulate processus;

x. noncomparable (Dinornithiformes).

Note.—See: Zusi and Bentz (1984: fig. 15).

1376. Extremitas proximalis humeri, crista deltopectoralis, facies caudalis, margo dorsalis, distinct variably deep concavity immediately distal to tuberculum dorsale and proximale to angulus cristae (or homologous situs) to form concavitas marginalis cristae (**new term**), which together with distal convexity of margo cristae, presenting a sinuous aspectus, status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes).

1377. Extremitas proximalis humeri, crista deltopectoralis (oblique *caudal* perspective), forma facialis (**unordered**):
a. concave, margo dorsalis oriented obliquely dorsocaudad;
b. planar;
c. convex, margo dorsalis oriented craniad;
x. noncomparable (Dinornithiformes).
Note.—See: Strauch (1978: character 43), reanalyzed by Björklund (1994: appendix) and Chu (1995); Gauthier (1986: 14, unindexed synapomorphy of Aves); Livezey (1986: appendix 1, character 25); Siegel-Causey (1988: characters 67–69); Livezey (1989: table 1, character 25); Andors (1992: table 2, character 29); Novas (1992: character 1); Sereno et al. (1993: legend for fig. 3a); Novas (1994 [1993]: appendix, character 2); Elzanowski (1995: character N'5); Livezey (1996b: appendix 1, character 21); Ericson (1997: table 1, character 55); Livezey (1998b: appendix A, character 206); Makovicky and Sues (1998: appendix 1, character 64); Sereno et al. (1998: footnote 22, characters 3 and 31); Azuma and Currie (2000: appendix 1, character 55); Holtz (2000 [1998]: appendix I, character 241); J. A. Clarke and Chiappe (2001: character 3); Cracraft and Clarke (2001: appendix 2, character 23); Norell and Clarke (2001: appendix I, characters 113 and 115); J. A. Clarke (2002: appendix I, characters 112 and 114); J. A. Clarke and Norell (2002: appendix 2, characters 112 and 114); Zhou and Zhang (2002: appendix III, characters 113 and 115); J. A. Clarke (2004: appendix 1, characters 112 and 114); Ji et al. (2005: supplement, part I, characters 113 and 115).

1378. Extremitas proximalis humeri, crista deltopectoralis (oblique caudal perspective), maximal dorsal width relative to co-aligned diameter of adjacent corpus humeri, forma (**ordered**):
a. crista narrower than corpus;
b. crista of equal breadth with corpus;
c. crista broader than corpus;
x. noncomparable (Dinornithiformes).
Note.—See: Payne and Risley (1976: character 24), regarding Ardeidae; Norell and Clarke (2001: appendix I, character 114), treated similarly by J. A. Clarke (2002: appendix I, character 113), J. A. Clarke and Norell (2002: appendix 2, character 113), and J. A. Clarke (2004: appendix 1, character 113); Maryanska et al. (2002: appendix 1, character 129); Zhou and Zhang (2002: appendix III, character 114); Ji et al. (2005: supplement, part I, character 114).

1379. Extremitas proximalis humeri, crista deltopectoralis, quadrangular margo (craniocaudal perspective), status:
a. absent; **b.** present.
Note.—See: Bourdon (2006: supplement, character 79).

1380. Extremitas proximalis humeri, crista deltopectoralis (oblique caudal perspective), form in which margo dorsalis cristae parallel and aligned with margo dorsalis corporis throughout length of former, status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes, Sphenisciformes).

1381. Extremitas proximalis humeri, crista deltopectoralis, markedly shallow (dorsoventral) depth in combination with considerable proximocaudal extent of margo cristae, status:
a. absent; **b.** present.
Note.—See: Bourdon (2006: supplement, character 106).

1382. Extremitas proximalis humeri, crista deltopectoralis, comparative proximodistal length relative to that of corpus humeri:
a. great, well developed and extending at least one-third of length of corpus humeri;
b. small, diminutive, triangular eminentia, extending *less* than one-third of length of corpus humeri;
x. noncomparable (Dinornithiformes).
Note.—See: Rauhut (2003: character 142).

1383. Extremitas proximalis humeri, crista deltopectoralis (oblique caudal perspective), proximodistal extent relative to that of crista bicipitalis, magnitudo (**ordered**):
a. majority distal to latter;
b. substantial minority distal to latter;
c. slight or moderate minority distal to latter;
d. approximately equal to latter;
x. noncomparable (Dinornithiformes) or crista (*Struthio*, Rheidae, *Apteryx*).
Note.—See: Cracraft (1982: series 4, character 3), regarding *Gestalt* of extremitas proximalis humeri of loons and grebes; Cracraft (1985: character 30); Chu (1998: appendix 1, character 87); Dyke (2001a: appendix 1, character 5); Maryanska et al. (2002: appendix 1, character 132).

1384. Extremitas proximalis humeri, crista deltopectoralis, facies cranialis, margo dorsalis, cristula (sulcus) marginalis distale (**new term**), status:
a. absent, crista deltopectoralis uniformly smooth to margo;

b. present, crista deltopectoralis marked by distinct sulcus or jugum, especially distinct near terminus distalis cristae;
x. noncomparable (Dinornithiformes).
Note.—Ancora of aponeurosis origii m. scapulohumeralis caudalis (Ballmann 1969a) similar but nonhomologous (treated below). See: Azuma and Currie (2000: appendix 1, character 55); Norell et al. (2001: appendix 1, character 142); J. M. Clark et al. (2002a: appendix 2.2, character 144); Xu (2002: suite II, character 169); Xu et al. (2002a: supplement, character 114); Hwang et al. (2004: supplement, character 141); Xu and Norell (2004: supplement, character 141).

1385. Extremitas proximalis humeri, crista deltopectoralis, facies caudalis, foramen pneumaticum, status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes).

1386. Extremitas proximalis humeri, crista deltopectoralis, facies caudalis, margo dorsalis, cristula (sulcus) aponeurosis m. scapulo-humeralis caudalis (**new term**), status:
a. absent or indiscernable;
b. present, especially pronounced proximally;
x. noncomparable (ratites).
Note.—Apomorphic state typically appears as sloping extension of tuberculum dorsale along margo dorsalis cristae. See: Bannasch (1986a–b: fig. 38); Bannasch (1987); Livezey (1998b: appendix A, character 205).

1387. Extremitas proximalis humeri, crista deltopectoralis, facies caudalis, distinct concavitas under margo distalis capitis et tuberculae dorsale, status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes).
Note.—Evidently serves as margo proximalis of caput dorsale of m. scapulohumeralis.

1388. Extremitas proximalis humeri, notably tuberculum ventrale, distinct distal counterclockwise rotation (caudal perspective) effecting: (*i*) ventrodistal shift and associated virtual alignment of margo dorsalis corporis et crista deltopectoralis, margo dorsalis; and (*ii*) subperpendicularity between margo ventralis of crista bicipitalis and margo ventralis corporis, status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes).

1389. Extremitas proximalis humeri, facies caudalis et margo dorsalis, tuberculum ventrale, distal position of tuberculum such that it is directly dorsal to fossa pneumotricipitalis, status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes).
Note.—See: McGowan (1982).

1390. Extremitas proximalis humeri, facies caudalis et margo dorsalis, proximodorsal separation of caput et tuberculum dorsale by deep, wide sulcus that is positioned distad such that it is directly dorsal to fossa pneumotricipitalis, status:
a. absent;
b. present, crista broad and triangular (*Casuarius*) or crista narrow;
x. noncomparable (Dinornithiformes).

1391. Extremitas proximalis humeri, crista deltopectoralis, facies caudalis, ala subtubercularis (**new term**), status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes).
Note.—New term refers to rounded “flange” on margo dorsalis cristae deltopectoralis immediately distodorsal to tuberculum dorsale.

1392. Extremitas proximalis humeri, crista deltopectoralis, facies caudalis, cavitas pneumaticum cristae (**new term**), status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes).
Note.—This feature does *not* perforate crista craniocaudally, appearing only as imperforate, translucent concavitas on facies caudalis cristae.

1393. Extremitas proximalis humeri, crista deltopectoralis, facies caudalis, pila transversa cristae (**new term**), status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes).
Note.—New feature refers to reinforcing, rounded strut incorporated into crista at approximate midpoint, directed towards angulus cristae (where present).

1394. Extremitas proximalis humeri, crista deltopectoralis, fonticulus cristae (**new term**), status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes).
Note.—Fonticulus presumably occluded by membrana in life. Minute, bilobate fenestra present unilaterally in Berlin specimen of *Archaeopteryx*.

1395. Extremitas proximalis humeri, crista deltopectoralis, angulus cristae aut tuberculum angulae (**new term**), status et forma (**unordered**):
a. absent, margo cristae essentially rounded;
b. present, represented by simple but distinct angulus;
c. present, represented by tuberculum angulae;
x. noncomparable (Dinornithiformes).
Note.—Preferable to define myological implications of angulus, the latter qualifying if angularity of eminentia marginalis exceeds elliptical form.

See: Cracraft (1985: character 45); Cracraft (1988: series IX, character 6); Houde (1988: table 27, character 32); Livezey (1998b: appendix A, characters 204 and 208).

1396. Extremitas proximalis humeri, crista deltopectoralis, angulus cristae, prominence and orientation relative to corpus humeri such that: (*i*) crista is at least as prominently extended dorsad, (*ii*) angulus cristae sharply acuminate, and (*iii*) margo proximalis cristae concave, status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes).
Note.—Reflects both angulus cristae and forma cristae marginalis.

1397. Extremitas proximalis humeri, crista deltopectoralis, angulus cristae (if present) or homologous locus, situs (**unordered**):
a. proximal; **b.** dorsal; **c.** distal;
d. cranial, perpendicular to crista propria.
Note.—See: Ericson (1997: table 1, character 56).

1398. Extremitas proximalis humeri, crista deltopectoralis, facies caudalis, immediately ventral to margo cristae et impressio insertii m. scapulohumeralis caudalis, foramen neurovascularium et/aut pneumaticum, status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes).
Note.—See: Bannasch (1986a–b: fig. 38); Bannasch (1987).

1399. Extremitas proximalis humeri, facies caudalis, crista deltopectoralis, impressio (cristula) m. supracoracoidei exclusive of situs ancorae tuberculae dorsale, status et forma (**ordered**):
a. absent or indiscernable;
b. present, impressio, terminating proximad to basis cristae;
c. present, cristula, extending distad to basis cristae;
x. noncomparable (ratites).
Note.—Tendo insertii m. supracoracoidei humeri principally is anchored to tuberculum dorsale; in some taxa this ancora is continued (typically distad, proximate to basis cristae) by impressio aut crista faciei caudalis cristae deltopectoralis. In Dromornithidae, feature frequently enhanced by sulcus m. supracoracoideus. See: Archey (1941: figs. 52–53); Bannasch (1986a–b: fig. 38); Bannasch (1987); J. A. Clarke and Chiappe (2001: character 1); Dyke (2001a: appendix 1, character 13); J. A. Clarke (2002: appendix I, character 115); Dyke et al. (2003: appendix 1, character 58); J. A. Clarke (2004: appendix 1, character 115).

1400. Extremitas proximalis humeri, crista deltopectoralis, impressio aut tuberculum insertii m. pectoralis (partes sternobrachialis et costobrachialis), status et forma (**unordered**):
a. present, deep, elongate, elliptical depressio, or elevated, crescentic or ovate impressio;
b. present, modest tuberculum;
c. present, essentially sessile linea muscularis;
d. absent or indiscernable;
x. noncomparable (Dinornithiformes).
Note.—See: Archey (1941: figs. 52–53); Stephan (1979); Bannasch (1986a–b: fig. 38); Bannasch (1987); Siegel-Causey (1988: character 77); Chu (1998: appendix 1, character 86); Hughes (2000: appendix 2, character 110), after Seibel (1988: character HU 16).

1401. Extremitas proximalis humeri (facies cranialis), crista deltopectoralis, terminus distalis, tuberculum insertii m. pectoralis, pars subcutanea thoracica, status:
a. absent or mere impressio(nes);
b. present, prominent lobus;
x. noncomparable (Dinornithiformes).
Note.—See: Archey (1941: figs. 52–53); Livezey (1986: appendix 1, character 31); Bannasch (1986a–b: fig. 38); Bannasch (1987); Ericson (1997: table 2, character 34); Livezey (1997a: appendix 1, character 72; *corrigenda*, Livezey 1998a); Andors (1992: table 2, character 30); Dyke (2001b: appendix 1, character 72).

1402. Extremitas proximalis humeri, crista deltopectoralis, facies caudalis et/aut margo dorsalis, impressio (eminentia) insertii m. latissimi dorsi, status et forma (**ordered**):
a. absent or indistinguishable;
b. present, indistinct impressio aut eminentia linearis;
c. present, prominent, sublinear, variably elongate ruga;
d. present, conspicuous, broad sulcus;
x. noncomparable (Dinornithiformes).
Note.—See: Archey (1941: figs. 52–53); Chu (1998: appendix 1, character 88). Alternative term "eminentia musculi latissimi dorsi posterioris" proposed by Ballmann (1969a).

1403. Extremitas proximalis humeri, crista bicipitalis, status (**ordered**):
a. absent or rudimentary;
b. present, distinct;
c. present, but generally reduced;
x. noncomparable (Dinornithiformes).
Note.—See: Thulborn (1984: 126–127, character 16); Zusi and Bentz (1984: fig. 15); Houde (1988: table 27, character 31); Chatterjee (1995: character 11, part); Kurochkin (1995b: table 1, character 10); Sanz et al. (1995, 1997: character 72); Chatterjee (1999: appendix II, character 56); Sereno et al. (2002), regarding *Sinornis*; Vickers-Rich et al. (2002), concerning *Avimimus*.

1404. Extremitas proximalis humeri, facies caudalis, tuberculum ventrale, crista bicipitalis, crus ventrale fossae, enclosure within perforation by comparatively numerous pori pneumatici, status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes).

1405. Extremitas proximalis humeri, crista bicipitalis, facies cranialis, forma facialis *sensu* planarity or slight concavity, status:
a. absent, facies cranialis variably convex;
b. present; **x.** noncomparable (ratites).

1406. Extremitas proximalis humeri, facies cranialis, crista bicipitalis, (ventro)cranial prominence, status:
a. absent, negligible to moderate;
b. present, extreme rounded intumescentia;
x. noncomparable (ratites).
Note.—See: Siegel-Causey (1988: character 71); Chiappe and Calvo (1994: appendix II, character 8), listed as synapomorphy of Enantiornithes, the "bulky, cranioventrally projected" state of crista; Livezey (1998b: appendix A, character 214); Chiappe (2001a: appendix 1, character 87); Norell and Clarke (2001: appendix I, character 118), treated similarly by J. A. Clarke (2002: appendix I, character 117), J. A. Clarke and Norell (2002: appendix 2, character 117), and J. A. Clarke (2004: appendix 1, character 117); Chiappe (2002: appendix 20.2, character 87); Chiappe and Walker (2002: appendix 11.1, character 18); Zhou and Zhang (2002: appendix III, character 118); Dyke and van Tuinen (2004: appendix 1, character 52); Ji et al. (2005: supplement, part I, character 118).

1407. Extremitas proximalis humeri, facies cranialis, intumescentia, marked circumdelimitation by jugum, status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes).
Note.—Prominence of delimitation covariant with body size, i.e., least in *Gavia stellata* and greatest in *G. adamsii*. Comparatively pronounced jugum of intumescentia in Gaviidae evidently related to provision of exceptionally strong aponeurosis origii capitis m. biceps brachii (McKitrick 1992: fig. 13).

1408. Extremitas proximalis humeri, facies cranialis, crista bicipitalis, margines distalis et dorsalis (medianus), demarcation by shallow, narrow sulcus marginalis intumescentiae (**new term**) or distinct linea, status et forma (**unordered**):
a. absent;
b. present, limited to margo distalis intumescentiae;
c. present, includes margines distalis et dorsalis (medianus) intumescentiae;
x. noncomparable by absence (Dinornithiformes) or profound distortion of element (*Aepyornis*, *Aptornis*).
Note.—New term may be ventrolateral homologue of sulcus aut canalis n. coracobrachialis cranialis of Charadriiformes.

1409. Extremitas proximalis humeri, facies bicipitalis, margo ventralis immediately caudal to tuberculum ventrale, eminentia subcircularis marginale (**new term**), status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes).
Note.—Apomorphy refers to rounded flange in margin shortly distad to tuberculum, delimited both proximally and cranially by concavitates marginales.

1410. Extremitas proximalis humeri, tuberculum ventrale, crista bicipitalis, crus distale fossae (**new term**), situs insertii m. scapulohumeralis caudalis, status, forma et situs (**unordered**):
a. absent;
b. present, impressio craniodistales cristae;
c. present, impressio ventrodistalis apicali cristae;
d. present, sulcus aut fossa caudodistalis cristae;
x. noncomparable by absence of element or crista (Aepyornithiformes, Dinornithiformes).
Note.—New term refers to variably pronounced, often caudally concave extension of distal portion of crista bicipitalis (cf. Zhou and Zhang 2002). See: Livezey (1986: appendix 1, character 30); Livezey (1995b: appendix 1, character 12); Livezey (1995c: appendix II, character 15); Sanz et al. (1995, 1997: character 83) regarding facies lateralis, "small fossa for muscular attachment"; Livezey (1998b: appendix A, character 209); Siegel-Causey (1988: characters 72–73), regarding "bicipital furrow"; Chiappe (2001a: appendix 1, character 88); Norell and Clarke (2001: appendix I, character 117), treated similarly by J. A. Clarke (2002: appendix I, character 116), J. A. Clarke and Norell (2002: appendix 2, character 116), and J. A. Clarke (2004: appendix 1, character 116); Chiappe (2002: appendix 20.2, character 88); Chiappe and Walker (2002: appendix 11.1, character 19); Zhou and Zhang (2002: appendix III, character 117), respectively in reference to mark on facies cranialis aut distalis, and position of mark on margo cristae; Ji et al. (2005: supplement, part I, characters 116–117).

1411. Extremitas proximalis humeri, tuberculum ventrale, crista bicipitalis, crus distale fossae (**new term**), situs insertii m. scapulohumeralis caudalis, cristula terminalis (**new term**), status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes).
Note.—See: Archey (1941: figs. 52–53); Bannasch (1986a–b: fig. 38); Bannasch (1987); J. A. Clarke (2004: fig. 50).

1412. Extremitas proximalis humeri, crista bicipitalis, terminus distalis, lobus m. biceps (**new term**), status et forma (**unordered**):

a. absent;

b. present, small or homologue indicated by angular eminentia;

c. present, large lobus or tuberculum;

x. noncomparable (Dinornithiformes).

Note.—Evidently related to origo m. biceps brachii, caput humerale aut pars propatagialis.

1413. Extremitas proximalis humeri, crista bicipitalis, terminus on corpus humeri, margo ventralis, forma (**unordered**):

a. gradually continued by shallow, low but distinct jugum along corpus humeri, margo ventralis;

b. abruptly discontinued proximally on corpus humeri, margo ventralis;

c. abruptly discontinued, adorned by bulbus bicipitalis (**new term**) at terminus corporis;

x. noncomparable (ratites).

Fossa pneumotricipitalis

Note.—This fossa manifests extraordinary structural and functional variation among taxa, a diversity expected in light of its multiple anatomical and functional roles. Most notably, the fossa(e) can represent enclosures for capita musculi, atria externa of spatia pneumatica, or a combination of the two. Ultimately in reference to the "single," "double," and two components of the latter we adopted the following, narrowly delimited nomenclatural schema, respectively: (*i*) fossa pneumotricipitalis cingulus (**new term**), (*ii*) fossa pneumotricipitalis totalis (**new term**), and (*iii*) subfossae ventrale et dorsale pneumatica.

In reference to the plesiomorphic "single" or fossa (proprius) totalis, the enclosure serves as ancorae of origiones m. humeroscapularis (capita ventrale et dorsale), insertii m. scapulohumeralis cranialis, and foramen pneumaticum, and is bounded ventrally by crus ventrale fossae and dorsally by crus dorsale fossae. The dorsal (supplementary) component of the "doubled fossae," where present, typically is apneumatic and encloses origo capitis dorsale of m. humeroscapularis and situs insertii mm. scapulohumeralis cranialis et caudalis, as well as m. latissimus dorsi, and as it is apneumatic this dorsale component only appears to be "coupled" with the fossa pneumotricipitalis proprius (i.e., *sensu stricto*). Variation in this complex abounds, e.g., some taxa (e.g., *Dromaius*) possesses both a single pneumatic fossa pneumotricipitalis proprius with dorsal sulcus for m. triceps complex (part) lacking even the appearance of a fossa; whereas *Lophortyx*, and evidently the entire subfamily Odontiphorinae, is not only the only galliform group to manifest a "double" variant of this complex, but it also is characterized by substantial fossa quasi-pneumatica within each.

1414. Extremitas proximalis humeri, fossa pneumotricipitalis, foramen pneumaticum primus (**new term**), status (**ordered**):

a. absent; **b.** rudimentary or vestigial;

c. present, shallow, evidently related to subaquatic habit;

d. present, deep, (variably) significant;

x. noncomparable (Dinornithiformes).

Note.—See: G. Mayr and Clarke (2003: appendix A, character 77), in which *Colius* was incorrectly coded; Dyke and van Tuinen (2004: appendix 1, character 53); G. Mayr and Ericson (2004: appendix I, character 50).

1415. Extremitas proximalis humeri, fossa pneumotricipitalis (partes dorsalis et ventralis), status et forma pneumatica *vis-à-vis* fenestrae pneumaticae et pori pneumatici (**unordered**):

a. absent, fossa apneumatic;

b. present, fossa pneumatic, pneumaticity rudimentary, effected by pori pneumatici perforating largely occlusive lamina osseum;

c. present, fossa moderately pneumatic, effected by fenestra pneumatica prima (orientation principally proximodorsad) et pori pneumatici;

d. present, fossa pneumatic, pneumaticity moderate, effected by fenestra pneumatica accessoria (orientation principally dorsodistad) et pori pneumatici;

e. present, fossa pneumatic, pneumaticity great, effected by fenestra pneumatica prima (orientation principally proximodorsad), fenestra pneumatica accessoria (orientation principally dorsodistad), et pori pneumatici;

f. present, fossa doubly pneumatic, pneumaticity extreme, effected by both fenestrae prima et accessoria in fossa pneumotricipitalis pars ventralis, et fenestra pneumatica in fossa pneumotricipitalis pars dorsalis;

x. noncomparable by absence of entire element (Dinornithiformes) or fossa (Dromaiidae, *Apteryx*, Dromornithidae).

Note.—*Some* confamilials of trochilid exemplar *Glaucis* possess fenestra pneumatica cristae deltopectoralis (**new term**) on facies caudalis, apparently unique among Neornithes. See: Bock (1962), regarding state(s) in Passeres; Holman (1961, 1964), regarding "pneumatic fossa II"; Payne and Risley (1976: character 25), regarding Ardeidae; Thulborn (1984: 126–127, character 17), regarding *Archaeopteryx*; Cracraft (1986: appendix, character 66, part); Bannasch (1986a–b: fig. 38); Bannasch (1987); Livezey (1986: appendix 1, character 28); Bledsoe (1988: appendix, character 13), discounted by K. Lee et al. (1997: appendix 2) for ratites; Cracraft (1988: series V, character 11); Siegel-Causey (1988: character 76); Cracraft and Mindell (1989: table 1, character 11); Livezey (1995a: appendix 1, character 6); Livezey (1995b: appendix 1, character 11); Livezey (1995c: appendix II, character 13); Livezey (1996b: appendix 1, character 23); Livezey (1996c: character 4); Ericson (1997: table 1, character 51, part); Chiappe et al. (1998: character 44); Chu (1998: appendix 1, character 89); Ji et al. (1998: supplement, character 44); Livezey (1998b: appendix A, character 201); Chiappe et al. (1999); Hughes (2000: appendix 2, character 111); Chiappe (2001a: appendix 1, character 85); J. A. Clarke and Chiappe (2001: characters 7–8); Cracraft and Clarke (2001: appendix 2, character 24); Norell and Clarke (2001: appendix I, character 119), treated similarly by J. A. Clarke (2002: appendix I, character 118), J. A. Clarke and Norell (2002: appendix 2, character 118), and J. A. Clarke (2004: appendix 1, character 118); Chiappe (2002: appendix 20.2, character 85); Zhou and Zhang (2002: appendix III, character 119); Dyke et al. (2003: appendix 1, characters 56 and 60), regarding "secondary fossa pneumaticum"; Dyke (2003: table 1); G. Mayr and Clarke (2003: appendix A, character 77); G. Mayr (2004a: appendix 1, character 40); G. Mayr and Ericson (2004: appendix I, character 51); Ji et al. (2005: supplement, part I, character 119).

1416. Extremitas proximalis humeri, fossa pneumotricipitalis relative to tuberculum ventrale, forma et situs (**unordered**):

a. expansive over comparatively broad regio distodorsal to tuberculum;

b. limited to small ventral area on facies distalis of tuberculum ventrale;

c. restricted to recessus deep within incisura proximocraniad to basis tuberculum ventrale;

x. noncomparable (Dinornithiformes).

Note.—See: Zusi and Bentz (1984: fig. 15).

1417. Extremitas proximalis humeri, fossa pneumotricipitalis (primus in taxa with duplex fossae) relative to corpus humeri (distal perspective), situs (**unordered**):

a. ventrocaudal;

b. caudoventral, and approaching coplanarity with crista deltopectoralis;

c. strictly ventral, directly opposite basis cristae deltopectoralis;

x. noncomparable (ratites, Turnicidae).

1418. Extremitas proximalis humeri, fossa pneumotricipitalis (primus in taxa with duplex fossae), distinct, triangular, partitioned, caudally exposed subfossa subtubercularis (**new term**), status:

a. absent; **b.** present;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

1419. Extremitas proximalis humeri, fossa pneumotricipitalis, occluding caudal lamina, rendering fossa apneumatic, with three or more distinct, subovate depressiones, status:

a. absent; **b.** present;

x. noncomparable (Dinornithiformes, Dromornithidae).

1420. Extremitas proximalis humeri, fossa pneumotricipitalis, partially occluding caudal (superficial) lamina marginis distalis fossae, status et forma (**ordered**):

a. absent;

b. present, occluding minority of atrium fossae;

c. present, occluding majority of atrium fossae;

x. noncomparable (Dinornithiformes).

Note.—Feature in question is thin, osseous lamina originating at margo distalis fossae and extending variably proximad.

1421. Extremitas proximalis humeri, facies caudalis, fossa pneumotricipitalis, subdivision by impressio origii m. humerotriceps, caput dorsale, to delimit pars ventralis fossae (**new term**)—virtually universal among Aves—et pars dorsalis fossae (**new term**)—rarely pneumatic and of restricted expanse—status et forma (**unordered**):

a. absent, fossa unipartite, comprising only homologue of pars ventralis fossae;

b. rudimentary, fossa comprising pars ventralis et pars dorsalis incipiens, latter typified by rudimentary crus proximale (juxtaposed with margo distalis capitis), but lacking distinct, distal sulcus or delimiting margines dorsalis et ventralis;

c. partial, fossa comprising pars ventralis et pars dorsalis incompletus, latter typified by distinct crus proximale (juxtaposed with margo distalis capitis) and shallow, abbreviated distal sulcus;

d. present, fossa bipartite, comprising both partes ventralis et dorsalis, each well developed and typically of comparable size;

x. noncomparable (Dinornithiformes) or fossa (Dromaiidae, *Apteryx*, Dromornithidae).

Note.—This character is descriptive of the fossa *per se*, and not its (a)pneumatic nature. Musculus related to present osteological character synonymous with "m. supraspinatus" of Howard (1929: fig. 20). Ballmann (1969a) apparently derived this term within the context of the osteology of passerines. Pars dorsalis fossae is delimited dorsally by margo (crista) dorsalis, proximally by crus proximale fossae, and ventrally by neomorphous "crista coracoidea" (Komárek 1979) of impressio positioned in middle of fossa pneumotricipitalis propria. This subdivisional trend (Bock 1962) is not to be confused with that of fenestrae enclosed within the fossa pneumotricipitalis proprius (i.e., evident plesiomorphic state provisionally considered to be homologous with pars ventralis fossae) among Galliformes (Holman 1964; Dyke et al. 2003).

See: Archey (1941: figs. 52–53); Strauch (1978:

character 44), reanalyzed by Björklund (1994: appendix) and Chu (1995); Strauch (1985: character 17); Chu (1998: appendix 1, character 90); Livezey (1998b: appendix A, character 200); Dyke and Gulas (2002: appendix 1, character 21); Hughes (2000: appendix 2, character 109), after Seibel (1988: character HU 9); J. A. Clarke (2004: fig. 50); G. Mayr and Ericson (2004: appendix I, character 52).

1422. Extremitas proximalis humeri, facies caudalis, fossa pneumotricipitalis (caudal perspective), distinct circularity of densely rimmed atrium situated at approximate normality with respect to axis majoris corporis humeri, status (**unordered**):
a. absent; **b.** present;
x. noncomparable by absence of element or fossa (ratites exclusive of Casuariidae; Dromornithidae).
Note.—See: Stephan (1979); Bannasch (1986a–b: fig. 38); Bannasch (1987).

1423. Extremitas proximalis humeri, facies caudalis, fossa pneumotricipitalis, planum distalis fossae, area:
a. limited, submarginal;
b. expansive, typically constituting majority of solum fossae;
x. noncomparable (Dinornithiformes).
Note.—Character, deemed present by delimiting criteria *a priori*, determinable whether fossa is unipartite or bipartite; in the former case (where fossa not obstructed by lamina), structural parameters virtually assure qualification for state "b," whereas in the latter case the state is conditional in part on the distal extent of the crus dorsale of pars ventralis.

1424. Extremitas proximalis humeri, fossa pneumotricipitalis, apparent torsion of element about axis proximodistalis (majoris) such that entire fossa is ventral to corpus humeri, status:
a. absent, no torsion apparent nor position altered;
b. present, torsion apparent and position altered;
x. noncomparable (Dinornithiformes).
Note.—See: Stephan (1979); Bannasch (1986a–b: fig. 38); Bannasch (1987).

1425. Extremitas proximalis humeri, fossa pneumotricipitalis proprius (*sensu stricto*) or pars ventralis fossae, lamina crura dorsale fossae (**new term**), also serving as margo ventralis of incisura capitis, fenestra laminae, status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes).
Note.—See: Livezey (1986: appendix 1, character 36); Livezey (1995c: appendix II, character 19); Livezey (1998b: appendix A, character 202), regarding craniocaudal breadth of lamina fossae.

1426. Extremitas proximalis humeri, facies caudalis, fossa pneumotricipitalis, crus (proximalis) dorsale fossae (**new term**), pars ventralis aut proprius, distinctly angular cristula at junctura of incisura capitis et sulcus m. humerotriceps, status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes).

1427. Extremitas proximalis humeri, fossa pneumotricipitalis, crus (distalis) ventrale fossae (**new term**), status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes, Dromornithidae).
Note.—Corresponds to "lateral extension of internal tuberosity." See: Gauthier (1986: 14, unindexed synapomorphy of Aves); Elzanowski (1995: character N3).

1428. Extremitas proximalis humeri, facies (palmaris) cranialis, planum intertuberculare, sulcus (canalis) nervi coracobrachialis, status:
a. absent or indistinguishable;
b. present, represented by sulcus et/aut canalis;
x. noncomparable (Dinornithiformes).
Note.—See: Ericson (1997: table 1, character 58); Ballmann (1979); S. L. Olson and Steadman (1981: 14).

1429. Extremitas proximalis humeri, facies (palmaris) cranialis, planum intertuberculare, intumescentia humeri (proximal perspective), facies cranialis, forma superficialis (**ordered**):
a. convex; **b.** (sub)planar;
c. concave, defining fossa on midline and making facies articularis proximalis appear valliform, i.e., chevroniform-concave or "V-shaped";
x. noncomparable (Dinornithiformes).
Note.—See: Baumel and Witmer (1993: annotation 181); Livezey (1998b: appendix A, character 216), raising possibility that *Aptornis* noncomparable; G. Mayr (2003c: appendix, character 12); Norell and Clarke (2001: appendix I, character 110), in reference to "fossa on midline making the proximal articular surface appear "V-shaped" in proximal view," treated similarly by J. A. Clarke (2002: appendix I, character 110), J. A. Clarke and Norell (2002: appendix 2, character 110), and J. A. Clarke (2004: appendix 1, character 110); Zhou and Zhang (2002: appendix III, character 110); Ji et al. (2005: supplement, part I, character 110).

1430. Extremitas proximalis humeri, facies (palmaris) cranialis, planum intertuberculare, intumescentia humeri, margo distalis, cranially elevated and forming distinct, subcristulate plica aut jugum—cristula intumescentiae (**new term**), status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes).
Note.—See: Zusi and Bentz (1984: fig. 15).

1431. Extremitas proximalis humeri, facies (palmaris) cranialis, sulcus ligamentosus transversus, status et forma *sensu* dorsoventral extent (**ordered**):

a. absent or obsolete, at most suggested by shallow, abbreviate depressio or dorsally restricted fovea;

b. present, shallow and abbreviate, typically limited to (virtually entire) margo proximalis of facies bicipitalis and reaching midpoint of extremitas proximalis humeri, facies cranialis;

c. present, deep and long, extending dorsoventrally across extremitas proximalis humeri to intersect bases tuberculorum dorsale et ventrale humeri;

x. noncomparable (ratites).

Note.—See: Payne and Risley (1976: character 26); Cracraft (1985: character 29); Bledsoe (1988: appendix, character 12); Cracraft (1988: series VII, character 4; series XVI, character 4); Siegel-Causey (1988: characters 64–66); Chiappe (1995b: character 39); Sanz et al. (1995, 1997: character 37); Chiappe (1996b: character 36); K. Lee et al. (1997: appendix 1, character 17); Chiappe et al. (1998: character 43); Ji et al. (1998: supplement, character 43); Forster et al. (1998: supplement, character 56); Chatterjee (1999: appendix II, character 52); Chiappe (2001a: appendix 1, character 84); J. A. Clarke and Chiappe (2001: character 6); Norell and Clarke (2001: appendix I, character 112), treated similarly by J. A. Clarke (2002: appendix I, character 111), J. A. Clarke and Norell (2002: appendix 2, character 111), and J. A. Clarke (2004: appendix 1, character 111); Chiappe (2002: appendix 20.2, character 84); Zhou and Zhang (2002: appendix III, character 112); G. Mayr (2003b: appendix I, character 10), regarding Trogonidae and Steatornithidae; G. Mayr et al. (2003: appendix 1, character 36); Ji et al. (2005: supplement, part I, character 112).

1432. Extremitas proximalis humeri, facies (palmaris) cranialis, sulcus ligamentosus transversus, sectio ventralis, marked triangular raised subplanar regio delimited by pronounced cristae marginales and enclosing deep ventral fovea, status:

a. absent; **b.** present.

Note.—State superficially similar to apomorphic state occurs in Apodiformes. See: Bannasch (1986a–b: fig. 38); Bannasch (1987).

1433. Extremitas proximalis humeri, facies (palmaris) cranialis, impressio m. coracobrachialis cranialis (**emended term**), forma (**unordered**):

a. indistinct or vaguely delimited;

b. moderately deep, moderately delimited (typically margo ventralis), modally subtriangular and comparatively proximal, i.e., margo proximalis bordering sulcus ligamentosus transversus;

c. moderately to very deep, margines distinctly elliptical, typically opposite in entirety crista deltopectoralis or proximal thereto;

d. very deep and delimited dorsally and ventrally by long, distinct cristulae, fossa elongate and triangular, joining perpendicularly with sulcus ligamentosa transversus;

x. noncomparable (ratites).

Note.—In at least some ratites (e.g., *Struthio*, *Rhea*), obsolescence of impressio, related to distal extent of m. coracobrachialis cranialis, occurs.

See: Archey (1941: figs. 52–53); S. L. Olson and Feduccia (1980b: 20); Ericson (1997: table 1, character 57); Chu (1998: appendix 1, characters 91–93); J. A. Clarke (2004: fig. 50); G. Mayr and Ericson (2004: appendix I, character 49).

1434. Extremitas proximalis humeri, facies (palmaris) cranialis, impressio m. coracobrachialis cranialis (**emended term**), deeply ovate and enclosed ostia pneumatici marginales, status impressiorum et poricium (**unordered**):

a. absent, both forma et pori;

b. present, pori absent;

c. present, pori present;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—See: Archey (1941: figs. 52–53); J. A. Clarke (2004: fig. 50).

Corpus humeri

1435. Corpus humeri (lateral perspective), forma generalis:

a. sigmoidal; **b.** linear.

Note.—See: Holtz (1994a: appendix 1, characters 52 [sigmoidality] and 72 [linearity]); Rauhut (2003: character 143).

1436. Corpus humeri, departures from bilinearity by marginalis with respect to both plana dorsoventralis et craniocaudalis, forma (**unordered**):

a. bi-linear—linear both craniocaudad et dorsoventrad;

b. dorsoventrally sigmoidal and craniocaudally linear—principally effected by ventral prominence of extremitas proximalis and dorsal prominence of extremitas distalis;

c. bi-sigmoidal—sigmoidal in both plana, craniocaudal component with extremitas proximalis caudad and extremitas distalis craniad;

d. dorsoventrally linear and craniocaudally sigmoid—principally effected by caudal prominence of extremitas proximalis and cranial prominence of extremitas distalis;

e. dorsoventrally curvilinear, craniocaudally linear—margo dorsalis linear and margo ventralis concave;

f. dorsoventrally curvilinear, craniocaudally sigmoidal—margo dorsalis linear and margo ventralis concave;

g. moderately curvilinear craniocaudally—facies caudalis concave et facies cranialis convex;

h. moderately curvilinear craniocaudally—facies caudalis convex et facies cranialis concave;

i. strongly curvilinear or semilunate craniocaudally—facies caudalis concave et facies cranialis convex;

j. curvilinear dorsoventrally, sigmoid craniocaudally—margo dorsalis convex;

x. noncomparable (*Aepyornis*, Dinornithiformes, Sphenisciformes).

Note.—"Doubly sigmoid" state problematic to differentiate from bi-linear in cases disproportionately affected by extremitates distalis et proximalis. Apparent "torsion" of corpus treated separately. See: Houde (1988: table 27, character 33); Pérez-Moreno et al. (1994: legend for fig. 3, character 15); Holtz (1994a: appendix 1, characters 52 [sigmoidality] and 72 [linearity]); J. D. Harris (1998: appendix 2, character 72); Livezey (1998b: appendix A, character 217); Azuma and Currie (2000: appendix 1, character 59); Currie and Carpenter (2000: appendix 1, character 93); Holtz (2000 [1998]: appendix I, character 235), limited to sigmoidality; G. Mayr (2002a: legend fig. 9, node 1, character 1) [angularity]; G. Mayr (2003a: appendix I, character 30).

1437. Corpus humeri, extremitates proximalis et distalis, mutual dorsoventral (mediolateral) expansion relative to diameter at midpoint of corpus humeri, status:

a. small, maximal breadth of both extremitates less than 150% of diameter of corpus at midpoint;

b. large, maximal breadth of both extremitates exceeding 150% of diameter of corpus at midpoint;

x. noncomparable (Dinornithiformes).

Note.—See: Holtz (2000 [1998]: appendix I, character 240); Holtz (2000 [1998]: appendix I, character 240), in a general descriptor of probably minimal utility.

1438. Corpus humeri, apparent torsion of corpus about axis majoris (i.e., axis proximodistalis, in which extremitates are of maximal width within different, mutually oblique plana), status:

a. absent, extremitates proximalis et distalis coplanar;

b. present; **x.** noncomparable (ratites).

Note.—See: Pérez-Moreno et al. (1993); Chiappe and Calvo (1994: appendix I, character 35); Chiappe (1995b: character 35); Sanz et al. (1995, 1997: character 33); Chiappe (1996b: character 32); Chiappe et al. (1996: appendix 1, character 31); Novas (1996: appendix, character 71); Novas (1997: appendix, character 72); Novas and Puerta (1997), see identical characters in Novas (1997); Chiappe et al. (1998: character 41); Ji et al. (1998: supplement, character 41); Forster et al. (1998: supplement, character 67); Chatterjee (1999: appendix II, character 51); Holtz (2000 [1998]: appendix I, character 234), regarding apparent "torsion" of element about axis proximodistalis (majoris); Chiappe (2001a: appendix 1, character 80); Chiappe (2002: appendix 20.2, character 80).

1439. Corpus humeri, bilateral compression or departure from essentially elliptical form (planum transversus), status (**unordered**):

a. absent, elliptical, lacking notable flattening or bifacial compression throughout;

b. present, subelliptical with significant flattening or bifacial compression evident (typically craniocaudal) in a majority of the entirety of corpus;

c. present, strongly craniocaudally compressed, virtually laminate throughout;

x. noncomparable (Dinornithiformes).

Note.—See: Spring (1971); Bledsoe (1988: appendix, character 21), discounted by K. Lee et al. (1997: appendix 2) for ratites. Axis majoris of elliptical cross sections essentially within planum dorsoventrale; significant number of taxa with minor, unilateral flattening of facies cranialis of corpus (e.g., some Pelecaniformes and Columbiformes) coded herein as "elliptical."

1440. Corpus humeri, facies caudalis, margo caudalis, angulus caudalis corporis (**new term**), proximodistal extent and proximal orientation, status et forma (**unordered**):

a. absent essentially throughout;

b. present, distinctly angular and prominent throughout variably extensive portion of corpus humeri, proximally directed toward caput humeri;

c. present, variably distinct distally but proximally directed toward tuberculum ventrale;

d. present, distinct throughout majority of corpus humeri, proximally directed toward incisura capitis;

e. present, distinctly angular and prominent throughout variably extensive portion of corpus humeri, proximally directed toward tuberculum dorsale;

x. noncomparable (ratites, Dromornithidae, Alcidae, Strigidae).

Note.—Angulus in ratites not linea muscularis; ordering provisional, broadly based on (*i*) retention and (*ii*) ventral-dorsal orientation. See: Woolfenden (1961: 6–21); Livezey (1986: appendix 1, character 22), in reference to "capital shaft ridge"; Livezey (1989: table 1, character 22); Livezey (1996a: appendix 1, character 51); Livezey (1996b: appendix 1, character 25); Ericson (1997: table 2, character 33); Livezey (1997b: appendix 1, character 9); Livezey (1998b: appendix A, character 215).

1441. Corpus humeri, margo ventralis, linea insertio m. latissimi dorsi (especially or solely pars caudalis), forma (**ordered**):

a. linea aut impressio linearis, abbreviate;

b. eminentia aut sulcus, extensive;

c. cristula, extensive, elevated;

x. noncomparable (Dinornithiformes) or structural peculiarities (*Aepyornis*, Sphenisciformes).

Note.—See: Archey (1941: figs. 52–53); McGowan (1982: fig. 5); Livezey (1986: appendix 1, character 29); Livezey (1995c: appendix II, character 14); J. A. Clarke (2004: fig. 50).

1442. Corpus humeri, margo dorsalis, sulcus nervi radialis, status:

a. absent or indiscernable; **b.** present;

x. noncomparable (Dinornithiformes, *Aptornis*).

Note.—See: Baumel and Witmer (1993: annotation 191), who described it as "distinct" and occuring "only rarely," citing presence in "*Casuarius*, hummingbirds and swifts (Apodiformes)."

Extremitas distalis humeri

1443. Extremitas distalis humeri, pronounced and generalized craniocaudal compression, producing sublaminar form, status:

a. absent; **b.** present;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—See: Lowe (1939a) and Livezey (1989), regarding Sphenisciformes of Miocene; Chiappe and Calvo (1994: appendix II, character 9), listed as synapomorphy of Enantiornithes; Chiappe et al. (1998: character 51); Chiappe (2001a: appendix 1, character 93); Norell and Clarke (2001: appendix I, character 124), descriptive of craniocaudal compression and dorsoventral expansion of extremitas distalis humeri; Chiappe (2002: appendix 20.2, character 93); Chiappe and Walker (2002: appendix 11.1, character 20); J. A. Clarke (2002: appendix I, character 123); J. A. Clarke and Norell (2002: appendix 2, character 123); Zhou and Zhang (2002: appendix III, character 124); J. A. Clarke (2004: appendix 1, character 123); Ji et al. (2005: supplement, part I, character 100); Ji et al. (2005: supplement, part I, character 124).

1444. Extremitas distalis humeri, margo distalis humeri, principal orientation relative to axis majoris corporis, forma:

a. approximately perpendicular;

b. angulus strongly ventrad, significantly distad to pars dorsodistalis (**new term**), sometimes synonymous with prominence of processus flexorius.

Note.—See: Norell and Clarke (2001: appendix I, character 123), treated similarly by J. A. Clarke (2002: appendix I, character 122), J. A. Clarke and Norell (2002: appendix 2, character 122), and J. A. Clarke (2004: appendix 1, character 122); Zhou and Zhang (2002: appendix III, character 123); J. A. Clarke (2004: appendix 1, character 123); Ji et al. (2005: supplement, part I, character 123).

1445. Extremitas distalis humeri, condylus dorsalis humeri, axis majoris condylae relative to axis majoris of corpus humeri, typus:

a. subparallel, angulus at most weakly proximoventral;

b. subtransverse, angulus including strong craniocaudal component;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—See: Chiappe and Calvo (1994: appendix II, character 10); Sereno (2000: table 4, character 4), listed as synapomorphy of Enantiornithes; Elzanowski (1995: character E2); Norell and Clarke (2001: appendix I, character 121), treated similarly by J. A. Clarke (2002: appendix I, character 120), J. A. Clarke and Norell (2002: appendix 2, character 120), and J. A. Clarke (2004: appendix 1, character 120); Zhou and Zhang (2002: appendix III, character 121); Ji et al. (2005: supplement, part I, character 121).

1446. Extremitas distalis humeri, facies cranialis, condylus dorsalis humeri, apex termini condylae dorsalis, forma (**unordered**):

a. rounded, sessile upon facies cranialis humeri, and gradually merging with facies cranialis humeri;

b. flattened or subrectangular;

c. cornuate, cranially elevated with apex undercut, and/or distinctly pointed;

x. noncomparable (Dinornithiformes, Sphenisciformes).

Note.—See: Hughes (2000: appendix 2, character 114); Sereno (2000: table 4, character 4); Dyke and Gulas (2002: appendix 1, character 20); Dyke et al. (2003: appendix 1, character 55), employed again by Dyke (2003: table 1).

1447. Extremitas distalis humeri, facies cranialis, condylus dorsalis humeri, proximal extent relative to margo distalis fossae m. brachialis, (**ordered**):

a. condylus distal to fossa, and typically separated from margo distalis fossae m. brachialis by smooth area of bone from latter;

b. condylus (margo proximalis) typically extending at least proximad to margo distalis fossae m. brachialis;

c. condylus markedly proximal to fossa, including extremitates proximalis condylorum dorsalis et ventralis;

x. noncomparable (ratites, *Aptornis*, Sphenisciformes).

Note.—See: Zusi and Bentz (1984: fig. 15); Livezey (1986: appendix 1, character 35); Siegel-Causey (1988: character 83); Livezey (1995c: appendix II, character 18); G. Mayr (2004d: appendix I, character 16), treating relative medial position of fossa; G. Mayr (2005a: appendix 1, character 16).

1448. Extremitas distalis humeri, condylus ventralis (including "ulnar condyle" or "ulnar facet"), status:
a. absent or small;
b. present, often expanded;
x. noncomparable (Dinornithiformes).
Note.—See: Gauthier (1986: 14, unindexed synapomorphy of Aves), in reference to orientation of "ulnar crest"; Russell and Dong (1994a [1993a]: table 2, character 36), regarding the prominence of "ulnar facet" of humerus with respect to entepicondyle; Sereno (1994 [1993]: appendix, character 5); Xu et al. (1999a: character 59); Azuma and Currie (2000: appendix 1, character 57); Holtz (2000 [1998]: appendix I, character 244).

1449. Extremitas distalis humeri, condylae distales, numerus modalis, i.e., retention of condylus dorsalis and progressive loss of condylus ventralis, status:
a. present, both condyli dorsalis et ventralis humeri;
b. absent, condylus dorsalis humeri or (most probably) condylus ventralis humeri obsolete or lost;
x. noncomparable (Dinornithiformes).
Note.—See: Chiappe et al. (1996: appendix 1, character 79); Novas (1996: appendix, character 9, part); Novas (1997: appendix, character 9, part); Novas and Puerta (1997), identically by Novas (1997); Chiappe et al. (1998: character 46); Ji et al. (1998: supplement, character 46); Sereno et al. (1998: footnote 22, character 30); Chatterjee (1999: appendix II, character 54, in part), in reference to "carinate" aspect of distal condyles; Chiappe (2001a: appendix 1, character 90); Chiappe (2002: appendix 20.2, character 90).

1450. Extremitas distalis humeri, asymmetric "carinate" condylus dorsalis et condylus ventralis (including a strongly projecting condylus ventralis and well-defined epicondylus ventralis), status:
a. absent; **b.** present;
x. noncomparable (Dromornithidae).
Note.—See: Cracraft (1986: appendix, character 68); Chatterjee (1995: character 11, part); Azuma and Currie (2000: appendix 1, character 56), in which apomorphy was defined as extremitas distalis being 150% of diameter of corpus humeri.

1451. Extremitas distalis humeri, facies cranialis, condyli dorsalis et ventralis humeri, forma generalis (**unordered**):
a. suborbiculate, bulbous;
b. lorate ("straplike");
c. lamellate or scapulate ("bladelike");
x. noncomparable (Aepyornithiformes, Dinornithiformes).
Note.—See: Lowe (1939a), regarding Miocene Sphenisciformes; Stephan (1979); Cracraft (1988: series XV, character 6); Norell and Clarke (2001: appendix I, character 122); J. A. Clarke (2002: appendix I, character 121); J. A. Clarke and Norell (2002: appendix 2, character 121); Zhou and Zhang (2002: appendix III, character 122); J. A. Clarke (2004: appendix 1, character 121); Ji et al. (2005: supplement, part I, character 122).

1452. Extremitas distalis humeri, facies cranialis, condylae dorsalis et ventralis humeri, aspectus principalis corporis:
a. distalis; **b.** cranialis;
x. noncomparable (Dinornithiformes).
Note.—See: Cracraft (1988: series III, character 9); Perle et al. (1993); Chiappe and Calvo (1994: appendix I, character 40); Chiappe (1995b: character 40); Sanz et al. (1995, 1997: character 38); Chiappe (1996b: character 37); Chiappe et al. (1996: appendix 1, character 36); Chiappe et al. (1998: character 45); Forster et al. (1998: supplement, character 54); Ji et al. (1998: supplement, character 45); Xu et al. (1999a: character 56); Xu et al. (1999b: character 43); Holtz (2000 [1998]: appendix I, character 242), citing Novas (1996); Xu et al. (2000: supplement, character 30), with respect to "distal condyles . . . located mainly on the distal or cranial aspect"; Chiappe (2001a: appendix 1, character 89); Norell and Clarke (2001: appendix I, character 120), treated similarly by J. A. Clarke (2002: appendix I, character 119), J. A. Clarke and Norell (2002: appendix 2, character 119), and J. A. Clarke (2004: appendix 1, character 119); Chiappe (2002: appendix 20.2, character 89); Maryanska et al. (2002: appendix 1, character 131); Zhou and Zhang (2002: appendix III, character 120). See also Livezey (1998b: appendix A, character 212), regarding the relative prominence of key proximal features (e.g., crista bicipitalis, tuberculum ventrale) and distal features (e.g., processus flexorius) relative to corpus humeri, facies ventralis; Ji et al. (2005: supplement, part I, character 120).

1453. Extremitas distalis humeri, facies cranialis, condylus ventralis, length of axis majoris condyli relative to that of condylus dorsalis:
a. former less than latter;
b. former subequal to or greater than latter;
x. noncomparable (Dinornithiformes).
Note.—See: Norell and Clarke (2001: appendix I, character 126); J. A. Clarke (2002: appendix I, character 125); J. A. Clarke and Norell (2002: appendix 2, character 125); Zhou and Zhang (2002: appendix III, character 126); Dyke et al. (2003: appendix 1, character 59), employed again by Dyke (2003: table 1); J. A. Clarke (2004: appendix 1, character 125); Ji et al. (2005: supplement, part I, character 126).

1454. Extremitas distalis humeri, facies cranialis, incisura intercondylaris, forma:
a. shallow and wide; **b.** deep and narrow;
x. noncomparable (Dinornithiformes).

Note.—See: Novas (1996: appendix, character 9, part); Novas (1997: appendix, character 9, part); Novas and Puerta (1997), see identical characters in Novas (1997); Xu et al. (1999a: character 58), with respect to "flexor groove between ulnar and radial condyles."

1455. Extremitas distalis humeri, facies cranialis, incisura intercondylaris, lamina mediana sulci (**new term**) serving as boundary for sulcus ligamenti m. scapulotriceps, status et magnitudo (**ordered**):

a. absent; **b.** present, small;
c. present, moderate; **d.** present, large;
x. noncomparable (Dinornithiformes).

Note.—See: Zusi and Bentz (1984: fig. 15).

1456. Extremitas distalis humeri, facies cranialis, fossa m. brachialis, status et forma *sensu* depth (**ordered**):

a. absent;

b. present, rudimentary or vestigial;

c. present, moderately limited;

d. present, deep, typically including recessus ventralis fossae;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—See: Cracraft (1986: appendix, character 71); Bledsoe (1988: appendix, character 17), for ratites; Cracraft (1988: series III, character 12); Siegel-Causey (1988: character 82); Holdaway (1991: appendix 5.1, character 101); Chatterjee (1995: character 11, part); Chatterjee (1999: appendix II, character 57); Chiappe (2001a: appendix 1, character 91); J. A. Clarke and Chiappe (2001: character 9); Norell and Clarke (2001: appendix I, character 125), treated similarly by J. A. Clarke (2002: appendix I, character 124), J. A. Clarke and Norell (2002: appendix 2, character 124), and J. A. Clarke (2004: appendix 1, character 124); Chiappe (2002: appendix 20.2, character 91); G. Mayr (2003c: appendix, character 11); Vickers-Rich et al. (2002), concerning *Avimimus*; Zhou and Zhang (2002: appendix III, character 125); G. Mayr (2003b: appendix I, character 11), regarding Trogonidae; G. Mayr and Clarke (2003: appendix A, characters 79–80); G. Mayr et al. (2003: appendix 1, character 37); G. Mayr (2004d: appendix I, character 16); Dyke and van Tuinen (2004: appendix 1, characters 55–56); G. Mayr (2005a: appendix 1, character 16); G. Mayr 2005b: appendix A, character 26); Ji et al. (2005: supplement, part I, character 125).

1457. Extremitas distalis humeri, facies cranialis, fossa m. brachialis, proximodistal elongation, status:

a. absent, fossa of typical formation, variably subelliptical or subtriangular;

b. present, fossa elongate, approximating isosceles triangle with basis distalis much shorter than margines dorsalis et ventralis;

x. noncomparable (Dinornithiformes).

1458. Extremitas distalis humeri, facies cranialis, fossa m. brachialis, aspectus of elongate rhombus, obliquely oriented proximodistad from margo dorsalis to margo ventralis, status:

a. absent; **b.** present;
x. noncomparable (Dinornithiformes).

1459. Extremitas distalis humeri, facies cranialis, fossa m. brachialis, pori, foramina, aut fenestrae pneumaticae, status (**ordered**):

a. absent;

b. present, but limited to pori aut foramina in margo distalis fossae;

c. present, involving comparatively numerous and large fenestrae;

x. noncomparable (Dinornithiformes, Sphenisciformes).

Note.—See: Lowe (1939a) and Livezey (1989), regarding Miocene Sphenisciformes.

1460. Extremitas distalis humeri, fossa m. brachialis (cranial perspective), dorsoventral position relative to axis medianus of corpus humeri (**ordered**):

a. dorsal; **b.** medial; **c.** ventral;
x. noncomparable by absence of fossa (*Struthio*, *Rhea*, *Apteryx*).

Note.—See: Hughes (2000: appendix 2, character 112), after Seibel (1988: character HU 47).

1461. Extremitas distalis humeri, epicondylus dorsalis (ectepicondylus), status et forma *sensu* promimentia dorsalis (**ordered**):

a. absent or virtually coplanar with facies dorsalis of extremitas dorsalis humeri, vertically intersecting curva terminalis condyli at vertex dorsodistalis of element;

b. present, moderately prominent, latter approximating one-half the transverse width of condylus ventralis;

c. present, prominent, latter distinctly exceeding one-half the transverse width of condylus ventralis, in some approaching equality;

x. noncomparable, ossa alae absent (Dinornithiformes).

Note.—"Dorsal prominence" was estimated by chord between margines dorsales of corpus humeri et condylus dorsalis, *exclusive* of variably adjoined, proximal tuberculum supracondylare dorsale. See: Yudin (1957: fig. 5); Strauch (1978: character 45), reanalyzed by Björklund (1994: appendix) and Chu (1995); Bledsoe (1988: appendix, character 19); Siegel-Causey (1988: character 79); Ericson (1997: table 1, character 59); K. Lee et al. (1997: appendix 1, character 18); Sereno (2000: table 4, character 5), with respect to purported synapomorphy of "humeral epicondylar width very broad" for Enantiornithes. Also related are characterizations of caudal ("anconal") prominence; Livezey (1986: appendix 1, character 33); Livezey (1989: table 1, character 33);

Livezey (1991: appendix 1, character 152); Livezey (1996c: character 5); Livezey (1997b: appendix 1, character 10); Maryanska et al. (2002: appendix 1, character 133).

1462. Extremitas distalis humeri, epicondylus dorsalis (ectepicondylus), foramen epicondylae dorsale (**new term**), status:

a. present; **b.** absent.

Note.—See: Benton (1990a).

1463. Extremitas distalis humeri et corpus humeri, facies cranialis, tuberculum (fossa) origii m. pronator superficialis (**new term**), status:

a. absent or indiscernable; **b.** present.

Note.—Identification of musculus associated with feature provisional. See: G. Mayr (2004d: fig. 4), in reference to “tubercle above condylus dorsalis.”

1464. Extremitas distalis humeri et corpus humeri, epicondylus ventralis (entepicondylus), ancora origii m. pronator profundus (**new term**), forma et situs:

a. fovea on epicondylus ventralis;

b. facet on ancora m. pronator profundus;

x. noncomparable (Dinornithiformes).

Note.—See: McGowan (1982: fig. 7); Zusi and Bentz (1984: fig. 15); G. Mayr (2003c: appendix, character 14); G. Mayr (2005b: appendix A, character 26).

1465. Extremitas distalis humeri et corpus humeri, epicondylus dorsalis (ectepicondylus), ancora origii m. deltoideus pars propatagialis (**new term**), pars cranialis, situs et forma (**ordered**):

a. distal, a facet on epicondylus dorsalis;

b. subdistal, on cristula on margo dorsalis corporis shared with ancorae origii m. extensor digitorum communis;

c. distinctly proximal, on eminentia on margo dorsalis corporis distinct from more-distal ancorae origii m. extensor digitorum communis;

x. noncomparable (Dinornithiformes).

Note.—See: Zusi and Bentz (1984: fig. 15); G. Mayr (2003c: appendix, character 15); G. Mayr (2005b: appendix A, character 30).

1466. Extremitas distalis humeri et corpus humeri, epicondylus dorsalis (ectepicondylus), ancora origii m. extensor digitorum communis (**new term**), situs et forma (**ordered**):

a. distal, a fovea on epicondylus dorsalis;

b. subdistal, a tuberculum proximal to epicondylus dorsalis;

c. subproximal, an elongate impressio or jugum on margo dorsalis corporis;

x. noncomparable (Dinornithiformes).

Note.—See: Zusi and Bentz (1984: fig. 15); G. Mayr (2003c: appendix, character 9), with which tuberculum m. extensor carpi radialis may be confounded; G. Mayr (2005b: appendix A, character 24).

1467. Extremitas distalis humeri, tuberculum (processus) supracondylaris dorsalis (as distinct from epicondylus dorsalis), status et forma (**ordered**):

a. present, very prominent (exceeding dorsad extremitas distalis), subrectangular processus oriented dorsad;

b. present, prominent (exceeding dorsad extremitas distalis), subtriangular processus oriented dorsoproximad;

c. present, moderately large (approximating dorsad extremitas distalis), tuberculum;

d. present, small (exceeded dorsad by extremitas distalis), jugum or torus;

e. absent;

x. noncomparable (Dinornithiformes).

Note.—In some cases, partial union with epicondylus dorsalis obscured forma (e.g., *Ptilonorhynchus*). “Absent” refers to sites of attachment (e.g., those of mm. extensor carpi radialis et pronator superficialis) that are discernable but limited to small impressiones of margo dorsalis humeri.

See: Ericson (1997: table 1, character 59); Chu (1998: appendix 1, character 95); G. Mayr (2003a: appendix I, character 34); G. Mayr (2003c: appendix, characters 9 and 14); J. A. Clarke (2004: fig. 50); G. Mayr (2004a: appendix 1, character 42); G. Mayr (2004b: appendix 1, character 40); G. Mayr and Ericson (2004: appendix I, character 54); G. Mayr (2005b: appendix A, character 29).

1468. Extremitas distalis humeri, tuberculum (processus) supracondylaris dorsalis et epicondylus dorsalis, forma combining exceptional dorsal extension and robust conjoining of two structural components, status:

a. absent; **b.** present;

x. noncomparable (Dinornithiformes).

1469. Extremitas distalis humeri, tuberculum (processus) supracondylaris dorsalis relative to (epi)condylus dorsalis, situs proximodistalis:

a. variably conjoined; **b.** distinctly proximal;

x. noncomparable (Dinornithiformes).

Note.—See: Cracraft (1988: series XV, character 3), with respect to variable union of epicondylus dorsalis with tuberculum supracondylare dorsale; Sereno (2000: table 4, character 5); Livezey (1998b: appendix A, character 221).

1470. Extremitas distalis humeri, tuberculum (processus) supracondylaris dorsalis, ancora origii m. extensor (meta)carpi radialis (or nonavian homologue), status, situs, et forma (**unordered**):

a. absent or indiscernable;

b. distal, united, typically as impressio aut fovea on epicondylus dorsalis;

c. distal, separated by sulcus, a distinct tuberculum of processus supracondylaris dorsalis;

d. proximal, on conspicuous, subrectangular processus on margo dorsalis corporis closely distal to crista deltopectoralis;

x. noncomparable (Dinornithiformes).

Note.—See: Zusi and Bentz (1984: fig. 15); Cracraft (1988: series XV, character 4); Livezey (1998b: appendix A, character 220); G. Mayr (2003c: appendix, character 8); J. A. Clarke and Chiappe (2001: characters 10–11); Dyke (2001a: appendix 1, characters 1–2), but see J. A. Clarke (2002: appendix I, character 126); J. A. Clarke and Norell (2002: appendix 2, character 126); J. A. Clarke (2004: appendix 1, character 126); G. Mayr (2005b: appendix A, character 23).

1471. Extremitas distalis humeri, tuberculum (processus) supracondylaris dorsalis, ancora origii m. pronator superficialis (or nonavian homologue), comparative situs et forma:

a. distal, on epicondylus dorsalis;

b. proximal, on tuberculum or facet on margo ventralis corporis;

x. noncomparable (Dinornithiformes).

Note.—See: Zusi and Bentz (1984: fig. 15); G. Mayr (2003c: appendix, character 14); G. Mayr (2005b: appendix A, character 29).

1472. Extremitas distalis humeri, epicondylus ventralis (entepicondylus), forma:

a. sessile boss or torus;

b. variably elevated cristula or jugum;

x. noncomparable (Dinornithiformes).

Note.—Assessments intended to exclude effects of tuberculum supracondylare ventrale et processus flexorius, former especially challenging and state "a" variable; also affects apparent depth of fossa olecrani. See: Lowe (1939a), regarding Miocene Sphenisciformes; Cracraft (1985: character 31); Cracraft (1988: series XV, character 5); Novas (1996: appendix, character P5), with respect to entepicondyle and presence of "longitudinal prominence on the anteromedial margin of distal humerus"; Livezey (1998b: appendix A, character 218).

1473. Extremitas distalis humeri, epicondylus ventralis (entepicondylus), impressio origii m. entepicondylo-ulnaris (or nonavian homologue), status:

a. absent or indistinct;

b. present, prominent with cranial and caudal delimiting depressiones;

x. noncomparable (ratites).

Note.—See: Ballmann (1969a: fig. 7c); Sereno (1994 [1993]: appendix, character 4); Makovicky and Sues (1998: appendix 1, character 66); Holtz (2000 [1998]: appendix I, character 243).

1474. Extremitas distalis humeri, facies ventralis et/aut epicondylus dorsalis (entepicondylus), impressio m. extensor digitorum communis (or nonavian homologue), status et situs proximodistalis (**ordered**):

a. absent or not discernable;

b. distal, on epicondylus proprius;

c. proximal, encompassing relatively elongate area on margo ventralis between tuberculum m. extensor carpi radialis et epicondylus;

x. noncomparable (Dinornithiformes).

Note.—See: Ballmann (1969a: fig. 7c).

1475. Extremitas distalis humeri, facies caudalis, epicondylus ventralis (entepicondylus), situs proximodistalis relative to those of epicondylus dorsalis (ectepicondylus) et condylus ventralis, forma:

a. former proximal to latter;

b. former approximately equal or distal to latter;

x. noncomparable (ratites).

1476. Extremitas distalis humeri, processus flexorius (caudal perspective), status et forma (**ordered**):

a. absent or indiscernable as distinct processus, although homologous situs typically indicated by impressio (angulus) tendinis origii (fossa muscularis) m. flexor (meta)carpi ulnaris;

b. present, limited to proximally restricted jugum;

c. present, moderately prominent, equaling complement of extremitas distalis distocaudally;

d. present, conspicuous, exceeding complement of extremitas distalis distocaudally;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—See: Livezey (1998b: appendix A, character 219); Hughes (2000: appendix 2, character 113), after Seibel (1988: character HU 14); Dyke and Gulas (2002: appendix 1, character 22); Dyke et al. (2003: appendix 1, character 57); G. Mayr et al. (2003: appendix 1, character 38); G. Mayr and Ericson (2004: appendix I, character 55).

1477. Extremitas distalis humeri, processus flexorius, conspicuously elongate-triangular, caudal inflation, status (**ordered**):

a. absent; **b.** present, great;

c. present, exceptional;

x. noncomparable (Dinornithiformes).

1478. Extremitas distalis humeri, processus flexorius, condylus ventralis et condylus dorsalis, ventral displacement and craniocaudal compression into multilaminar structure, status:

a. absent; **b.** present;

x. noncomparable (Dinornithiformes).

Note.—See: Lowe (1939a), regarding Miocene Sphenisciformes; S. L. Olson and Hasegawa (1979); Stephan (1979); S. L. Olson (1980); Schreiweis (1982); G. Mayr (2004b: appendix 1, character 37).

1479. Extremitas distalis humeri, processus flexorius, forma combining exceptional distal extension, ventrocaudal torsion, and caudal lamination, status:

a. absent; **b.** present;

x. noncomparable (Dinornithiformes).

Note.—Basal passeriforms variably intermediate.

1480. Extremitas distalis humeri, processus flexorius, impressio origii m. flexor (meta)carpi ulnaris (or nonavian homologue), status:

a. absent; **b.** present;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—Apomorphic state presents significant variation in position of the impressio or fovea upon processus flexorius. See: Ballmann (1969a: fig. 7c); Butendieck (1980: fig. 36), Butendieck and Wissdorf (1981), Butendieck et al. (1981), termed "fossa muscularis"; Sereno (1994 [1993]: appendix, character 3), in reference to "circular pit on distal margin of humeral ectepicondyle"; Livezey (1986: appendix 1, character 34); Livezey (1995c: appendix II, character 17); Ericson (1997: table 1, character 60 and fig. 23), evidently confusing single impressio origii m. flexor digitorum communis (possibly m. pronator profundus aut m. entepicondylo-ulnaris) with the averred second impressio origii m. flexor carpi ulnaris, whereas the latter is limited to a single ancora in most or all Neornithes (Ballmann 1969a: fig. 7c).

1481. Extremitas distalis humeri, tuberculum supracondylare ventrale, status et forma (**unordered**):

a. absent or indiscernible;

b. present, sessile, comparatively truncate aspectus ancorae or weakly developed, proximally truncate eminentia, depressed and subparallel to facies cranialis of corpus humeri;

c. present, (sub)sessile, comparatively elongate (typically distinctly defined, ovate) aspectus ancorae, depressed and subparallel to facies cranialis of corpus humeri;

d. present, well-developed tuberculum, distal fovea angled distally and elevated, basal structure proximally extensive;

e. present, prominent processus distinctly proximal to epicondylus ventralis;

f. present, trenchant tuberculum well proximal to epicondylus ventralis;

x. noncomparable (Dinornithiformes, Sphenisciformes).

Note.—See: Lowe (1939a), regarding Miocene Sphenisciformes; Livezey (1986: appendix 1, character 26); Livezey (1989: table 1, character 26), Livezey (1995a: appendix 1, character 3); Livezey (1995c: appendix II, character 12); Livezey (1996b: appendix 1, character 26), in reference to "attachment for anterior articular ligament"; G. Mayr (2003c: appendix, character 16); G. Mayr (2005b: appendix A, character 31).

1482. Extremitas distalis humeri, facies caudalis, fossa olecrani, status et forma (**ordered**):

a. absent or obsolete, rudimentum aut vestigium;

b. present, limited depth and proximodistal width;

c. present, markedly deep, proximodistally broad, and (typically) sharply delimited;

d. present, extremely deep cavitas;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—See: Lowe (1939a), regarding Miocene Sphenisciformes; Bledsoe (1988: appendix, character 23); Cracraft (1988: series XV, character 5); Kurochkin (1995b: table 1, character 12); Chiappe et al. (1998: character 47); Ji et al. (1998: supplement, character 47); Chiappe (2001a: appendix 1, character 92); Chiappe (2002: appendix 20.2, character 92).

1483. Extremitas distalis humeri, facies caudalis, fossa olecrani, proximal extent and prominence of sulcus inter-epicondylaris caudalis (**new term**), status:

a. absent or obsolete, sulcus essentially minimal transition from fossa olecrani to margo caudalis humeri;

b. present and prominent, sulcus distinctly emarginated, extending significantly proximad to fossa olecrani et termina proximales epicondylarum;

x. noncomparable (Dinornithiformes).

Note.—The variably deep and broad sulcus between epicondyli humeralium and including (*sensu lato*) sulcus m. humerotricipitis—not individuated nomenclaturally by Howard (1929), Butendieck (1980), Butendieck and Wissdorf (1981), Butendieck et al. (1981), or Baumel and Witmer (1993). See: G. Mayr and Clarke (2003: appendix A, character 81), pertaining principally to sulcus scapulotricipitalis; Dyke and van Tuinen (2004: appendix 1, character 57).

1484. Extremitas distalis humeri, facies caudalis, fossa olecrani (and cranially delimiting condylus ventralis), situs dorsoventralis relative to midpoint of concavitas distalis of sulcus inter-epicondylaris caudalis (**ordered**):

a. (ventro)medial—opposite (or only slightly ventral to) midpoint of concavitas, typically centered between sulci mm. humerotricipitis ventrad et scapulotricipitis dorsad;

b. medioventral—opposite ventral half of concavitas, pars ventralis of concavitas opposite terminus of sulcus m. humerotricipitis;

c. ventral—opposite margo ventralis of concavitas, pars medianus of concavitas opposite terminus of sulcus m. humerotricipitis, concavitas approximately opposite processus flexorius;

x. noncomparable by uniquely derived or absent elements (Aepyornithiformes, Dinornithiformes, Sphenisciformes) or absence of fossa (other ratites).

1485. Extremitas distalis humeri, facies caudalis, fossa olecrani, fossa aut pori pneumatica[ici], status:
a. absent; **b.** present;
x. noncomparable (Aepyornithiformes, Dinornithiformes).
Note.—*Sula* possessed of exceptionally deep fossa olecrani.

1486. Extremitas distalis humeri, facies caudalis, fossa olecrani, forma in which fossa is broad, deep, and cranially unobstructed by condylus ventralis, status:
a. absent; **b.** present;
x. noncomparable (Aepyornithiformes, Dinornithiformes).
Note.—See: Zusi and Bentz (1984: fig. 15).

1487. Extremitas distalis humeri, facies caudalis, sulcus tendinis m. humerotricipitalis (*sensu stricto*), status et forma (**ordered**):
a. absent; **b.** rudimentary or vestigial;
c. present;
x. noncomparable (Dinornithiformes, Sphenisciformes).
Note.—See: Houde (1988: table 27, character 36, part); J. A. Clarke and Chiappe (2001: character 18); Norell and Clarke (2001: appendix I, character 127), treated similarly by J. A. Clarke (2002: appendix I, character 127), J. A. Clarke and Norell (2002: appendix 2, character 127), and J. A. Clarke (2004: appendix 1, character 127); Zhou and Zhang (2002: appendix III, character 127); Ji et al. (2005: supplement, part I, character 127).

1488. Extremitas distalis humeri, facies caudalis, sulcus tendinis m. scapulotricipitalis, status et forma (**ordered**):
a. absent;
b. present, weakly defined, typically comparatively broad, shallow, and truncate;
c. present, conspicuously defined, typically comparatively narrow, deep, and elongate;
x. noncomparable (Aepyornithiformes, Dinornithiformes, Sphenisciformes).
Note.—See: Houde (1988: table 27, character 36, part); Chu (1998: appendix 1, character 96); Livezey (1998b: appendix A, character 222); Norell and Clarke (2001: appendix I, character 128); J. A. Clarke (2002: appendix I, character 128); J. A. Clarke and Norell (2002: appendix 2, character 128); Zhou and Zhang (2002: appendix III, character 128); J. A. Clarke (2004: appendix 1, character 128); Ji et al. (2005: supplement, part I, character 128).

Ulna

1489. Os ulna, status et forma generalis (**ordered**):
a. present, of typical prominence and structural detail;
b. present, moderate in relative length but retaining majority of structural details;
c. present, truncate in relative length and many structural details, especially of extremitates proximalis et distalis or simplified to subcylindrical vestigium in which extremitas distalis is synostotic with that of radius and ossa proximalia carpi;
d. present, vestigium broadly synostotic with other ossa antebrachii et manus or reduced to mere angularity;
e. absent.
Note.—See: Friant (1945b, 1959).

1490. Os ulna, corpus ulnaris, virtually linear form coincident with extreme relative elongation, status:
a. absent; **b.** present.
Note.—See: Bourdon (2006: supplement, character 63).

Extremitas proximalis ulnae

1491. Extremitas proximalis ulnae, processus cotylaris dorsalis, cotyla dorsalis, forma (**ordered**):
a. typical proportion or elongate;
b. distinctly diminutive, regressed toward olecranon;
c. regressed toward olecranon and with margo cranialis concave, narrowing cotyla dorsalis still further;
x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromornithidae).
Note.—See: Hughes (2000: appendix 2, character 117), extreme cases those in which cotyla dorsalis approximately one-half size of ventralis.

1492. Extremitas proximalis ulnae, processus cotylaris dorsalis, pronounced ventral orientation such that apex processi is approximately coplanar with facies dorsalis corporis, status:
a. absent, apex processi variably elevated dorsad to corpus;
b. present;
x. noncomparable (Dinornithiformes, Sphenisciformes, *Aptornis*).
Note.—See: Livezey (1998b: appendix A, character 225), pertaining to prominence of processus.

1493. Extremitas proximalis ulnae, processus cotylaris dorsalis, cristula apicalis (**new term**), status:
a. absent or indistinct;
b. present, prominently developed, distally oriented, hamulate ala;
x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromornithidae).
Note.—Cristula in question is a dorsoventrally compressed, sublaminate, distal augmentation of the processus cotylaris dorsalis. See: Hughes (2000: appendix 2, character 118), describing a "prominent spur."

1494. Extremitas proximalis ulnae, processus cotylaris dorsalis, cotyla dorsalis, forma superficialis:

a. concave or planar; **b.** convex;

x. noncomparable (Dinornithiformes, Dromornithidae).

Note.—See: Norell and Clarke (2001: appendix I, character 130), treated similarly by J. A. Clarke (2002: appendix I, character 130), J. A. Clarke and Norell (2002: appendix 2, character 130); J. A. Clarke (2004: appendix 1, character 130); Zhou and Zhang (2002: appendix III, character 130); Ji et al. (2005: supplement, part I, character 130).

1495. Extremitas proximalis ulnae, processes cotylares dorsalis et ventralis, conspicuous craniocaudal compression and distodorsal angulation such that cotylae form an angular dorsocaudal prominentia, status:

a. absent; **b.** present;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromornithidae).

Note.—See: Stephan (1979); Hughes (2000: appendix 2, character 119), after Seibel (1988: character UL 4), regarding "mesodistal to lateroproximal" orientation in Musophagidae and *Opisthocomus*, not sustainably diagnosable throughout exemplars; G. Mayr et al. (2003: appendix 1, character 41), with respect to elongate midline ridge distal to cotyla ventralis.

1496. Extremitas proximalis ulnae, processus cotylaris dorsalis, cotyla dorsalis, facies articularis relative to cotyla ventralis, forma (**ordered**):

a. less expansive; **b.** subequal in expanse;

c. more expansive;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromornithidae, Sphenisciformes, *Aptornis*).

Note.—Related to characters pertaining to impact on cotyla ventralis of concavity of margines and incisura radialis, but treated separately as these features are readily separable and not identically distributed. See: Bledsoe (1988: appendix, characters 24 and 26), discounted by K. Lee et al. (1997: appendix 2) for ratites; Chiappe et al. (1996: appendix 1, character 96), regarding "subequal cotyla of ulna"; J. A. Wilson and Sereno (1998: appendix, character 5), regarding Sauropoda; Hughes (2000: appendix 2, character 115), after Seibel (1988: character UL 1).

1497. Extremitas proximalis ulnae, processus cotylaris dorsalis, crista intercotylaris, status et forma (**ordered**):

a. absent, proximal extent distinctly less than that of olecranon, a single cotylus evident;

b. rudimentary, crista indicated, but aspect exaggerated (extremitas proximalis apparently dominated by medial angularity) by sloping, depressed cotylae;

c. present, crista rudimentary but evident despite more typically conformed cotylae;

d. present, variably prominent, cotylae dorsalis et ventralis distinct;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromornithidae).

Note.—See: Cracraft (1986: appendix, character 16); Gauthier (1986: 13, unindexed synapomorphy of Ornithurae); Cracraft (1988: series III, character 4); Chiappe (1995b: character 41); Elzanowski (1995: 38, character unindexed); Kurochkin (1995b: table 1, character 15); Sanz et al. (1995, 1997: character 39); Chiappe (1996b: character 38); Chu (1998: appendix 1, character 98); Makovicky and Sues (1998: appendix 1, character 68); J. A. Clarke and Chiappe (2001: characters 20–21); Norell et al. (2001: appendix 1, character 145); Chiappe and Walker (2002: appendix 11.1, character 21), regarding separation of cotyla dorsalis from olecranon by jugum; J. M. Clark et al. (2002a: appendix 2.2, character 147); Xu (2002: suite II, character 172); Xu et al. (2002a: supplement, character 117), in terms "articular facet" and "median ridge"; Hwang et al. (2004: supplement, character 144); Xu and Norell (2004: supplement, character 144).

1498. Extremitas proximalis ulnae, crista intercotylaris, tuberculum cristae (**new term**), status:

a. absent; **b**. present.

Note.—Presumably serves as ancora distalis ligamenti craniale cubiti.

1499. Extremitas proximalis ulnae, processus cotylaris dorsalis, crista intercotylaris, caudalmost orientation with respect to olecranon, forma (**unordered**):

a. dorsal to olecranon, truncate, intersecting jugum linearis aut angularis transversus cranial to olecranon, thereby demarcating a facies comprising two cotylae cranially and one variably shaped area subolecrani (**new term**) caudodorsally, typically isolating single eminentia intercotylaris (**new term**) at intersection;

b. dorsal to olecranon, elongate and continuous to terminus of extremitas proximalis ulnae;

c. toward olecranon;

x. noncomparable (Dinornithiformes, Sphenisciformes, *Aptornis*).

Note.—See: G. Mayr (2003c: appendix, character 19), in terms of dubiously related cristula relative to cotyla ventralis ulnae; G. Mayr (2005b: appendix A, character 34).

1500. Extremitas proximalis ulnae, processus cotylaris dorsalis, crista intercotylaris, forma:

a. variably conformed, inconspicuous eminentia or cristula;

b. prominent processus approaching olecranon in proximal extent;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

1501. Extremitas proximalis ulnae, processus cotylaris dorsalis, crista intercotylaris, area intercotylaris caudale (**new term**), fossa pneumatica, status:

a. absent; **b.** present.

Note.—New term refers to variably sloping surface on extremitas proximalis ulnae, caudal or proximal to crista intercotylaris and dorsal to olecranon.

1502. Extremitas proximalis ulnae, margo interosseus (cranialis), impressio insertii m. brachialis, forma (**ordered**):

a. impressio planum aut facies ancorae, margo proximocaudalis only (rarely) slightly elevated;

b. concavum modestus—moderately deep, with margo proximocaudalis or crista brachialis (**new term**) elevated only proximally, and typically not undercutting cotylae proximales;

c. concavum profundus—very deep, margo proximocaudalis or crista brachialis (**new term**) elevated for at least half of impressio, and typically undercutting cotylae proximales significantly;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromornithidae, Sphensciformes).

Note.—Challenging characterization because of combined effects of minor differences in depth and apparent positive allometry with body size. See: Holdaway (1991: appendix 5.1, character 101); Livezey (1996a: appendix 1, character 53); Livezey (1998b: appendix A, character 224); Chiappe (2001a: appendix 1, character 97); J. A. Clarke and Chiappe (2001: character 19); Norell and Clarke (2001: appendix I, character 134); Chiappe (2002: appendix 20.2, character 97), using synonym “M. brachialis anticus”; Chiappe and Walker (2002: fig. 11.8), regarding *Enantiornis*; J. A. Clarke (2002: appendix I, character 134); J. A. Clarke and Norell (2002: appendix 2, character 134); Zhou and Zhang (2002: appendix III, character 134); J. A. Clarke (2004: appendix 1, character 134); Ji et al. (2005: supplement, part I, character 134).

1503. Extremitas proximalis ulnae, impressio insertii m. brachialis, foramina pneumatica, status:

a. absent; **b.** present;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

1504. Extremitas proximalis ulnae, ancora insertii m. scapulotricipitis, forma (**unordered**):

a. impressio (infrequently barely discernable) or slightly elevated cristula or jugum;

b. facies ancorae subplanaris aut depressio subfovealis, of intermediate proximity to cotylae;

c. fovea, distinct and adjacent to rima cotylae dorsalis;

d. tuberculum, small but elevated;

e. torus, variably broad, suborbiculate, convex;

x. noncomparable (Sphenisciformes).

Note.—See: Stephan (1979), a comprehensive atlas of Spheniscidae; J. A. Clarke et al. (2003), regarding Paleogene Sphenisciformes.

1505. Extremitas proximalis ulnae, processus cotylaris dorsalis, incisura radialis, status:

a. absent or indistinct, sulcus narrow, cotylae closely juxtaposed, and process rounded-triangular and with distinct apex;

b. present and variably pronounced, sulcus wide and cotylae distales well separated, margo dorsalis invaginated by incisura, rendering subrectangular, less-expansive processus;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromornithidae, Sphenisciformes, *Aptornis*).

Note.—In many “plesiomorphic” conditions, intrusion of incisura into cotyla is absent because the incisura is positioned in the natural dorsal division between the two cotylae. Confirmed for *Archaeopteryx* based on well-preserved elements in articulation (Berlin specimen).

See: Livezey (1998b: appendix A, character 226); Sereno et al. (1998: footnote 22, character 33), regarding both “radial external tuberosity and ulnar internal tuberosity, size”; Hughes (2000: appendix 2, character 116), after Seibel (1988: character UL 1), feature in reference to “fossa” between processes cotylae dorsalis et ventralis; Norell and Clarke (2001: appendix I, character 129), treated similarly by J. A. Clarke (2002: appendix I, character 129), J. A. Clarke and Norell (2002: appendix 2, character 129), and J. A. Clarke (2004: appendix 1, character 129); Zhou and Zhang (2002: appendix III, character 129); Ji et al. (2005: supplement, part I, character 129).

1506. Extremitas proximalis ulnae, incisura radialis, accessory refinements for accommodation of radius, status et forma (**unordered**):

a. absent or obsolete, incisura simple and comparatively shallow and/or restricted;

b. present, fovea or fossa of variable diameter and depth;

c. present, but limited to dorsoventrally bracing tuberositates, cristula, and/or facies articularis;

x. noncomparable (ratites, Sphenisciformes, *Aptornis*).

Note.—See: Livezey (1998b: appendix A, character 223), regarding possible confusion between fovea aut facies articularis radialis and impressio aut tuberculum origii m. extensor longus alulae.

1507. Extremitas proximalis ulnae, incisura radialis, facies articularis radii, fossa pneumaticum, status et/aut forma:

a. absent or rudimentary, i.e., small and flat;

b. present, expanded transversely and concave.

Note.—See: Holtz (2000 [1998]: appendix I, character 249).

1508. Extremitas proximalis ulnae, incisura radialis, facies articularis radii, fossa pneumaticum, status:

a. absent; **b.** present;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—Pneumatic passage continued distad via pori pneumatici on extremitas distalis ulnaris.

1509. Extremitas proximalis ulnae, olecranon, status et forma (**unordered**):

a. absent;

b. present, distal to cotylae dorsalis et ventralis;

c. present, proximal to cotylae dorsalis et ventralis;

x. noncomparable (Dinornithiformes).

Note.—See: Stephan (1979); Holdaway (1991: appendix 5.1, character 116); G. Mayr (1998a: fig. 10H); J. A. Clarke et al. (2003), regarding Paleogene Sphenisciformes; G. Mayr (2003c: appendix, character 18); G. Mayr et al. (2003: appendix 1, character 42); G. Mayr (2005b: appendix A, character 33).

1510. Extremitas proximalis ulnae, olecranon, length (**unordered**):

a. relatively small, significantly less than one-third of length of corpus ulnae;

b. moderately developed, approaching one-third of length of corpus ulnae;

c. very prominent, approaching one-half of length of corpus ulnae;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromornithidae).

Note.—See: Bledsoe (1988: appendix, character 25); Chiappe et al. (1996: appendix 1, character 75); Novas (1996: appendix, character 10); Novas (1997: appendix, character 10); Novas and Puerta (1997), see identical characters in Novas (1997); Ji et al. (1998: supplement, character 50); Novas (1998); J. A. Wilson and Sereno (1998: appendix, character 4), regarding Sauropoda; Chiappe (2001a: appendix 1, character 96); Norell et al. (2001: appendix 1, character 143); Chiappe (2002: appendix 20.2, character 96); J. M. Clark et al. (2002a: appendix 2.2, character 145); Xu (2002: suite II, character 170); Xu et al. (2002a: supplement, character 115), with respect to prominence of "olecranon process," and limited to binary discrimination; G. Mayr et al. (2003: appendix 1, character 42); Rauhut (2003: character 144); G. Mayr (2004d: appendix I, character 19); Hwang et al. (2004: supplement, character 142); Xu and Norell (2004: supplement, character 142); G. Mayr (2005a: appendix 1, character 19).

1511. Extremitas proximalis ulnae, olecranon, especially as related to impressio (tuberculum) insertii m. humerotriceps (proximally) et/aut impressio (fovea) trochlearis humeroulnaris (ventrally), status et forma (**unordered**):

a. indiscernable, or an impressio not effecting distinct angular departure;

b. olecranon truncated, disproportionately blunted, in some taxa evidently replaced at least in part by ossa sesamoidea;

c. variably blunt angulus or tuberositas offset from olecranon (tuberculum insertii m. humerotriceps), and/or ventral subfoveate impressio (trochlea humeroulnaris) creating appearance of hamulation;

d. subtriangular tuberculum, aligned with olecranon proprius but distinguished by caudal prominence or proximal extension, typically acuminate;

x. noncomparable (ratites, Sphenisciformes, Raphidae).

Note.—See: Zusi and Bentz (1984); Baumel and Witmer (1993: annotation 201–202); Kurochkin (1995b: table 1, character 14); Livezey (1998b: appendix A, characters 227–228).

1512. Extremitas proximalis ulnae, processus cotylaris dorsalis, sulcus tendinosus, status:

a. absent or obsolete, space between cotyla ventralis et olecranon flat to convex;

b. present, sulcus between cotyla ventralis et olecranon distinctly concave;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromornithidae, *Aptornis*).

Note.—Sulcus tendinosus is located between cotyla ventralis et olecranon, conducting tendo m. flexor carpo-ulnaris, and sometimes is referred to simply as a concave "area" near the olecranon. Among Neornithes, a challenging assessment is required, as many taxa show terminal segments of sulcus on facies dorsalis et ventralis of element, but fail to form sulcus or concavity between cotyla ventralis and olecranon. See: Chiappe and Calvo (1994: appendix II, characters 11–12), listed as synapomorphy of Enantiornithes; Sanz et al. (1995, 1997: character 73); J. A. Clarke and Chiappe (2001: character 22).

1513. Extremitas proximalis ulnae, cotyla ventralis, situs insertii m. biceps brachii (tuberculum bicipitale ulnae), status et forma (**unordered**):

a. absent or vaguely indicated;

b. present, as distinct but modest impressio, jugum, or tumulus, typically manifested as enlargement at basis proximalis of impressio insertii m. brachialis;

c. present, as moderately prominent tuberculum or processus, in some passerines tending toward foveate form;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromornithidae, Sphenisciformes).

Note.—See: Norell and Clarke (2001: appendix I, character 133), treated similarly by J. A. Clarke (2002: appendix I, character 133), J. A. Clarke and Norell (2002: appendix 2, character 133), and J. A.

Clarke (2004: appendix 1, character 133); Zhou and Zhang (2002: appendix III, character 133); Ji et al. (2005: supplement, part I, character 133). Baumel and Witmer (1993: annotation 210) listed feature as that of radius, whereas evidently it can pertain to one or both elements among Neornithes.

1514. Extremitas proximalis ulnae, impressio ligamenti collateralis ventralis, forma:

a. variably shaped (often suborbiculate to ovate), comparatively proximal impressio;

b. proximodistally elongated, elevated, subplanar jugum, extending distally for a considerable section of margo caudalis of impressio insertii m. brachialis;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromornithidae).

Note.—Frequent adjacency of impressio biceps brachii (typically more cranial) and impressio ligamenti collateralis ventralis (typically more proximocaudal) mandates that care be exercised in differentiation of these two features. See: Chu (1998: appendix 1, character 99), regarding extent of tuberculum relative to margo ventralis of processus cotylaris dorsalis; J. A. Clarke and Chiappe (2001: character 23).

Corpus ulnae

1515. Corpus ulnae, diameter (at midpoint) relative to that of corpus radii, expressed as multiplicative factor (**ordered**):

a. similar, factor less than 1.25;

b. moderately greater, factor 1.25–1.50;

c. substantially greater, factor at least 1.50;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—See: Tarsitano and Hecht (1980); Gauthier (1986: 13, unindexed synapomorphy of Ornithurae); Bledsoe (1988: appendix, character 28), discounted by K. Lee et al. (1997: appendix 2) for ratites; Sanz and Buscalioni (1992: character 1); Sereno and Rao (1992); Perle et al. (1993); Chiappe and Calvo (1994: appendix I, character 42); Chiappe (1995a: legend for fig. 1); Chiappe (1995b: character 42); Elzanowski (1995: character O6); Sanz et al. (1995, 1997: character 40); Chiappe (1996b: character 39); Chiappe et al. (1996: appendix 1, character 38); Chiappe et al. (1998: character 49); Forster et al. (1998: supplement, character 59); Ji et al. (1998: supplement, character 49); Xu et al. (1999b: character 44); Holtz (2000 [1998]: appendix I, character 247), qualitatively diagnosed; G. Mayr (2003c: appendix, character 17), for related index to relative ulnar breadth; Xu et al. (2000: supplement, character 31); Chiappe (2001a: appendix 1, character 95); Ji et al. (2001), regarding unnamed dromaeosaurid NGMC 91-A; Chiappe (2002: appendix 20.2, character 95); Sereno et al. (2002), regarding *Sinornis*; Ji et al. (2003a: 22) regarding *Shenzhouraptor*; G. Mayr (2005b: appendix A, character 32).

1516. Corpus ulnae, pronounced craniocaudal compression such that element assumes sublaminate shape, status (**ordered**):

a. absent; **b.** present, moderate;

c. present, pronounced;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—Nonexemplary Alcidae include taxa qualifying for state "c," notably *Pinguinus* and *Mancalla* (Livezey 1989, 1993). Extreme dorsoventral compression of antebrachial elements progressively reduces four facies corporalia (cranialis, caudalis, caudodorsalis, et caudoventralis) to two (dorsalis et ventralis).

1517. Corpus ulnae, facies (caudo)dorsalis, forma generalis (dorsoventral perspective):

a. subcylindrical, small diameter, slight craniocaudal curvature;

b. dorsoventrally compressed and laminar, rounded margines, margo cranialis essentially linear, and margo caudalis strongly angular with maximal craniocaudal width immediately distal to extremitas proximalis;

x. noncomparable (Dinornithiformes).

Note.—See: S. L. Olson and Hasegawa (1979); Stephan (1979), regarding Spheniscidae; S. L. Olson (1980); G. Mayr (2004b: appendix 1, character 41).

1518. Corpus ulnae, facies (caudo)dorsalis, forma (**unordered**):

a. linear or essentially straight;

b. variably convex, comparatively uniformly rounded or abruptly subangular;

c. subrectangular, subplanar;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—See: Holtz (2000 [1998]: appendix I, character 246); Maryanska et al. (2002: appendix 1, character 134). Assessments typically paralleled by those for facies caudoventralis.

1519. Corpus ulnae, facies cranialis (dorsoventral perspective), margo interosseus (cranialis), forma superficialis (**unordered**):

a. essentially linear or vaguely sigmoidal;

b. slightly concave, magnitude uniform or greater distally than proximally;

c. moderately concave, with concavity distinctly greater through proximal one-third of element;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—Assessments paralleled by those for facies caudalis, margo caudalis; literature replete with descriptive terms like "bowing." See: Gauthier (1986: character 74); Sanz and Buscalioni (1992: character 2); Russell and Dong (1994a [1993a]: table 2, character 37); Russell and Dong (1994b [1993b]: list B, character 7); Holtz (1994a: appendix 1, character 40); Novas (1996: appendix, character 11); Novas (1997: appendix, character 11); Novas and Puerta (1997), identically by Novas (1997); Sues (1997: appendix 1, character 31); Forster et al. (1998: supplement, character 69); J. D. Harris (1998: appendix 2, character 94); Makovicky and Sues (1998: appendix 1, character 67); Xu et al. (1999a: character 60); Xu et al. (1999b: character 51); Azuma and Currie (2000: appendix 1, character 109); Currie and Carpenter (2000: appendix 1, character 73); Holtz (2000 [1998]: appendix I, character 245); Xu et al. (2000: supplement, character 38); Ji et al. (2001), regarding unnamed dromaeosaurid NGMC 91-A; Ji et al. (2003a: 22).

1520. Corpus ulnae (craniocaudal perspective), margo dorsalis, forma superficialis:
a. dorsally sublinear to concave;
b. dorsally convex;
x. noncomparable by absence (Dinornithiformes).

1521. Corpus ulnae, papillae remigales caudales dorsales (caudales), status et forma (**ordered**):
a. absent or indiscernable;
b. present, small impressiones or tumula;
c. present, substantial tuberositates;
d. present, prominent tuberculae;
x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—Pertain to the "*papillae ulnares anconales*" of Lambrecht (1933) and the "quill knobs" of Edington and Miller (1941). See: Gauthier (1986: 13, unindexed synapomorphy of Ornithurae); Sanz and Buscalioni (1992: excluded character 1); Elzanowski (1995: character N4); Ji et al. (2001), regarding unnamed dromaeosaurid NGMC 91-A; G. Mayr and Ericson (2004: appendix I, character 57).

1522. Corpus ulnae, papillae remigales ventrales, status et forma:
a. absent or indiscernable;
b. present, modest impressiones or tumula;
x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—The papillae ventrales alternate with their dorsal counterparts, suggesting that the former may pertain to bases of tectrices majores ventrales as opposed to serving secondary ligamenta remigiorum.

Extremitas distalis ulnae

1523. Extremitas distalis ulnae, facies craniodorsalis, incisura (impressio, sulcus) tendinosa—sulcus tendineus *fide* Butendieck (1980: 90); Butendieck and Wissdorf (1981); Butendieck et al. (1981)—status:
a. absent, indiscernible, or obsolete;
b. present, variably distinguished by lineae, tuberositates;
x. noncomparable (Aepyornithiformes, Dinornithiformes, Sphenisciformes).

Note.—Situated immediately dorsal to rima dorsalis of trochlea carpalis, accommodates tendines mm. extensor carpi ulnaris et extensor digitorum communis, augmented by retinaculum ligamentosum. Distinct from and distal to a poorly known feature named "impressio tendinea" by Buendieck (1980: 86), the latter comparatively infrequent and apparently uniformative. Claim by Baumel and Witmer (1993: annotation 209) that *Gavia* possessed ossified retinaculae was not substantiated. See: J. A. Clarke and Chiappe (2001: character 29), in reference to "transverse muscle impression" on caudal surface of distal end of ulna; Dyke and Gulas (2002: appendix 1, character 25); Dyke et al. (2003: appendix 1, character 64), under "incisura tendinosa."

1524. Extremitas distalis ulnae, depressio radialis, status et forma (**unordered**):
a. absent or indiscernable, regio sometimes convex;
b. present, shallow and nondescript;
c. present, moderately deep, distinctly triangular;
d. present, deep, foveate apneumatica;
e. present, deep, ovoid fossula pneumatica;
x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromornithidae).

Note.—"Depressio radialis"—a variably configured, shallow facies articularis—nomenclaturally implies a relationship with the radius, and therefore is depicted on the wrong side of the tuberculum carpale by Baumel and Witmer (1993: fig. 4.13); the depressio indicated there instead should be "depressio carpo-ulnaris" (**new term**) to reflect the relationship with os carpi ulnare. See: Dyke and Gulas (2002: appendix 1, character 24, polarity reversed); G. Mayr and Clarke (2003: appendix A, character 84); Dyke et al. (2003: appendix 1, character 63); Dyke and van Tuinen (2004: appendix 1, character 59); G. Mayr (2004a: appendix 1, character 44).

1525. Extremitas distalis ulnae, depressio carpo-ulnaris (**new term**), status:
a. present, variably distinct; **b.** absent;
x. noncomparable (Aepyornithiformes, Dinornithiformes, Sphenisciformes).

Note.—See: Baumel and Witmer (1993: fig. 4.13), regarding nomenclature; Livezey (1998b: appendix A, character 231).

1526. Extremitas distalis ulnae, trochlea carpalis, condylus dorsalis ulnae, labrum condyli dorsalis (dorsal perspective), forma marginalis distale (**unordered**):
a. essentially flat;
b. uniformly rounded (orbiculate) throughout, ap-

proximate midpoint of arcus aligned with axis majoris ulnae;

c. generally rounded but with margo distalis flattened, resulting in rounded subrectangular profile with distinct, rounded, subangular vertices cranialis et caudalis;

d. rounded throughout, but with distinct increase in slope caudally, placing intersection of axis majoris ulnae cranial to midpoint of arcus;

x. noncomparable (Dinornithiformes, Sphenisciformes).

Note.—See: Ericson (1997: character 61); J. A. Clarke and Chiappe (2001); J. A. Clarke (2002: appendix I, character 132); G. Mayr and Clarke (2003: appendix A, character 83); J. A. Clarke (2004: appendix 1, character 132).

1527. Extremitas distalis ulnae, trochlea carpalis, condylus dorsalis ulnae, labrum condyli dorsalis (dorsal perspective), low but distinct convexity or lobus immediately proximal to rima, status:

a. absent; **b.** present;

x. noncomparable (Dinornithiformes, Sphenisciformes).

Note.—Limited intraspecific variability within some Piciformes.

1528. Extremitas distalis ulnae, trochlea carpalis, condylus dorsalis ulnae, labrum condyli dorsalis (“semilunate ridge”), terminal extension (including facies articularis with os carpi ulnaris), status et forma apicalis (**ordered**):

a. absent, no extension of condylus dorsalis onto corpus;

b. present, intersecting with corpus from condylus dorsalis at obtuse, subdiagonal, to subperpendicular angulae, typically lacking extension on corpus as jugum;

c. present, apex (terminus) of condylus dorsalis extended, acuminate, variably elevated from margo dorsalis corporis;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromornithidae).

Note.—See: Cracraft (1986: appendix, character 16); Chiappe and Calvo (1994: appendix I, character 41); Sanz et al. (1995, 1997: character 39); Chiappe et al. (1996: appendix 1, character 37); Chiappe et al. (1998: character 52); Ji et al. (1998: supplement, character 52); Forster et al. (1998: supplement, character 58); Chatterjee (1999: appendix II, character 59), for “semilunate ridge on ulnar dorsal condyle”; Chiappe (2001a: appendix 1, character 98); Norell et al. (2001: appendix 1, character 144); Chiappe (2002: appendix 20.2, character 98); J. M. Clark et al. (2002a: appendix 2.2, character 146); Xu (2002: suite II, character 171); J. A. Clarke and Chiappe (2001: character 25); Norell and Clarke (2001: appendix I, character 131); J. A. Clarke (2002: appendix I, character 131); J. A. Clarke and Norell (2002: appendix 2, character 131); Zhou and Zhang (2002: appendix III, character 131); J. A. Clarke (2004: appendix 1, character 131); Hwang et al. (2004: supplement, character 143); Xu and Norell (2004: supplement, character 143); Ji et al. (2005: supplement, part I, character 131).

1529. Extremitas distalis ulnae, trochlea carpalis, condylae dorsalis et ventralis ulnae, forma intercondylaris:

a. subrectangular or “flat,” pars distalis dorsoventrally compressed and pars proximalis craniocaudally extended in planum of flexion-extension of ulna relative to humerus;

b. subtriangular or “convex, semilunate,” pars distalis subtriangular “with a dorsomedial condyle,” with 54° torsion of terminus distalis relative to terminus proximalis;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromornithidae).

Note.—See: Novas (1996: appendix, character 64); Novas (1997: appendix, character 65); Novas and Puerta (1997: appendix, character 65); Ji et al. (1998: supplement, character 51); Forster et al. (1998: supplement, character 68); Xu et al. (1999b: character 50); Holtz (2000 [1998]: appendix I, character 248); Xu et al. (2000: supplement, character 37); Xu et al. (2002a: supplement, character 116); Xu et al. (2002a: supplement, character 118).

1530. Extremitas distalis ulnae, trochlea carpalis, condylus dorsalis et ventralis ulnae, proximodistal extent:

a. approximately equal;

b. condylus dorsalis distinctly proximal to condylus ventralis;

x. noncomparable (Dinornithiformes).

Note.—See: S. L. Olson and Hasegawa (1979); Stephan (1979), a comprehensive atlas of Sphenisci-dae; S. L. Olson (1980); Ji et al. (2005: supplement, part I, character 132).

1531. Extremitas distalis ulnae, trochlea carpalis, condylus ventralis ulnae, craniocaudal depth, and associated relative width of adjacent sulcus intercondylaris (distal perspective), forma:

a. condylus reduced, comparatively shallow, and abbreviated ventrally, with condylus typically remaining discernable (rarely obsolete), with sulcus intercondylaris accordingly broad and shallow;

b. condylus comparatively deep and not abbreviated ventrally, delimiting one side of narrow and deep sulcus intercondylaris;

x. noncomparable (ratites, Dromornithidae, Sphenisciformes).

Note.—See: Sereno (1994 [1993]: appendix, character 6), regarding this feature and associated tuberculum and included facies articularis carpale “concavoconvex with size disparity”; Ericson (1997: table

1, character 62); Livezey (1998b: appendix A, characters 229–230), regarding gruiforms.

1532. Extremitas distalis ulnae, trochlea carpalis et tuberculum carpale, sulcus intercondylaris, condylus ventralis, margo distalis of tuberculum carpale, and (especially) condylus dorsalis ulnae (distal perspective), broad, flattened facies articulares, status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes, Sphenisciformes).

1533. Extremitas distalis ulnae, tuberculum carpale, status et forma *sensu* cranial prominence (**ordered**):
a. absent, i.e., no extension beyond margo cranialis;
b. present, small, i.e., tuberculum appearing as mere angulus of extremitas distalis ulnae;
c. present, moderately large, i.e., tuberculum distinct but significantly less prominent than width of corpus caudal to tuberculum;
d. present, very prominent, i.e., tuberculum distinct, at least as prominent as width of corpus caudal to tuberculum;
x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromornithidae).
Note.—See: J. A. Clarke and Chiappe (2001: character 28), in reference to "tubercle adjacent to tendinal groove" of ulna, codings for which conflicted significantly with present assessment.

1534. Extremitas distalis ulnae, tuberculum carpale, jugum tuberculae cranialis (**new term**), status:
a. absent or incompletely developed or indistinct;
b. present, distinctly curving (margo proximalis concave) and extending across facies dorsalis from tuberculum carpale caudad to margo caudalis ulnae;
x. noncomparable (Dinornithiformes, Sphenisciformes).
Note.—Jugum enhanced in some taxa by adjacent impressio tendinea (Butendieck 1980: 90, feature 23); Butendieck and Wissdorf (1981); Butendieck et al. (1981).

1535. Extremitas distalis ulnae, tuberculum carpale, facies craniodorsalis, fossa pneumatica et/aut pori pneumatici, status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes, Sphenisciformes).
Note.—See: Baumel and Witmer (1993: annotation 207).

1536. Extremitas distalis ulnae, tuberculum carpale, status et forma apicalis (**unordered**):
a. cuneate, proximodistally wide, dorsoventrally thick;
b. blunt, unilobate, but some taxa with irregular facetae et tuberositates terminales;
c. bifurcate;
d. crescentiform;
x. noncomparable (ratites, Sphenisciformes, Pelecanidae, *Aptornis*).
Note.—See: Baumel and Witmer (1993: annotation 207).

Radius

Extremitas proximalis radii

1537. Extremitas proximalis radii, comparative differentiation of caput radii from adjacent corpus radii in diameter, and qualitative features, e.g., pronounced collum radii (**new term**), status:
a. present, distinct;
b. absent, weak, or obsolete;
x. noncomparable (Aepyornithiformes, Dinornithiformes).

1538. Extremitas proximalis radii, caput radii, cotyla humeralis, forma:
a. subplanar to concave;
b. angular or convex;
x. noncomparable (Aepyornithiformes, Dinornithiformes).

1539. Extremitas proximalis radii, margo cranialis (rima externa), facies articularis ulnaris, forma marginalis:
a. facies indistinguishable from caput radii;
b. limited to superficially defined facies or boss elevated by comparatively subtle, subtending eminentia;
x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromornithidae).
Note.—See: Novas (1996: appendix, character M11); Chu (1998: appendix 1, character 100); Sereno et al. (1998: footnote 22, character 33), in terms of prominence of "radial external tuberosity and ulnar internal tuberosity, size"; J. A. Clarke and Chiappe (2001: character 31), in reference to "prominent tubercle on edge of humeral cotyla [= cotyla humeralis radii]."

1540. Extremitas proximalis radii, facies ventralis, tuberculum bicipitale radii, status et forma (**unordered**):
a. absent;
b. present, a modest boss or tuberculum, essentially sessile on corpus;
c. present, a prominent, comparatively proximal tuberculum, including extreme position on margo cotylae;
d. present, impressio on prominent jugum;
e. present, an elevated, foveate processus or tuba;
x. noncomparable (Dinornithiformes).
Note.—See: Ballmann (1969a); Sereno et al. (1998: footnote 22, character 33), regarding both "ra-

dial external tuberosity and ulnar internal tuberosity, size"; J. A. Clarke and Chiappe (2001: character 30); Xu et al. (2003).

1541. Extremitas proximalis radii, facies dorsalis, sulcus obliquus m. brachialis (**new term**), status:

a. absent; **b.** present;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—See: S. L. Olson and Hasegawa (1979, 1985, 1996); Stephan (1979); S. L. Olson (1980).

1542. Corpus radii, margo cranialis, facies ventralis, jugum aut ala cranialis et sulcus muscularis (**new term**), latter primarily supporting insertio m. deltoideus, pars propatagialis, caput craniale (pars longus), status:

a. absent; **b.** present;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—See: S. L. Olson and Hasegawa (1979, 1985, 1996); Stephan (1979); S. L. Olson (1980).

1543. Corpus radii, distinct, moderate flattening, attaining maximum distal to midpoint of corpus, resulting in segment being flattened on facies interosseus whereas corpus "hemi-cylindrical" (planum transversus), status:

a. absent; **b.** present;

x. noncomparable (Dinornithiformes, Sphenisciformes).

Note.—See: Livezey (1998b: appendix A, character 233). Similar but mid-corporal flattening characterizes *Phalacrocorax*.

1544. Corpus radii, pronounced dorsoventral compression throughout such that element assumes sublaminate shape, status:

a. absent; **b.** present;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—See: S. L. Olson and Hasegawa (1979, 1985, 1996); Stephan (1979); S. L. Olson (1980).

1545. Corpus radii, facies (ventro)caudalis, lineae intermusculares (mm. pronator superficialis et profundus, extensor longus digiti majoris pars proximalis, et extensor longus alulae, caput radiale), status et proximodistal extent (**unordered**):

a. absent or obsolete;

b. present, moderate impressio(nes) extending majority of corpus;

c. present, deep sulcus(ci) extending majority of corpus;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—See: Chiappe and Calvo (1994: appendix II, character 13), for "longitudinal groove on ventrocaudal surface" synapomorphic of Enantiornithes; Kurochkin (1995b: table 1, character 16); Chiappe (2001a: appendix 1, character 99); Norell and Clarke (2001: appendix I, character 135); Chiappe (2002: appendix 20.2, character 99); Chiappe and Walker (2002: appendix 11.1, character 22); J. A. Clarke (2002: appendix I, character 135); J. A. Clarke and Norell (2002: appendix 2, character 135); Zhou and Zhang (2002: appendix III, character 135); J. A. Clarke (2004: appendix 1, character 135); Ji et al. (2005: supplement, part I, character 135).

1546. Corpus radii, facies (ventro)caudalis, lineae intermusculares, linea m. extensor longus alulae, caput radiale, status:

a. absent or indistinct;

b. present and conspicuously delimited;

x. noncomparable (Dinornithiformes, Sphenisciformes).

1547. Corpus radii, margo cranialis, pronounced dorsoventral compression and cranial extension into blunt angularity, status:

a. absent;

b. present, producing calcar radialis (**new term**), facies dorsalis of which manifests proximodistal sulcus tendinis m. extensor (meta)carpi radialis;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—See: Beddard (1898a: fig. 70); Rand (1954: figs. 1F, 1I).

1548. Corpus radii, margo interosseus (caudalis), foramen neurovascularia, status:

a. present; **b.** absent;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—Foramen typically opposite parallel structure in ulna.

1549. Corpus radii, margo interosseus (caudalis), arcus origii m. extensor longus digiti majoris, pars proximalis (**new term**), status:

a. absent; **b.** present;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—See: Bock and McEvey (1969a) regarding this "nutrient foramen." Arcus evidently serves as both situs insertii m. pronator profundus et origii m. extensor longus digiti majoris pars proximalis; some variation noted among taxa, including partial arca in some taxa (Shufeldt 1900a: 673; Pycraft 1903c: 43).

1550. Corpus radii, margines cranialis et caudalis, curvature or bowing, status et forma (**unordered**):

a. absent;

b. present, negligible or slight, approximately uniform;

c. present, moderate, more pronounced distally;

x. noncomparable (Dinornithiformes).

Note.—Curvature evidently alters articulatio radiocarpalis to comparatively cranial position. See related osteological aspect of distal broadening and myological character regarding tendo insertii m. (meta)carpi radialis.

1551. Extremitas distalis radii (distal perspective), forma transversa (**unordered**):
a. subcylindrical; **b.** subrectangular;
c. sublaminar;
x. noncomparable (Aepyornithiformes, Dinornithiformes).
Note.—See: J. A. Wilson and Sereno (1998: appendix, character 6) with respect to Sauropoda.

1552. Extremitas distalis radii, exostosis continuous with that of extremitas proximalis carpometacarpalia, status:
a. absent; **b.** present.
Note.—See: Livezey (1993).

1553. Extremitates distales radii et ulnae, syn(ex) ostosis ulnoradialis, status:
a. absent; **b.** present.
Note.—See: Livezey (1996a: appendix 1, character 52); Makovicky and Norell (2004: character 211); Xu and Norell (2004: supplement, character 211).

1554. Extremitas distalis radii, facies articularis radiocarpalis, forma superficialis:
a. linear or slightly convex, subcylindrical;
b. concave, sub-bicondylar;
x. noncomparable (Aepyornithiformes, Dinornithiformes).
Note.—See: Novas (1996: appendix, character M12); Livezey (1998b: appendix A, character 234); Hughes (2000: appendix 2, character 120).

1555. Extremitas distalis radii, facies ventralis, tuberculum aponeurosis ventralis, forma (**unordered**):
a. inconspicuous, rounded;
b. prominent, angular or hemispheroidal tumulus;
c. conspicuously developed, peglike processus;
d. carinate;
x. noncomparable (Aepyornithiformes, Dinornithiformes).
Note.—See: Andors (1992: table 2, character 31), in reference to "elongate, distal, external tubercle [crest] near its [radius] distal end"; Baumel and Witmer (1993: annotation 213).

1556. Extremitas distalis radii, facies ventralis, tuberculum aponeurosis ventralis et facies dorsalis, tumulus rotundus (**new term**), unique bitubercular facies articulares with deep, dividing, obliquely oriented sulcus ligamentosus, status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes).
Note.—See: Stephan (1979), a comprehensive atlas of Spheniscidae.

1557. Extremitas distalis radii, facies ventralis, depressio ligamentosa, cristula(e) sulci longitudinales (**new term**), status, numerus et forma (**unordered**):
a. absent;
b. present, two (cranialis et caudalis), moderately conspicuous to very prominent;
c. present, three (cranialis, mediana, et caudalis), moderately prominent;
x. noncomparable (Aepyornithiformes, Dinornithiformes).
Note.—See: McKitrick (1991a); Chu (1998: appendix 1, character 102). Presence of cristulae typically associated with disproportionate distal broadening of element, as well as proximal extent and depth of depressio ligamentosa. Regarding latter, see: Livezey (1998b: appendix A, character 232); Chu (1998: appendix 1, character 101); J. A. Clarke and Chiappe (2001: character 32).

1558. Extremitas distalis radii, facies ventralis, depressio ligamentosa, fossa pneumatica aut foramina pneumatica sine fossa, status:
a. absent; **b.** present;
x. noncomparable (Aepyornithiformes, Dinornithiformes).

1559. Extremitas distalis radii, facies ventralis, sulcus (depressio) ligamentosus, disproportionately broad and deep effecting spatulate aspect, accentuated by pair of marginal sulci longitudinales, status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes, Sphenisciformes).

1560. Extremitas distalis radii, facies dorsalis, tumulus rotundus (**new term**), forma (**unordered**):
a. subplanar or shallowly rounded;
b. prominently, irregularly shaped and surfaced, elevated regio;
c. distinctly delimited, comparatively low, triangular area;
d. significantly elevated, rounded, subtrianguloid;
e. cristulate;
x. noncomparable (ratites, Sphenisciformes, *Pezophaps*).
Note.—New feature is variably prominent mound at dorsodistal vertex of element. See: G. Mayr (2003c: appendix, character 20); G. Mayr (2005b: appendix A, character 35).

1561. Extremitas distalis radii, margo dorsalis cristulate expansion and associated change in sulcus tendineus, status:
a. absent, margo dorsalis rounded or only slightly emarginate, sulcus typically angled with respect to axis majoris radii;
b. present, margo dorsalis enhanced by cristulate extension of margo cranialis of extremitas distalis radii, sulcus tendineus typically subparallel with axis majoris radii or broadened into indiscernability, ef-

fecting deflection of carpal passage of tendo m. extensor (meta)carpi radialis from cranial to craniodorsal;

x. noncomparable (ratites, Sphenisciformes, *Pezophaps*).

Note.—Sulcus accommodates tendo(ines) insertii(iorum) m. extensor (meta)carpi radialis, and apomorphic state effects shift of action from cranial to dorsal aspects of carpus et manus.

Ossa Carpi Proximalia

Note.—The carpus or "wrist" of Neornithes is comparatively refined for flight (Vazquez 1992, 1994) and skeletally simplified to comprise only ossa carpi proximalia et distalia. Previously employed characters of general form of ossa carpi proximalia (e.g., essentially cuboidal or discoidal) were put aside for this analysis due to challenges of assessment: Holtz (1994a: appendix 1, character 59); Holtz (2000 [1998]: appendix I, character 251); Ji et al. (2001), regarding unnamed dromaeosaurid NGMC 91-A.

Os carpi radiale

Note.—Synonymous with os scapholunare (Lambrecht 1933).

1562. Os carpi radiale, os proprius et facies articularis metacarpalis, status et forma (**unordered**):

a. present, including functional facies articulares metacarpalis, radialis, et ulnaris;

b. vestigial, meniscoid, typically substantially smaller and of reduced functionality than os carpi ulnare;

c. absent, collective loss of ossa alae distales.

Note.—See: Jeffries (1882a).

1563. Os carpi radiale, foramina pneumatica, status:

a. absent; **b.** present;

x. noncomparable (Dinornithiformes, Sphenisciformes).

Os carpi ulnare

Note.—Synonymous with os cuneiform (Lambrecht 1933).

1564. Os carpi ulnare, status et forma (**unordered**):

a. absent;

b. present, distinctly arcuate, effecting amplexus trochlearis (**new term**) comprising articulationes ulnocarpo-metacarpales ventrale et dorsale;

c. vestigial, cuneate, effecting articulationes planae;

d. obsolete, secondarily.

Note.—See: Gauthier (1986); Norell and Clarke (2001: appendix I, character 136), treated similarly by J. A. Clarke (2002: appendix I, character 136), J. A. Clarke and Norell (2002: appendix 2, character 136), and J. A. Clarke (2004: appendix 1, character 136); Zhou and Zhang (2002: appendix III, character 136); Ji et al. (2005: supplement, part I, character 136).

1565. Os carpi ulnare, corpus (craniocaudal perspective), forma (**unordered**):

a. orbiculate to subrectangular;

b. cordiform;

c. parabolic ("U-shaped") with deep incisura dorsocranialis carpi ulnaris (**new term**) delimiting two distinct crura;

d. equilaterally triangular, dorsoventrally compressed, sublaminate;

x. noncomparable (most ratites, *Aptornis*).

Note.—See: G. G. Simpson (1946); S. L. Olson and Hasegawa (1979, 1985, 1996); Stephan (1979); S. L. Olson (1980); Sereno and Rao (1992); Forster et al. (1998: supplement, character 70), regarding semilunate shape of "distal radial carpal"; Ji et al. (1998: supplement, character 53); Padian and Chiappe (1998b); Norell and Clarke (2001: appendix I, character 137), treated similarly by J. A. Clarke (2002: appendix I, character 137), J. A. Clarke and Norell (2002: appendix 2, character 137), and J. A. Clarke (2004: appendix 1, character 137); Norell et al. (2001: appendix 1, character 146); J. M. Clark et al. (2002a: appendix 2.2, character 148); Xu (2002: suite II, character 173); Zhou and Zhang (2002: appendix III, character 137); Hwang et al. (2004: supplement, character 145); G. Mayr (2004b: appendix 1, character 42); Xu and Norell (2004: supplement, character 145); Ji et al. (2005: supplement, part I, character 137).

Original description may have synonymized mistakenly os carpi ulnare with the "scapholunar," whereas the latter (correctly spelled scapholunare) is synonymous with os carpi radiale.

1566. Os carpi ulnare, ramus ventralis (**new term**), facies proximoventralis, sulcus tendineus radioulnaris (**new term**), status et forma (**ordered**):

a. absent or indistinct;

b. present, open sulcus throughout;

c. present, sulcus covered proximally by arcus, converting to partial canaliculis tendineus;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—New term is synonymous with crus longum. See: J. A. Clarke and Chiappe (2001: character 34). Probably involving tendines insertii mm. flexores digitorum superficialis et profundus.

1567. Os carpi ulnare, ramus ventralis (**new term**), incisura metacarpalis, et processus muscularis, foramina pneumatica, status:

a. absent; **b.** present;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—New term is synonymous with crus longum.

1568. Os carpi ulnare, ramus ventralis (**new term**), terminus cruralis, semiglobular tuberculum, status:

a. absent; **b.** present;

x. noncomparable (Dinornithiformes).

Note.—New term is synonymous with crus longum.

1569. Os carpi ulnare, ramus ventralis (**new term**), forma (**unordered**):

a. sublinear;

b. curved dorsally, acuminate;

c. curved dorsally, blunt;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—New term is synonymous with crus longum. See: Hughes (2000: appendix 2, character 122), after Seibel (1988: character CU 2); G. Mayr (2003c: appendix I, character 20); G. Mayr et al. (2003: appendix 1, character 46), in reference to Cuculiformes; G. Mayr (2005b: appendix I, character 36).

1570. Os carpi ulnare, relative lengths of ramus ventralis (**new term**) and ramus dorsalis (**new term**), forma (**ordered**):

a. ventralis shorter than dorsalis;

b. ventralis (sub)equal to dorsalis;

c. ventralis distinctly longer than dorsalis;

x. noncomparable (ratites).

Note.—New terms are synonymous with crura longum et breve, respectively. See: Hughes (2000: appendix 2, character 123), after Seibel (1988: character CU 3), regarding relative dorsoventral thickness of crurae ventralis et dorsalis; J. A. Clarke and Chiappe (2001: character 33); Norell and Clarke (2001: appendix I, character 138), treated similarly by J. A. Clarke (2002: appendix I, character 138), J. A. Clarke and Norell (2002: appendix 2, character 138), and J. A. Clarke (2004: appendix 1, character 138); Zhou and Zhang (2002: appendix III, character 138); G. Mayr (2003b: appendix I, character 12), regarding Trogonidae; G. Mayr and Clarke (2003: appendix A, character 87), regarding truncation of crus longum; Dyke and van Tuinen (2004: appendix 1, character 63); G. Mayr et al. (2003: appendix 1, character 45); G. Mayr and Ericson (2004: appendix I, character 61); Ji et al. (2005: supplement, part I, character 138).

1571. Os carpi ulnare, incisura metacarpalis, status:

a. present; **b.** absent;

x. noncomparable (Dinornithiformes).

Note.—See: Stephan (1979); G. Mayr (2004b: appendix 1, character 42).

1572. Os carpi ulnare, incisura metacarpalis, angulus:

a. acute (angulus less than 90°), predominantly subdiagonal (angulus approximating 45°);

b. perpendicular (angulus approximating 90°;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—See: Hughes (2000: appendix 2, character 121), after Seibel (1988: character CU 1).

1573. Os carpi ulnare, facies cranialis aut margo proximalis incisurae, processus muscularis, status et forma (**unordered**):

a. absent or obsolete;

b. present, positioned away from margo incisurae, subtly developed;

c. present, positioned at margo incisurae, variably prominent;

x. noncomparable by absence or fundamental apomorphy of element (ratites).

Note.—See: Ericson (1997: table 1, character 63), with whom current codings disagree with respect to taxa *Turnix*, *Jacana*, *Burhinus*, and *Rynchops*; Hughes (2000: appendix 2, character 124), in reference to "distal end"; J. A. Clarke and Chiappe (2001a: character 35); G. Mayr and Clarke (2003: appendix A, character 88), in terms of status of tuberculum insertii ligamentum humerocarpale; G. Mayr and Ericson (2004: appendix I, character 60), terming feature tuberculum insertii ligamentum humerocarpale. Tuberculum evidently serves as ancora insertii m. flexor carpi ulnaris, and, together with retinaculum ulnocarporemigiale et ligamentum humerocarpale, constitutes processus muscularis.

Os Prominens

1574. Os prominens, status et forma (**unordered**):

a. absent;

b. present, as comparatively small, variably ossified, simply shaped os sesamoideum;

c. present, as comparatively substantial, typically well-ossified, hamulate os sesamoideum;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—Os prominens is an os sesamoideum upon which tendo m. deltoideus propatagialis (formerly m. tensor propatagialis, pars longus) inserts. See: Shufeldt (1881a); Jeffries (1882a); F. A. Lucas (1882); Kuroda (1954); Hoff (1966); Bock and McEvey (1969a); Hudson et al. (1969).

Ossa Carpi Intermedia

Note.—During the evolutionary history of Archosauromorpha, a reduction in the "wrist" paralleled a similar trend in the manus. The plesiomorphic carpus of Archosauromorpha comprised two or (perhaps) three ossa carpi proximalia associated with antebranchial elements—ulnare, radiale, and often the interposed intermedium—and a variably complete and/or synostotic complement of ossa carpi intermedia (typically lost in Neornithes) that are proximal to ossa carpi (one to five corresponding to retained ossa metacarpalia, in Ornithurae typically incorporated into carpometacarpus).

The ossa carpi intermedia (Romer 1956: figs. 178–184) comprise ossa carpi: (*i*) proximalis centrale, medialis centrale, lateralis centrale, et distalis centrale; (*ii*) mesocuneiformis et ectocuneiformis; (*iii*) pisiformis, navicularis, magnus, centrale, et cuboidale. Despite uncertainty in identification of specific elements lost and problems of differentiation between loss and synostosis, a primary role of ossa carpi ulnare et radiale, a lesser, ephemeral role of os carpi pisiformis, uncertainty about os carpi intermedium pertains to Neornithes. See: Sereno (1994 [1993]: appendix, character 7), which referred to "centrale distal to radiale" in the basal theropod *Herrerasaurus* but not in several other Dinosauria (e.g., *Coelophysis*, *Staurikosaurus*, *Plateosaurus*, and *Lesothrosaurus*. Similarly, J. A. Wilson and Sereno (1998: appendix, character 79) referred to a number of "carpal bones" among Sauropoda.

1575. Ossa carpi intermedia, numerus modalis definitivum (**ordered**):

a. two to four; **b.** one to two; **c.** zero.

Note.—Tallies estimated by difference between total number of ossa carpi and five (latter accounts for two ossa carpi proximalia, and three ossa carpi distalia). Loss can be genuine or apparent (latter by synostosis).

Ossa Carpi Distalia

Note.—G. P. Wagner and Gauthier (1999) inferred that three condensations, corresponding to the primordia of ossa carpi distalia, can be identified in embryonic Aves; this interpretation was confirmed by Chatterjee (1998b). G. P. Wagner and Gauthier (1999) concluded that all five primordia undergo some condensation during early embryogenesis: (**a**) the "first" condensation is abortive but incorporated with the basis of the primordium and destined to become os metacarpale I (topographically near the processus extensorius); (**b**) the "second through fourth" condensations being those detected in the earlier work as giving rise to the trochlea carpalis; and (**c**) the fifth not even persisting as a cartilago and effectively "absent" in (at least adult) Neornithes. Alternatively, Padian and Chiappe (1998b: fig. 11), based on a comparison of *Coelophysis*, *Deinonychus*, and *Archaeopteryx*, concluded that "distal carpals 1 and 2" unite to form the trochlea carpalis, and "distal carpal 3" merges into margo caudalis of the trochlea at the basis os metacarpale III (see also Currie and Padian 1997). Regardless of the ontogenetic details, the primordia or "distal carpals" which ultimately coalesce to produce the definitive trochlea carpalis collectively are homologous to the traditional "semilunate carpal." The latter element poses some problems of homoplasy in form (Chure 2001) This morphological variation and a dearth of embryological insights justify caution in heavy reliance on this feature for purposes of diagnoses of fossils.

At least two structural components of the trochlea are detectable, and these correspond to the two facies articulares (dorsal and ventral) associated with the two os carpi proximalia (os carpi radiale with facies articularis radiocarpalis trochlearis, and os carpi ulnare with facies articularis ulnocarpalis trochlearis). The third primordium of the ossa carpi distalia is the last to form; if detected, it is associated with the basis of os metacarpale I. However, like the primordia for the ossa carpi distalia associated with ossa metacarpalia IV et V, the third primordium may be lost in Neornithes; alternatively, it may contribute to the cranial extremity of the trochlea carpalis or the processus pisiformis (latter alternative supported by *Sinosauropteryx*; cf. Currie and Chen 2001). See Sereno (1994 [1993]: appendix, character 8), in which size of "distal carpal 4" relative to os carpi ulnare is assessed for selected Dinosauria including *Herrerasaurus*.

Identities of ossa carpometacarpales and associated digiti have caused considerable debate, largely divided along lines between developmental and paleontological schools, including: Hinchliffe (1977, 1985, 1989); Tarsitano and Hecht (1980); Hinchliffe and Griffiths (1983); Hinchliffe and Hecht (1984); Thulborn (1984: 126–127, character 19); Burke and Feduccia (1997); Chatterjee (1998b); G. P. Wagner and Gauthier (1999); Chure (2001), regarding *Allosaurus*; Feduccia and Nowicki (2002); Larsson and Wagner (2002, 2003). Paleontological interpretations of quasi-avian manus began in the late 19th century (Huxley 1870), and sustained by Lambrecht (1914, 1931, 1933), and Romer (1956: fig. 385F)—in the absence of explicit support for the membership of Aves among Theropoda. This hypothesis currently is accepted by a prominent majority of systematists (e.g., Chiappe and Witmer 2002).

This division of opinion led the authors of the *Nomina Anatomica Avium* (Baumel et al. 1993) to adopt a nomenclatural compromise designating the elements (in craniocaudal order) as digiti alularis, majoris, et minoris (Baumel and Witmer 1993). Currently, embryological and paleontological data support the identification of the three digiti manus avium as homologous with digiti I, II, et III of nonavialian Theropoda. Enumeration aside, embryonic Neornithes (especially palaeognathous taxa) variably manifest an ephemeral cartilago ossis metacarpale IV (Degen 1894; Beddard 1898a).

1576. Ossa carpi distalia, status:
a. present; **b.** absent *in toto*;
x. noncomparable (*Aepyornis*).

1577. Ossa carpi distalia, forma generalis:
a. cuboid, facies articulares distinct;
b. subplanar, facies articulares indistinct;
x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—See: Holtz (1994a: appendix 1, character 59); Holtz (2000 [1998]: appendix I, character 251).

1578. Ossa carpi distalia, os scapholunare ("semilunate carpal"), status et forma *sensu* size, articulationes carpo-carpometacarpalia (**ordered**):
a. present and distinct, large, articulatio(nes) including *entirety* of extremitates proximales of ossa metacarpalia I (primus, alularis) et II (secundus, majus);
b. present and distinct, small, but articulatio(nes) including *entirety* of extremitates proximales of ossa metacarpalia I (primus, alularis) et II (secundus, majus);
c. present and distinct, small, and articulatio(nes) including only extremitates proximales of ossa metacarpalia I (primus, alularis) et II (secundus, majus);
d. absent as distinct element, incorporated by synostosis with extremitates proximales of both ossa metacarpalia majus et minus;
x. noncomparable (Dinornithiformes).

Note.—Here, "present" means discernable as separate element and not incorporated with ossa metacarpalia, and "absent" means not discernable as separate element in adults and hence synostotic with ossa metacarpalia; i.e., presumably the element or its homologue is present in all Theropoda. See: Steiner (1922); Montagna (1945); Holmgren (1955); Romanoff (1960); Berger (1966); Seichert and Reichter (1972); and Hinchliffe (1985). Limited ontogenetic data precludes firm inferences concerning whether the "semilunate carpal" element comprises one or two carpal primordia, confounding issues of coverage of extremitates metacarpalia by "semilunate carpal" or subunits thereof (treated as separate characters by Norell et al. (2001), J. M. Clark et al. (2001), and Xu (2002).

See: Ostrom (1969) on *Deinonychus* or Ostrom (1976a) on *Archaeopteryx*, concerning nomenclatural confusion pertaining to the "semilunate carpal"; Gauthier (1986: text characters 21 and 75); Sereno and Rao (1992); Russell and Dong (1994b [1993b]: list B, character 8); Holtz (1994a: appendix 1, character 42); Novas (1996: appendix, character 46); Sues (1997: appendix 1, character 32); Makovicky and Sues (1998: appendix 1, character 69); Chatterjee (1999: appendix II, character 60); Xu et al. (1999a: character 62), in reference to presence of "semilunate distal carpal"; Holtz (2000 [1998]: appendix I, characters 252–253) distinguish os carpi distale from synostosis carpometacarpus; Chiappe (2001a: appendix 1, character 101, part); Ji et al. (2001), regarding unnamed dromaeosaurid NGMC 91-A; Norell and Clarke (2001: appendix I, character 139), treated similarly by J. A. Clarke (2002: appendix I, character 139), J. A. Clarke and Norell (2002: appendix 2, character 139), and J. A. Clarke (2004: appendix 1, character 139); Norell et al. (2001: appendix 1, characters 147 and 149); Norell and Clarke (2001: appendix I, character 140); Chiappe (2002: appendix 20.2, characters 100 [presence] and 101 [synostosis]); J. M. Clark et al. (2002a: appendix 2.2, characters 149 and 151); Maryanska et al. (2002: appendix 1, characters 136–137); Sereno et al. (2002), regarding *Sinornis*; Xu (2002: suite II, characters 174 and 176); Xu et al. (2002a: supplement, character 121); Zhou and Zhang (2002: appendix III, characters 139–140); Hwang et al. (2004: characters 146 and 148); Xu and Norell (2004: supplement, characters 146 and 148); Ji et al. (2005: supplement, part I, character 139).

1579. Ossa carpi distalia, "os scapholunare" ("semilunate carpal"), status et forma generalis (**ordered**):
a. absent;
b. present, (*i*) aspectus proximalis semilunate, aspectus cranialis rectangular (*Coelophysis*, *Dilophosaurus*, *Syntarsus*, *Allosaurus*), or (*ii*) (sub)discoid;
c. present, (semi)lunate, typically including transverse sulcus trochlearis;
x. noncomparable by reduction or absence of ossa alae (Aepyornithiformes, Dinornithiformes).

Note.—Most Neornithes assessed by ontogenetic evidence. See: Gauthier (1986: text character 75); Sereno and Rao (1992); Pérez-Moreno et al. (1994: legend for fig. 3, character 18); Sereno et al. (1994: footnote 12); Chatterjee (1995: character 13); Sereno et al. (1996: footnote 45, character 9); Novas (1997: appendix, character 47); Novas and Puerta (1997), see identical characters in Novas (1997); Chiappe et al. (1998: character 53); Forster et al. (1998: supplement, character 70); J. D. Harris (1998: appendix 2, character 96); Xu et al. (1999b: character 52), in reference to "distal radial carpal, proximodistally flattened or semilunate"; Azuma and Currie (2000: appendix 1, character 18); Currie and Carpenter (2000: appendix 1, character 75); Holtz (2000 [1998]: appendix I, character 255), regarding "full development" of transverse trochlea; Chiappe (2001a: appendix 1, character 100); Sereno (2001: table 2, character 46); Sereno et al. (2002), regarding *Sinornis*; Ji et al.

(2003a: 23), regarding *Shenzhouraptor*; Rauhut (2003: character 146). See: Steiner (1922); Montagna (1945); Holmgren (1955); Romanoff (1960); Berger (1966); Seichert and Reichter (1972); Hinchliffe (1985); Padian and Chiappe (1998b), concerning synostosis of ossa carpalia distales.

Ossa Metacarpalia

Note.—See: Larsson and Wagner (2002), in which a pentadactyl *Grundplan* for ala avium is proposed.

1580. Os metacarpale primus (I, alulare), status et typus (**ordered**):
a. present, distinguishable, comparatively elongate, extending significantly distad to symphysis intermetacarpalis proximalis;
b. present, distinguishable, comparatively truncate, extending no farther distad than symphysis intermetacarpalis proximalis;
c. present, diminutive, synostotic with os metacarpale II (margo cranialis) et phalanx proximalis digiti I;
d. present, vestigial; **e.** absent;
x. noncomparable (Dinornithiformes).
Note.—See: W. K. Parker (1888a, c) and Lowe (1928a); S. L. Olson and Hasegawa (1979, 1985, 1996); Stephan (1979); S. L. Olson (1980).

1581. Os metacarpale secundus (II, majus), typus (**unordered**):
a. structurally distinguishable from ossa metacarpalia I et III, spatium intermetacarpale wide;
b. closely synchondrotic with ossa metacarpalia I et III, spatium intermetacarpale fissuriform;
c. closely synchondrotic with ossa metacarpalia I et III, spatium intermetacarpale obsolete or absent;
x. noncomparable (Dinornithiformes).
Note.—See: W. K. Parker (1888a, c) and Lowe (1928a), concerning ratites; Romanoff (1960).

1582. Os metacarpale tertius (III, minus), status (**ordered**):
a. present during ontogeny and functional in adult;
b. present during ontogeny, but rendered indistinguishable in adult through synchondrosis, resulting in status definitivum as eminentia on basis metacarpale II or vestigium;
c. absent;
x. noncomparable (Dinornithiformes).
Note.—See: W. K. Parker (1888c), concerning ungues of ratites; Romanoff (1960).

1583. Ossa metacarpalia quartus (IV), status definitivum:
a. present, os metacarpale IV retained as separate, (semi)functional remnant, some taxa retaining corresponding digiti;
b. absent, but perhaps present during early ontogeny, but rendered indistinguishable in adult by synchondrosis with os metacarpale III;
x. noncomparable (Dinornithiformes).
Note.—See: Romanoff (1960); interpretation of the identity of ossa metacarpalia avium renders differentiation of states given problematic. Under scheme followed herein, os metacarpale V is absent entirely in all avialians, and os metacarpale IV is small or absent.

1584. Ossa metacarpalia quintus (V), status definituvum:
a. present, os metacarpale V retained as separate, semifunctional remnant, some taxa retaining corresponding digiti;
b. absent;
x. noncomparable (Dinornithiformes).
Note.—See: Romanoff (1960); Weishampel et al. (1990). Interpretation of the identity of ossa metacarpalia avium renders differentiation of states given problematic. Under scheme followed herein, os metacarpale V is absent entirely in all avialians, and os metacarpale IV is small or absent.

1585. Os metacarpale alulare (I, primus), foramen intermetacarpale, status:
a. absent;
b. present, at least typical of *Genyornis*.
Note.—Foramen intermetacarpale is a subcircular passage between ossa metacarpalia I et II in some or most Dromornithidae.

1586. Os metacarpale alulare (I, primus), size relative to that of os metacarpale II (**ordered**):
a. less than one-third of latter;
b. between one-third and one-half of latter;
c. greater than one-half but less than totality of latter;
d. subequal to latter;
x. noncomparable (Aepyornithiformes, Dinornithiformes).
Note.—See: W. K. Parker (1888c), concerning ungues of ratites; Gauthier (1986: text character 61), in which os metacarpale I is compared to ossa metacarpalia II (especially) and III, Holtz (1994a: appendix 1, character 124); J. D. Harris (1998: appendix 2, character 98); Currie and Carpenter (2000: appendix 1, character 77); Holtz (2000 [1998]: appendix I, character 260), revised to permit logical ordering; Xu et al. (2002a: supplement, character 122), in which states were delimited differently.

1587. Os metacarpale alulare (I, primus), facies cranialis, forma:
a. hyperbolic (“hourglass-shaped”) and moderately craniocaudally expanded, constricted immediately proximal to facies articularis alularis;
b. broadly convex or cylindrical;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—See: Chiappe (2001a: appendix 1, character 106); Norell and Clarke (2001: appendix I, character 143); treated similarly by J. A. Clarke (2002: appendix I, character 143), J. A. Clarke and Norell (2002: appendix 2, character 143), and J. A. Clarke (2004: appendix 1, character 143); Chiappe (2002: appendix 20.2, character 106); Chiappe and Walker (2002: appendix 11.1, character 23); Zhou and Zhang (2002: appendix III, character 143); Ji et al. (2005: supplement, part I, character 143).

1588. Os metacarpale majus (II, secundus), facies ventralis (internus, palmeris), situs dorsoventralis relative to that of os metacarpale minus (III, tertius):

a. equal, bases metacarpalia majus et minus coplanar dorsoventrally;

b. former dorsal to latter.

Note.—See: Holtz (2000 [1998]: appendix I, character 266, revised).

1589. Os metacarpale minus (III, tertius), forma *sensu* comparative width (especially to that of os metacarpale II):

a. absent, robust, width subequal to that of os metacarpale II;

b. present, "long and slender," width less than 70% that of os metacarpale II;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—See: Gauthier (1986); Holtz (1994a: appendix 1, character 14); J. D. Harris (1998: appendix 2, character 99); Azuma and Currie (2000: appendix 1, character 79); Currie and Carpenter (2000: appendix 1, character 78); Rauhut (2003: character 151).

1590. Os metacarpale minus (III, tertius), corpus metacarpale, facies caudalis, sectiones proximalis et intermedius, forma superficialis (**ordered**):

a. (sub)cylindrical;

b. (sub)laminar, flat;

c. slightly to moderately concave proximally;

d. deeply concave, forming conspicuous, longitudinal sulcus;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Sphenisciformes, *Aptornis*).

Note.—Not explicitly involving distal extent of sulcus caudalis metacarpi minoris (**new term**), but deep sulci tend to be more extensive. See: Livezey (1998b: appendix A, character 252).

1591. Ossa metacarpalia minus (III, tertius) et majus (II, secundus), corpus metacarpale, forma *sensu* relative lengths, primarily as reflected by relative distal extents of extremitates distales metacarpalia, facies articulares digitales (**ordered**):

a. os metacarpale II equal to or longer than os metacarpale III;

b. os metacarpale II moderately shorter than os metacarpale III, extremitas distalis of latter typically curving craniad to terminate between ossa metacarpalia et phalanges;

c. os metacarpale II conspicuously shorter than os metacarpale III, extremitas distalis of latter typically extending steplike distad to former;

x. noncomparable (*Aepyornis*, Dinornithiformes, *Apteryx*, *Aptornis*).

Note.—Condition in ascertained most readily with juvenile specimens, in which os metacarpale III can be seen passing distad to os metacarpale II and partly between extremitas distalis of latter and facies articularis proximalis of phalanx proximalis metacarpi majoris (e.g., specimen for Otididae).

See: W. K. Parker (1888c), concerning ungues of ratites; Livezey (1986: appendix 1, character 45); Livezey (1989: table 1, character 45); Pérez-Moreno et al. (1993); Holtz (1994a: appendix 1, character 44); Russell and Dong (1994a [1993a]: table 2, characters 39–40); Livezey (1996a: appendix 1, character 61); Ericson (1997: table 2, character 41); Sanz et al. (1997: footnote 29, character *viii*), especially with respect to state "c"; Xu et al. (1999a: character 67); De Klerk et al. (2000: 330, character 8), citing in turn Holtz (2000 [1998]); Holtz (2000 [1998]: appendix I, character 263, revised); Chiappe (2001a: appendix 1, character 105); J. A. Clarke and Chiappe (2001: character 48); Norell and Clarke (2001: appendix I, character 148), treated similarly by J. A. Clarke (2002: appendix I, character 148), J. A. Clarke and Norell (2002: appendix 2, character 148), and J. A. Clarke (2004: appendix 1, character 148); Chiappe (2002: appendix 20.2, character 105); Chiappe and Walker (2002: appendix 11.1, character 24); Dyke and Gulas (2002: appendix 1, character 29, polarity reversed), in reference to "projection"; Maryanska et al. (2002: appendix 1, character 142); G. Mayr (2002a: legend fig. 9, node 5, character 4); Zhou and Zhang (2002: appendix III, character 148); Ji et al. (2005: supplement, part I, character 148).

1592. Os metacarpale minus (III, tertius), corpus metacarpale, facies articularis proximalis, forma *sensu* width relative to homologous segment of ossa metacarpalia I et II:

a. expanded, width subequal to those of latter;

b. not expanded, very slender relative to latter.

Note.—See: Gauthier (1986); Rauhut (2003: character 152).

1593. Os metacarpale IV, status et forma, latter *sensu* length relative to that of os metacarpale II, and retention of phalanges (**ordered**):

a. present, more than half length of os metacarpale II, in articulation with two or more phalanges, including distalmost phalanx ungualis;

b. present but vestigial, possessed of digit but lacking distalmost phalanx ungualis;

c. present but vestigial, lacking phalanges entirely;
d. absent entirely;
x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—See: Gauthier (1986), considered synapomorphic of Tetanurae; Novas (1994 [1993]: appendix, character 37, appended), with respect to os metacarpale and basic condition; Novas (1994 [1993]: appendix, character 15) with respect to associated numbers of phalanges (three or fewer, more than three) in corresponding digitus; J. D. Harris (1998: appendix 2, character 100); Currie and Carpenter (2000: appendix 1, character 79); Holtz (2000 [1998]: appendix I, character 257).

1594. Os metacarpale alulare (I, primus), forma superficialis (**unordered**):
a. unremarkable, essentially a semi-elongate, rectangular, dorsoventrad laminate corpus;
b. massive, depressed, and quadrangular;
c. short, vestigial, oriented craniad or (rarely) distad.

Note.—See: Andors (1992: table 2, character 34); Chiappe et al. (1998: character 57); Ji et al. (1998: supplement, character 57); Chiappe (2002: appendix 20.2, character 107).

1595. Os metacarpale alulare (I, primus), length relative to breadth:
a. significantly longer than broad;
b. approximately as broad as long.

Note.—See: Rauhut (2003: character 164).

1596. Os metacarpale alulare (I, primus), length relative to that of os metacarpale majus (II, secundus):
a. former greater than one-third of latter;
b. former less than one-third of latter;
x. noncomparable, ossa absent entirely (Dinornithiformes, *Aptornis*).

Note.—See: Tarsitano and Hecht (1980); Gauthier (1986: text character 61); Pérez-Moreno et al. (1994: legend for fig. 3, character 19); Russell and Dong (1994a [1993a]: table 2, character 41); Russell and Dong (1994b [1993b]: list A, character 9, part), combining both length and robustness; Holtz (1994a: appendix 1, character 124); Chiappe et al. (1998: character 56); Forster et al. (1998: supplement, character 62); Ji et al. (1998: supplement, character 56); Xu et al. (1999a: character 64); Xu et al. (1999b: character 45); Azuma and Currie (2000: appendix 1, character 69); Holtz (2000 [1998]: appendix I, character 260); Xu et al. (2000: supplement, character 32); Norell et al. (2001: appendix 1, character 150); J. M. Clark et al. (2002a: appendix 2.2, character 152); Maryanska et al. (2002: appendix 1, character 140); Xu (2002: suite II, character 177); Hwang et al. (2004: supplement, character 149); Xu and Norell (2004: supplement, character 149).

1597. Os metacarpale alulare (I, primus), facies articularis phalanx alularis (et articulatio metacarpophalangealis alulae), status:
a. present; **b.** absent;
x. noncomparable, ossa alae absent (Dinornithiformes), modally synostotic (*Aptornis*).

Note.—See: Bledsoe (1988: appendix, character 31); Livezey (1994); K. Lee et al. (1997: appendix 1, character 15).

1598. Os metacarpale alularis (I, primus), facies articularis distalis, symmetry condylorum, forma:
a. approximately symmetrical;
b. strongly asymmetrical, condylus medialis distinctly proximal to condylus lateralis.

Note.—See: Sereno (1993); Rauhut (2003: character 149).

1599. Ossa alulare (I, primus) et metacarpale majus (II, secundus), facies articularis (situs synostosis) intermetacarpalis proximalis, situs proximodistalis relative to corpus of os metacarpale I:
a. former coincident with terminus proximalis of os metacarpale I;
b. former extending distally well into corpus ("diaphysis") of os metacarpale I;
x. noncomparable by absence of spatium intermetacarpale (Dromornithidae).

Note.—See: Holtz (2000 [1998]: appendix I, character 261).

1600. Os metacarpale minus (III, tertius), corpus metacarpalia, robustness (craniocaudal diameter) relative to that of os metacarpale II, forma:
a. substantial and subequal, diameter at least one-half that of latter;
b. diminutive and markedly disparate, diameter less than one-half that of latter;
x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—See: Gauthier (1986: text character 76, part); Bledsoe (1988: appendix, character 33), discounted by K. Lee et al. (1997: appendix 2) for ratites; Pérez-Moreno et al. (1993); Russell and Dong (1994b [1993b]: list B, character 9, part); Elzanowski (1995: characters E1 and E4, at least with respect to relative diameters); Sereno et al. (1996: footnote 45, character 10); Sues (1997: appendix 1, character 34); Livezey (1998b: appendix A, character 247); Sereno (1999: character 20); Xu et al. (1999a: character 66); Holtz (2000 [1998]: appendix I, character 264), resequenced above to permit logical ordination of states; Norell and Clarke (2001: appendix I, character 141), treated similarly by J. A. Clarke (2002: appendix I, character 141), J. A. Clarke and Norell (2002: appendix 2, character 141), and J. A. Clarke (2004: appendix 1, character 141); Maryanska et al. (2002: appendix 1, characters 144–145); Suzuki et al. (2002: character 15); Zhou and Zhang (2002: appendix III, character 141); Ji et al. (2005: supplement, part I, character 141).

1601. Os metacarpale minus (III, tertius), diameter of corpus relative to that of os metacarpale majus (II, secundus), forma:

a. equal to moderately less;

b. conspicuously slimmer, apparently fragile, in sectiones translucent;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—An extension of previous character pertinent only to Neornithes; anomalous brachyptericine genus *Atelornis* (not primary exemplar herein), characterized by an exceptionally tumulous os metacarpale majus, exceeding diameter of os metacarpale III by a factor of at least two (Cracraft 1971a: fig. 8).

1602. Os metacarpale majus (II, secundus), comparative dorsoventral position of facies dorsalis and proximodistal alignment (caudal perspective) of element relative to that of os metacarpale minus (III, tertius), forma (**unordered**):

a. proximodistally parallel, os metacarpale majus dorsoventrally equal to os metacarpale minus throughout;

b. proximodistally parallel, os metacarpale majus variably but notably dorsal to os metacarpale minus throughout;

c. proximodistally sloping ventrad, latter parallel or partially ventral to former at synostosis proximalis and uniting at vertex ventralis of synostosis distalis, in part related to narrowing of os metacarpale minus distad;

d. proximodistally parallel, os metacarpale majus almost completely dorsal to os metacarpale minus, latter *ventral* to former at synostosis proximalis, parallels margo ventralis of former to vertex ventralis at synostosis distalis, in some taxa associated with dorsoventral curvature;

x. noncomparable (*Aepyornis*, Dinornithiformes, *Apteryx*, *Aptornis*).

Note.—Character related to proximodistal decrease in breadth of os metacarpale minus relative to os metacarpale majus, a sloping coincident with craniocaudal lamination or proximal concavitates; note especially pronounced reduction and laminar forma in Falconiformes and Strigiformes. See: Livezey (1998b: appendix A, character 246), with respect to orientation of os metacarpale minus (III), pars proximalis, facies caudalis, relative to os metacarpale majus; Livezey (1998b: appendix A, character 250), os metacarpale majus (II, secundus), regarding correlated prominence and alignment of jugum on facies ventrocaudalis (bordering spatium intermetacarpale) of os metacarpale majus (II, secundus); J. A. Clarke and Chiappe (2001: character 39).

1603. Os metacarpale majus (II, secundus), facies dorsalis, sulci tendinosi, pars proximalis (sulci tendinorum mm. extensor longus digiti majoris et extensor digitorum communis), forma superficialis *sensu* comparative proximodistal extent (**ordered**):

a. obsolete, facies dorsalis essentially unmarked;

b. present, extent limited to distal one-half of corpus;

c. present, extending for almost or actually the entire corpus, in some taxa distally prominent and forming pons aut arcus osseum;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—See: Cracraft (1971a), regarding hyperapomorphic state of purportedly brachyptericine genus *Atelornis*, a condition distinct from hypothetically confamilial (Leptosomatidae) *Leptosomus*; Livezey (1986: appendix 1, character 39); Livezey (1989: table 1, character 39); Livezey (1996a: appendix 1, character 58); Ericson (1997: table 2, character 36). See concerning sulci *per se*: Strauch (1978: character 48), reanalyzed by Björklund (1994: appendix) and Chu (1995); Livezey (1986: appendix 1, character 44); Livezey (1989: table 1, character 44); Livezey and Humphrey (1992: fig. 21); Livezey (1995c: appendix II, character 22); Livezey (1996a: appendix 1, character 59); Livezey (1998b: appendix A, character 253); J. A. Clarke and Chiappe (2001: characters 51–52); Dyke (2001a: appendix 1, character 24); G. Mayr (2001f: 2).

1604. Os metacarpale majus (II, secundus), pars proximalis, facies dorsalis, processus (lamina) intermetacarpalis (impressio aut tuberculum insertii m. extensor carpi ulnaris), status et forma (**unordered**):

a. absent;

b. impressio, situs on os metacarpale majus, tumulus aut tuberculum;

c. impressio, but situs shifted to os metacarpale minus, similar to that where processus (below) extends to latter element, impressio;

x. noncomparable (ratites, Dromornithidae, *Aptornis*).

Note.—Synonymous with "tuberositas muscularis" of Lambrecht (1914) and Stegmann (1965), serving as situs ancorae (tuberculum) insertii m. extensor carpi ulnaris (Baumel and Witmer 1993: annotation 221), *contra* statement by Ballmann (1969a: 25) associating feature with m. *flexo*r carpi ulnaris. Also referred to as "flexor tubercle" by Woolfenden (1961) and "tuberculum muscularis" by Stegmann (1978: fig. 7A). Schreiweis (1982: 12) described entirely tendinous condition of m. extensor carpi ulnaris and confirmed insertio on margo caudalis ossis metacarpale majus.

See: Holman (1961, 1964); Harrison (1969); Strauch (1978: character 47), reanalyzed by Björklund (1994: appendix) and Chu (1995); Livezey (1986: appendix 1, character 43); Livezey (1989: table 1, character 43); Livezey and Humphrey (1992: fig. 20), coding relative proximodistal position in *Tachyeres* (Anatidae); Livezey (1995b: appendix 1, character 14); Livezey (1995c: appendix II, character 21); Livezey (1996a: appendix 1, character 57); Livezey (1996b: appendix 1, character 33); Livezey (1996c: character 7); Ericson (1997: table 2, character 39); Livezey (1997a: appendix 1, character 74; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, characters 245 and 249); G. Mayr and Mourer-Chauviré (2000: fig. 11, node 2); J. A. Clarke and Chiappe (2001: character 45); Dyke (2001b: appendix 1, character 74); Norell and Clarke (2001: appendix I, character 149), treated similarly by J. A. Clarke (2002: appendix I, character 149), J. A. Clarke and Norell (2002: appendix 2, character 149), and J. A. Clarke (2004: appendix 1, character 149); Dyke and Gulas (2002: appendix 1, character 26); Zhou and Zhang (2002: appendix III, character 149); Dyke et al. (2003: appendix 1, character 66), employed again by Dyke (2003: table 1); G. Mayr et al. (2003: appendix 1, character 44), including finding by Stegmann (1965) that insertio m. extensor carpi ulnaris shifts to topographically similar situs on os metacarpale minus (III) in *Numida*, *Upupa*, *Phoeniculus*, and *Tockus* in clades otherwise characterized by prominent "processus intermetacarpalis"; G. Mayr (2004d: appendix I, character 22); G. Mayr (2005a: appendix 1, character 23); Ji et al. (2005: supplement, part I, character 149).

1605. Os metacarpale majus (II, secundus), pars proximalis, facies ventralis (medialis), expansion relative to pars distalis corporis, status:
a. present; **b.** absent.
Note.—See: Sereno (1993); Rauhut (2003: character 150).

1606. Os metacarpale minus (III, tertius), pars proximalis et intermedius, facies ventralis, distinct laminar broadening creating (*i*) oblique, caudodorsal orientation of element with terminus proximalis; (*ii*) uniquely broad and synchondrosis intermetacarpalis proximalis (**emended term**) extending from processus pisiformis to margo dorsalis of fovea carpalis caudalis; (*iii*) variably elongate, prominent jugum pisiformis (**new term**) extending from processus pisiformis and extending distoventrad to spatium intermetacarpale; and (*iv*) apparently truncated collum metacarpalis (**new term**), status:
a. absent;
b. present, causing an apparent truncation of collum carpometacarpalis (**new term**);
x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).
Note.—See: Ericson (1997: table 1, character 65), in reference to S. L. Olson (1985); Livezey (1998b: appendix A, character 248).

1607. Os metacarpale majus (II), pars proximalis, facies cranialis, protuberantia metacarpalis, status:
a. absent;
b. present, variably conformed tumulus or tuberositas;
x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromornithidae, Sphenisciformes, *Aptornis*).
Note.—New term endorsed by Baumel and Witmer (1993: annotation 221). Presumably serves as a guide for tendo m. extensor digiti majoris or possibly as ancora origii m. abductor digiti majoris. See: Stegmann (1962, 1965, 1978); Pocock (1966); Harrison (1969); Feduccia and Olson (1982: fig. 11); Gauthier (1986: text character 45); G. Mayr and Mourer-Chauviré (2000: fig. 10); G. Mayr (2004d: appendix I, character 23); G. Mayr (2005a: appendix 1, character 24).

1608. Os metacarpale majus (II, secundus), length relative to that of os metacarpale IV (quartus):
a. former more than half the latter;
b. former less than half the latter;
x. noncomparable by absence of os metacarpale IV (Neornithes).
Note.—See: Holtz (2000 [1998]: appendix I, character 268).

1609. Ossa metacarpalia majus (II) et minus (III), facies dorsalis, papillae remigiales caudales, status:
a. absent or indiscernable; **b.** present.
Note.—See: Chatterjee (1995: character 12).

1610. Os metacarpale minus (III), pars intermedius, margo caudalis, angulus m. ulnometacarpalis dorsalis (**new term**), status:
a. absent; **b.** present;
x. noncomparable (Aepyornithiformes, Dinornithiformes).
Note.—See: Stegmann (1978); Butendieck (1980: fig. 44); Butendieck and Wissdorf (1981); Butendieck et al. (1981); G. Mayr and Clarke (2003: appendix A, character 85), expressed in terms of bowing of element and resultant spatium intermetacarpale; Dyke and van Tuinen (2004: appendix 1, character 61). At least in some taxa, marks terminus distalis insertii m. ulnometacarpalis dorsalis and often is associated with torsion and variable concavitates et curvae of os metacarpale minus (III). This feature may serve analogously as the expanded and torqued sectio proximalis of os metacarpale minus, e.g., Cariamidae and Psophiidae.

1611. Os metacarpale minus (III), pars distalis, caudal divergence by caudal curvature or subangularity from os metacarpale majus (II) and craniocaudal broadening of symphysis intermetacarpalis distalis, creating distal broadening (typically maximal) of spatium intermetacarpalis, status:

a. absent; **b.** present, conspicuous;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Sphenisciformes, *Aptornis*).

Note.—See: G. Mayr and Clarke (2003: appendix A, character 86); G. Mayr et al. (2003: appendix 1, character 43); Dyke and van Tuinen (2004: appendix 1, character 62).

1612. Os metacarpale minus (III, tertius), extremitas proximalis metacarpalis, facies articularis proximalis, forma (planum transversus):

a. approximately quadrangular;

b. triangular, facies dorsalis with lamina oriented laterad and overlapping os metacarpale IV (if present), extremitas proximalis.

Note.—See: Holtz (2000 [1998]: appendix I, character 267), citing Russell and Dong (1994 [1993]); Rauhut (2003: character 156).

1613. Os metacarpale minus (III, tertius), forma *sensu* lateromedial curvature (*not* slant) of corpus relative to that of os metacarpale II:

a. straight, i.e., ossa metacarpalia II et III essentially linear in parallel;

b. dorsally (laterally) bowed, resulting in convexity of margo lateralis corporis.

Note.—See: Ligon (1967: table 5); Tarsitano and Hecht (1980); Gauthier (1986: text character 76, part); Andors (1992: table 2, character 35); Sanz and Buscalioni (1992: character 3, part); Russell and Dong (1994a [1993a]: table 2, character 42); Russell and Dong (1994b [1993b]: list B, character 9, part); Livezey (1997a: appendix 1, character 75; *corrigenda*, Livezey 1998a); Forster et al. (1998: supplement, character 63); Livezey (1998b: appendix A, character 251); Makovicky and Sues (1998: appendix 1, character 71); Xu et al. (1999b: character 46); Holtz (2000 [1998]: appendix I, character 265); Xu et al. (2000: supplement, character 33); Dyke (2001b: appendix 1, character 75); G. Mayr et al. (2003: appendix 1, character 43); Rauhut (2003: character 157); G. Mayr (2004a: appendix 1, character 45); G. Mayr and Ericson (2004: appendix I, character 59).

1614. Ossa metacarpalia majus (II, secundus) et minus (III, tertius), pronounced dorsal (lateral) curvature of corpora metacarpalia in parallel, status:

a. absent; **b.** present;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Sphenisciformes, *Aptornis*).

Note.—I.e., curvature characterized is common to both primary ossa metacarpalia relative to planum craniocaudalis.

1615. Ossa metacarpalia I, II, et III, foveae ligamentorum collateralium ("foveae distales"), status et forma (**unordered**):

a. present, weakly apparent;

b. present, distinct with prominent rima;

c. obsolete or absent.

Note.—See: Sereno et al. (1993: legend for fig. 3a); Novas (1994 [1993]: appendix, character 36) identified these as "extensor pits," explained in text as depressiones for origiones of mm. extensoria on the distal ends of ossa metacarpalia and acting on corresponding phalanges. It is not clear whether these did not reflect instead foveae ligamentorum collateralium in those taxa having separate ossa metacarpalia (as treated here for *Archaeopteryx*), and the possible manifestation of homologous features in taxa possessed of definitive carpometacarpi, averred to manifest them.

1616. Ossa metacarpalia I–II, articulationes metacarpophalangeales, forma:

a. "ginglymoid" or dorsoventrally compressed, subtrochlear;

b. subspheroidal.

Note.—See: Makovicky and Norell (2004: character 210); Xu and Norell (2004: supplement, character 210).

1617. Ossa metacarpalia I–III, articulationes metacarpophalangeales, hyperextensibility and correlated enlargement of impressiones (fossae) mm. extensorium (**new term**), status:

a. present; **b.** absent.

Note.—Synonymous with status of "extensor pits." See: Pérez-Moreno et al. (1994); Holtz (2000 [1998]: appendix I, character 269).

Carpometacarpus (Proprius)

Note.—Characters pertaining to individual ossa metacarpalia (i.e., partes majores carpometacarpi or ossa metacarpalia I (alulare, primus), II (majus, secundus), III (minus, tertius), and in basal taxa IV (quartus) et V (quintus) are treated sequentially in groupwise fashion in the first subsection of characters. Following this elementwise suite of characters, anatomical features intrinsically pertaining to the gradation of the synostotic (definitive) carpometacarpus of modern Aves are treated in the order given in the *Nomina* (Baumel and Witmer 1993), with new nomenclatural proposals inserted accordingly.

Also, the manus of ratites is strongly derived *sensu* manifesting progressive reduction, and this generality is associated with unusually high intraspecific variation in osteological characters, including such macro-characters as synchondrosis and loss of ossa metacarpalia, and numbers of phalanges (including ungues) retained by digiti manus (W. K. Parker 1888c).

Nomenclature of traditionally recognized osteological features of the manus, although stable for some, fails for the most part to associate the name of the skeletal feature with the associated aspect of the overlying musculature. For this reason, the following list of osteological terms and associated myological equivalents is provided:

Carpometacarpus:

- Processus extensorius—ancora tendinis longus propatagialis et/aut tendinis insertii m. extensor (meta)carpi radialis
- Processus intermetacarpalis—tuberculum insertionis tendinis m. extensor (meta)carpi ulnaris
- Processus distalis (Stegmann 1978)—tuberculum insertionis proximalis tendinis m. flexor digiti profundus

Phalanx digiti alularis:

- Extremitas proximalis phalangis, angulus cranialis—tuberculum insertii tendinis m. extensor longus alulae
- Margo (pila) cranialis phalangis—tuberculum tendinorum insertii mm. abductor alulae et flexor alulae
- Corpus phalangis, facies dorsalis—ancorae tendinorum insertii mm. extensor brevis alulae et extensor digitorum communis
- Corpus phalangis, facies caudalis—area insertii m. adductor alulae

Phalanx proximalis digiti majoris:

- Extremitas proximalis phalangis, angulus cranialis—tuberculum insertii tendinis m. flexor digiti majoris
- Margo (pila) cranialis phalangis, pars distalis—tuberculum insertii tendinis proximalis m. flexor digiti superficialis

Phalanx distalis digiti majoris:

- Extremitas proximalis phalangis, angulus cranialis—tuberculum insertii tendinis m. extensor longus digiti majoris
- Extremitas proximalis phalangis, angulus caudalis—tuberculum insertii tendinis m. interosseus dorsalis
- Extremitas distalis phalangis, margo cranialis—tuberculae tendinorum insertiorum distales mm. flexores digiti superficialis et profundus
- Extremitas distalis phalangis, margo caudalis—tumulus tendinis insertii m. interosseus ventralis

Phalanx digiti minoris:

- Extremitas proximalis phalangis, margo caudalis—tuberculum insertii tendinis m. flexor digiti minoris;
- Corpus phalangis, facies dorsalis—area tendinis insertii (ramus proximalis) m. interosseus ventralis (rare).

1618. Carpometacarpus, complexus ossium manus prodigitalis, status *in toto*:
a. present; **b.** absent;
x. noncomparable (*Aepyornis*).
Note.—See: Ji et al. (2003a: 23) regarding *Shenzhouraptor*.

Extremitas proximalis carpometacarpi

1619. Extremitas proximalis carpometacarpi, os metacarpale alulare, proximodistal length relative to that of digitus alularis (**ordered**):
a. longer; **b.** approximately equal;
c. smaller;
x. noncomparable by absence of ossa alae (Dinornithiformes), absence of digitus alulae (Dromornithidae).
Note.—Length of os metacarpale alulare is "basal," i.e., proximodistal length parallel to os metacarpale major; in some taxa (e.g., *Chauna*), length perpendicular to os metacarpale majus (including processus extensorius) is significantly greater.

1620. Extremitas proximalis carpometacarpi, os metacarpale alulare, ratio with that of phalanx proximalis digiti alularis, proximodistal length (**ordered**):
a. less than 1.0; **b.** between 1.0 and 1.5;
c. greater than 1.5.
Note.—See: Rauhut (2003: character 158).

1621. Extremitas proximalis carpometacarpi, processus alularis, facies articularis alularis, angulus interossea metacarpalia alularis et majus, forma:
a. essentially 0°, or mutually subparallel, in which typical position of digitus alularis is aligned with and parallel to margo cranialis of os metacarpale majus (II, secundus), and facies articularis alularis is approximately perpendicular to os metacarpale II, margo cranialis;
b. exceeding 45°, or supradiagonality, forming calcar phalangis alularis (**new term**), in which typical position of digitus alularis is diagonally craniodistal;
x. noncomparable (most ratites).
Note.—Apomorphy of Rheidae also was confirmed for *Pterocnemia*. Possibly associated with apomorphic modification of m. flexor alulae from corpus fibrosus into a strong tendo. See: Livezey (1986: appendix 1, character 41); Livezey (1996b: appendix 1, character 29); Dyke and Gulas (2002: appendix 1, character 27).

1622. Extremitas proximalis carpometacarpi, processus alularis, processus extensorius, status et cranial extent (**ordered**):
a. absent or rudimentary;
b. present, evidently functional, but extending marginally beyond margo cranialis of processus alularis;

c. present, evidently functional, comparatively prominent, processus exceeds facies articularis by at least one-half width of latter;

x. noncomparable (Dinornithiformes, Dromornithidae).

Note.—See: Chiappe and Calvo (1994: appendix I, character 44); Chiappe (1995b: character 44); Elzanowski (1995: character N'2); Sanz et al. (1995, 1997: character 42); Chiappe (1996b: character 41); Chiappe et al. (1996: appendix 1, character 40); Chu (1998: appendix 1, character 103); Chiappe et al. (1998: character 55); Ji et al. (1998: supplement, character 55); Forster et al. (1998: supplement, character 61); Chatterjee (1999: appendix II, character 63); Chiappe (2001a: appendix 1, character 104); J. A. Clarke and Chiappe (2001: character 41); Norell and Clarke (2001: appendix I, character 142), treated similarly by J. A. Clarke (2002: appendix I, character 142), J. A. Clarke and Norell (2002: appendix 2, character 142), and J. A. Clarke (2004: appendix 1, character 142); Chiappe (2002: appendix 20.2, character 104); Zhou and Zhang (2002: appendix III, character 142), regarding presence of "anteroproximally projected muscular process"; Ji et al. (2005: supplement, part I, character 142).

1623. Extremitas proximalis carpometacarpi, processus alularis, processus extensorius, length relative to craniocaudal width of trochlea carpalis including osseus basis calcarius (**unordered**):

a. less, not part of calcar alae;

b. greater, calcar an osseus core for blunt calcar alae;

c. greater, calcar an osseus core for narrowly based, acuminate, keratin-covered calcar alae;

d. greater, calcar an osseus core for broadly based, acuminate, keratin-covered calcar alae;

e. equal or greater, calcar an irregular, variable, subspherical, multituberculate, often enormous lobus calcarius, covered by keratinized integumentum in life;

x. noncomparable (Dinornithiformes).

Note.—See: Strauch (1978: character 46), reanalyzed by Björklund (1994: appendix) and Chu (1995); Strauch (1985: character 18); Livezey (1986: appendix 1, character 42); Livezey (1989: table 1, character 42); Livezey (1996a: appendix 1, character 56); Livezey (1996b: appendix 1, character 30); Ericson (1997: table 2, character 37); Livezey (1998b: appendix A, character 239).

1624. Extremitas proximalis carpometacarpi (**new term**), trochlea carpalis, relative *proximal* extents (craniocaudal perspective) of rima dorsalis (externum) et rima ventralis (internum) (**ordered**):

a. former conspicuously greater than latter, defining approximately diagonal angulus;

b. former significantly greater than latter;

c. former slightly greater than or subequal to latter;

d. former equal to latter;

x. noncomparable, ossa alae or carpometacarpus proprius lacking (Aepyornithiformes, Dinornithiformes, *Apteryx*, Dromornithidae).

Note.—See: Bledsoe (1988: appendix, character 30); K. Lee et al. (1997: appendix 1, character 14); G. Mayr (2004d: appendix I, character 20), in terms of proximal and cranial extent; G. Mayr (2005a: appendix 1, character 21). For purposes of this characterization, "proximal" extent is intended for context in which wing is extended.

1625. Extremitas proximalis carpometacarpi (**new term**), trochlea carpalis, comparative dorsoventral profile (craniocaudal perspective) of rima dorsalis (externum) et rima ventralis (internum), forma (**ordered**):

a. distinctly flattened, virtually planar;

b. intermediate, with shallow sulcus trochlearis between rimae;

c. distinctly sulcoid, with prominent sulcus trochlearis between rimae;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Apteryx*).

Note.—Perspective implies that assessment of depth is that of proximalmost segment of sulcus trochlearis. See: Livezey (1998b: appendix A, character 236), which is descriptive of general depth of the trochlear "groove," as opposed to the relative extents of the ventral and dorsal rimae. Excluded brachyptericine genus *Atelornis* differs from purportedly confamilial genus *Brachyptericias* in markedly subacuminate margo trochlearis (internus) ventralis (Cracraft 1971a: fig. 8).

1626. Extremitas proximalis carpometacarpi, trochlea carpalis, facies articularis ulnocarpalis, rima dorsalis trochlearis (**new term**) relative to that of rima ventralis trochlearis (caudal perspective), terminus distalis, situs proximodistalis (**ordered**):

a. slightly proximad or subequal, former only slightly proximal to latter, or termina of rimae approximately equal in distal extent;

b. moderately proximad, but extending at least (or approximately) half the distance distad as rima ventralis trochlearis;

c. well proximad, extending less than half as distad as rima ventralis trochlearis;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromaiidae, Casuariidae, *Apteryx*, Dromornithidae, *Aptornis*).

Note.—Rima dorsalis includes intumescentia aut tumuli at terminus rimae, but assessed at rima proximal to any marked ventral irregularities or sloping. See: Holman (1961, 1964); Ericson (1997: table 1, character 64; table 2, character 38); Livezey (1998b:

appendix A, character 237); J. A. Clarke and Chiappe (2001: character 38).

1627. Extremitas proximalis carpometacarpi, trochlea carpalis, facies dorsalis, facies articularis ulnocarpalis, rima dorsalis trochlearis, terminus distalis (caudal perspective), forma (**unordered**):

a. essentially undistinguished, including modest irregularities or uniform conformation in parallel to rima ventralis;

b. marked by modest tumulus, apparently result of subterminal incisura and remnant of rima isolated thereby;

c. marked by prominent intumescentia;

d. marked by apparent terminal incisura or truncation, reflecting *limited* amelioration of embryonic inequality between ossa carpalia distalia—i.e., geometry of "os scapholunare" (proximal trochlea) and os giving rise to distal facies articularis ulnocarpalis of many Neornithes (e.g., juvenile *Pavo*, CM 9395)—an initial state perhaps modified in some Neornithes;

e. marked by apparent terminal incisura or truncation, reflecting virtual *absence* of modification of embryonic inequality between ossa carpalia distalia;

x. noncomparable (Dinornithiformes, Dromaiidae, Casuariidae, *Apteryx*, *Aptornis*).

Note.—Some juvenile skeletons (e.g., Otididae) indicate that the variable modifications of terminus caudodistalis rimae dorsalis may reflect the contribution of a third primordium among those of ossa carpi distalis. States other than "undistinguished" often indicated by asymmetry with respect to rima ventralis trochlearis, terminus caudalis.

See: Livezey (1986: appendix 1, characters 37 [corrected], 38, and 47); Livezey (1989: table 1, character 38); Livezey (1995b: appendix 1, character 13); Livezey (1995c: appendix II, characters 20 and 23); Livezey (1996a: appendix 1, character 55); Livezey (1996b: appendix 1, characters 28 and 32); Livezey (1996c: character 6); Ericson (1997: table 2, character 35); Livezey (1997b: appendix 1, character 11).

1628. Extremitas proximalis carpometacarpi, trochlea carpalis, facies ventralis, facies articularis ulnocarpalis (caudal perspective), terminus distalis, forma (**unordered**):

a. essentially undistinguished from rest of rima;

b. modest tumulus, apparently result of subterminal incisura and remnant of rima isolated thereby;

c. prominent intumescentia;

d. caudally prominent arcus including discernable terminus at approximate mid planum of fovea caudalis;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromaiidae, Casuariidae, *Apteryx*, *Aptornis*).

Note.—States other than "undistinguished" often indicated by asymmetry with respect facies articularis radiocarpalis, terminus caudalis.

1629. Extremitas proximalis carpometacarpi, trochlea carpalis, facies articularis ulnocarpalis, rima trochlearis ventralis, terminus distalis (caudal perspective), proximodistal orientation relative to facies ventralis of corpus carpometacarpalis:

a. essentially parallel;

b. distinctly dorsad;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—Character essentially reflects angulus between axis (majoris) proximodistalis of os metacarpale minus and axis proximodistalis of rima ventralis trochlearis in caudal perspective. See: Livezey (1986: appendix 1, character 48); Livezey (1996c: character 8).

1630. Extremitas proximalis carpometacarpi, trochlea carpalis, rima dorsalis (dorsal perspective), apex proximalis of rima dorsalis trochlearis (**new term**), forma (**unordered**):

a. transversely flat;

b. broad, stout, and rounded;

c. narrow, elongate, and terminally rounded;

d. distinctly angular, subacuminate, elongated proximally;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromornithidae).

Note.—See: Livezey (1998b: appendix A, character 238). May be related to some degree with feature listed by Russell and Dong (1994a [1993a]: table 2, character 43) concerning the shape of the "proximal articulation of metacarpal III."

1631. Extremitas proximalis carpometacarpi, collum metacarpalis (**new term**)—i.e., carpometacarpus distal to trochlea carpalis and proximal to synchondrosis intermetacarpalis proximalis (**new term**)—relative to trochlea carpalis, situs proximodistalis:

a. typical, symphysis intermetacarpalis proximalis significantly distal;

b. truncate, symphysis intermetacarpalis proximalis (i.e., apex proximalis of spatium) essentially parallel;

x. noncomparable (ratites, Dromornithidae).

Note.—See: Andors (1992: table 2, character 33). Note that another character is associated with truncation of the collum, but those are but a subset of the continuum treated here.

1632. Extremitas proximalis carpometacarpi, os metacarpale minus (III), proximal to synchondrosis intermetacarpalis proximalis (**emended term**), fossa pneumatica, status et situs (**unordered**):

a. absent;

b. present, on facies cranialis et/aut vertex of synchondrosis;

c. present, on facies caudalis of os metacarpale III distad to synchondrosis;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—See: G. Mayr and Mourer-Chauviré (2000: fig. 11, node 3).

1633. Extremitas proximalis carpometacarpi, facies ventralis, processus pisiformis, status (**ordered**):

a. absent; **b.** rudimentary; **c.** present;

x. noncomparable (Dinornithiformes).

Note.—Processus pisiformis acts as a "pulley"—trochlea pisiformis (**new term**)—that redirects angulus retractionis ligamenti m. flexor digitorum communis. See: Holdaway (1991: appendix 5.1, character 124); Norell and Clarke (2001: appendix I, character 145), treated similarly by J. A. Clarke (2002: appendix I, character 145), J. A. Clarke and Norell (2002: appendix 2, character 145), and J. A. Clarke (2004: appendix 1, character 145); Dyke and Gulas (2002: appendix 1, character 30); Zhou and Zhang (2002: appendix III, character 145); Ji et al. (2005: supplement, part I, character 145).

1634. Extremitas proximalis carpometacarpi, facies ventralis, processus pisiformis, situs:

a. comparatively central;

b. shifted toward processus extensorius, near facies articularis radiocarpalis;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—States of Rhamphastidae problematic due to rudimentary condition of processus.

1635. Extremitas proximalis carpometacarpi, facies ligamentalis ventralis, depressio infratrochlearis ventralis (**new term**), status:

a. absent; **b.** present, typically conspicuous.

Note.—Evidently emphasized by adjacent intumescentia unique to these taxa. See: J. A. Clarke and Chiappe (2001: character 47), in reference to "conspicuous fossa caudodistal to pisiform process" (Butendieck 1980: fig. 45, feature 13); Butendieck and Wissdorf (1981); Butendieck et al. (1981).

1636. Extremitas proximalis carpometacarpi, processus pisiformis et facies ligamentalis ventralis, joint prominence and proximity creating bifurcated aspect of processus pisiformis, status:

a. absent, facies ligamentalis ventralis subsessile and processus pisiformis apparently single;

b. present, facies ligamentalis ventralis prominent and terminus processi pisiformis apparently double;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—See: Dyke et al. (2003: appendix 1, character 67), in which elevated facies ligamentalis ventralis mistaken for subterminus of processus pisiformis.

1637. Extremitas proximalis carpometacarpi, processus pisiformis et facies ligamentalis ventralis, shared elevation creating lobulate planum encompassing both and creating aspect of expanded processus pisiformis, status:

a. absent; **b.** present;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Sphenisciformes, *Aptornis*).

1638. Extremitas proximalis et collum carpometacarpalia, facies ventralis, synchondrosis intermetacarpalis proximalis and associated manifestation of jugum metacarpo-pisiformis (**new term**), situs relative to processus pisiformis (**ordered**):

a. well distal to processus pisiformis, jugum absent;

b. immediately distal or extending to processus pisiformis, jugum rudimentary or vestigial;

c. coincident, synchondrosis of os metacarpale minus continuous with processus pisiformis, jugum metacarpo-pisiformis (**new term**) present;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromornithidae, *Aptornis*).

Note.—New feature in reference to jugum or ridge between processus pisiformis and corpus os metacarpale minus (III). See: Kurochkin (1995b: table 1, character 17), regarding "under proc. pisiformis near os metacarp. minus"; Livezey (1998b: appendix A, character 243); J. A. Clarke and Chiappe (2001: character 40).

1639. Extremitas proximalis carpometacarpi, facies ventralis, fossa infratrochlearis ventralis (**emended term**), status et forma:

a. absent or rudimentary or shallow;

b. present, deep, foveate;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—See: J. A. Clarke and Chiappe (2001: character 37).

1640. Extremitas proximalis carpometacarpi, facies ventralis, fossa infratrochlearis ventralis (**emended term**), foramen pneumaticum, status:

a. absent; **b.** present;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—Variably numerous foramina neurovascularia in this fossa, comparatively widely distributed taxonomically, does not qualify as apomorphic in this context.

1641. Extremitas proximalis carpometacarpi, facies dorsalis, fossa supratrochlearis, status:

a. absent, rudimentary or vestigial;

b. present, substantial, apparently elevating processus pisiformis.

Note.—See: J. A. Clarke and Chiappe (2001: character 43); Norell and Clarke (2001: appendix I, character 146), treated similarly by J. A. Clarke (2002: appendix I, character 146), J. A. Clarke and Norell (2002: appendix 2, character 146), and J. A. Clarke

(2004: appendix 1, character 146); Zhou and Zhang (2002: appendix III, character 146). Situs of ancora of ligamentum ulnocarpo-metacarpalis dorsalis; Ji et al. (2005: supplement, part I, character 146).

1642. Extremitas proximalis carpometacarpi, facies dorsalis, fossa supratrochlearis, foramen pneumaticum, status:
a. absent; **b.** present;
x. noncomparable (Aepyornithiformes, Dinornithiformes).

1643. Extremitas proximalis carpometacarpi, facies dorsalis, fossa (sulcus) supra-extensorius (**new term**), status:
a. absent; **b.** present, apneumatic;
c. present, enclosing fossa et/aut foramen pneumatica;
x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—See: J. A. Clarke and Chiappe (2001: character 44), in reference to “fossa directly proximal and cranial to the supratrochlear fossa.” Depth of the present sulcus is loosely correlated with the clarity of the fovea carpalis cranialis et margo trochlearis cranialis.

1644. Extremitas proximalis carpometacarpi, fovea carpalis caudalis, status et forma (**ordered**):
a. absent or negligibly defined;
b. present, shallow to moderately deep;
c. present, markedly deep, ovate;
x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—Where well defined, the immediately proximal caudal edge or rima of the trochlea—margo caudalis trochlearis—typically also is well defined. See: Livezey (1986: appendix 1, character 46), with respect to “cuneiform fossa”; Livezey (1996b: appendix 1, character 31); Livezey (1998b: appendix A, character 241); J. A. Clarke and Chiappe (2001: character 42), with respect to absence in basal taxa. Intraspecific variation evident in some taxa (e.g., Rallidae).

1645. Extremitas proximalis carpometacarpi, fovea carpalis caudalis, linea fovealis caudalis, i.e., impressio (fovea) origii m. flexor digiti minoris (**new term**), status:
a. absent;
b. present, defining prominent margo fovealis distalis;
x. noncomparable (Aepyornithiformes, Dinornithiformes, Sphenisciformes, *Aptornis*).

Note.—Possibly homologous with similarly located tuberculum, of doubtful utility given currently detected pattern.

1646. Extremitas proximalis carpometacarpi, fovea carpalis caudalis, fossa et/aut foramina pneumatica, status:
a. absent; **b.** present;
x. noncomparable (Aepyornithiformes, Dinornithiformes, Sphenisciformes, *Aptornis*).

1647. Extremitas proximalis carpometacarpi, fovea carpalis cranialis, status:
a. absent to moderately distinct;
b. present, deep and marked;
x. noncomparable (Dinornithiformes).

Note.—See: Siegel-Causey (1988: character 90); Livezey (1998b: appendix A, character 240); G. Mayr and Ericson (2004: appendix I, character 58).

1648. Extremitas proximalis carpometacarpi, fovea carpalis cranialis, foramen pneumaticum, status:
a. absent; **b.** present;
x. noncomparable (Aepyornithiformes, Dinornithiformes).

1649. Extremitas proximalis carpometacarpi, facies ventralis, jugum infratrochlearis (**new term**), status:
a. absent;
b. present, moderately elevated jugum or robust cristula joining processus pisiformis and rima ventralis trochlearis;
x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—See: Siegel-Causey (1988: character 94); Livezey (1998b: appendix A, character 242), in reference to “jugum aut linea tuberculae between processus pisiformis proximad to trochlea carpalis.”

Corpus carpometacarpi

1650. Corpus carpometacarpi (or ossa carpometacarpalia I–III), facies dorsalis aut ventralis, total proximodistal length expressed as ratio with width (os metacarpale I, margo cranialis to os metacarpale III, margo caudalis), forma:
a. short and broad, ratio less than 2.0;
b. elongate and slender, ratio more than 2.2.

Note.—See: Gauthier (1986); Rauhut (2003: character 147). Width based on ossa metacarpalia I–III to preclude mensural effects of losses of digiti manus.

1651. Corpus carpometacarpi, os metacarpale majus (II), facies cranioventralis, impressio proprius m. abductor digiti majoris (**new term**), status et forma (**ordered**):
a. absent, corpus subcylindrical or subangular;
b. present, moderately deep and limited to distal half;
c. present, moderately or conspicuously deep, associated with planar facies ventralis corpus extend-

ing to margo distalis of basis ossis metacarpale alulae and to extremitas distalis carpometacarpi;

d. present, conspicuously deep, extends proximad to basis ossis metacarpale alulae or between processi extensorius et pisiformis and to extremitas distalis carpometacarpi;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromaiidae, Casuariidae, *Apteryx*, Dromornithidae, *Aptornis*).

Note.—Extreme robustness and extent of m. abductor digiti majoris proximally (e.g., *Opisthocomus*), where positioned typically on facies ventralis ossis carpometacarpale majus (II) is associated with presence of caput accessoria (**new term**)—the "supernumerary belly" of Hudson and Lanzillotti (1964: 30)—typically including (independently of tendo insertii m. abductor digiti majoris proprius) a slender tendo insertii to extremitas proximalis, phalangis proximalis digiti majoris.

1652. Corpus carpometacarpi, os metacarpale minus (III), facies ventralis, pars proximalis, eminentia retinaculum flexorium of aponeurosis ventralis (**new term**), status et forma (**ordered**):

a. absent or obsolete;

b. present, impressio or indistinct eminentia;

c. present, distinct tuberculum or cristula;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromaiidae, Casuariidae, *Apteryx*, Dromornithidae, *Aptornis*).

Note.—Aspect that of cristulate expansion of jugum metacarpo-pisiformis (**new term**), where present. Character referred to by Hesse (1990) as "*Fortsatz*." Stegmann (1978) implies this feature, if not strictly ventral in orientation (in which case probably related to retinaculum), pertains to insertio m. ulnometacarpalis dorsalis.

See: Stephan (1979); Livezey (1998b: appendix A, character 244); G. Mayr and Mourer-Chauviré (2000: fig. 11, node 1), in reference to "os metacarpale minus with small ventrally projecting tubercle."

1653. Corpus carpometacarpi, os metacarpale minus (III), facies ventralis, pars proximalis, eminentia retinaculum flexorium of aponeurosis ventralis (**new term**), presence accompanied by enclosed foramen neurovascularia, status:

a. absent; **b.** present.

1654. Corpus carpometacarpi, foramina pneumatica corporis, status et situs (**unordered**):

a. absent;

b. present, os metacarpale majus, sectio distalis, facies ventralis;

c. present, os metacarpale minus, sectio proximalis, margines cranialis et/aut caudalis by perforata;

d. present, os metacarpalia majus et minus, partes symphysiales intermetacarpales proximalis et/aut distalis, facies dorsalis et/aut ventralis;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

1655. Corpus carpometacarpi, os metacarpale minus (III), facies articularis phalangis digiti minoris (et articulatio metacarpophalangealis digiti minoris), status et typus (**unordered**):

a. present, articulatio sellaris;

b. present, articulatio synovialis—simplex, plana, aut ellipsoidea;

c. absent, by secondary reduction of manus;

x. noncomparable, ossa alae absent (Dinornithiformes).

Note.—See: Bledsoe (1988: appendix, character 34, modified), K. Lee et al. (1997: appendix 1, character 16, modified).

1656. Corpus carpometacarpi, os metacarpale minus, angulus distalis with symphysialis intermetacarpalis distalis, forma (**ordered**):

a. shallowly acute, with os metacarpale minus comparatively proximate and parallel and joining os metacarpale majus in narrow osseus corpus symphysialis;

b. moderately acute, with os metacarpale minus moderately proximate and subparallel;

c. subperpendicular, curving sharply to unite with symphysis intermetacarpalis distalis;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—Partially correlated with distal divergence of ossa metacarpalia and width of spatium intermetacarpale, and confounded as well with width of pars symphysialis intermetacarpalis distalis (**new term**).

1657. Corpus carpometacarpi, os metacarpale minus, margo caudalis, angulus (tuberositas) proximodistalis (**new term**), status:

a. absent or virtually distinguishable;

b. present, effecting distinct angularity of os metacarpale minus.

Note.—Angulus marks margo distalis of impressio insertii m. ulnometacarpalis dorsalis (Stegmann 1965).

1658. Corpus carpometacarpi, os metacarpale minus, margo caudalis, sulcus (impressio) origii m. flexor digiti minoris (**new term**), status et forma (**ordered**):

a. absent;

b. present, principally limited to proximal half of corpus;

c. present, extending entire length of corpus;

d. present, extending entire length of corpus, augmented by distal lamella marginis.

Note.—Sulcus accommodates comparatively large m. flexor digiti minoris (George and Berger 1966).

1659. Corpus carpometacarpi, os metacarpale minus, margo caudalis, angulus caudodistalis, apical adornment including rectangular margo, causing "squaring" of angulus caudally and proximal to facies articularis digiti minoris, regardless of magnitude of angulus *per se*, status (**ordered**):
a. absent; **b.** rudimentary; **c.** present;
x. noncomparable (Aepyornithiformes, Dinornithiformes).

1660. Corpus carpometacarpi, spatium intermetacarpale (dorsoventral perspective), status et forma (**ordered**):
a. absent, spatium precluded by proximodistally complete synostosis intermetacarpalis;
b. present, terminating proximad to terminus distalis of os metacarpale I;
c. present, extending distad to terminus distalis of os metacarpale I but proximad to extremitates ossa metacarpalia II et III;
d. present, extending distad to terminus distalis of os metacarpale II;
e. secondarily absent, diagnosable by profound truncation of manus (e.g., corollary of flightlessness) and/or secondary longitudinal synostosis between ossa metacarpalia majus et minus;
x. noncomparable (Aepyornithiformes, Dinornithiformes).
Note.—See: Livezey (1996a: appendix 1, character 60), in some flightless anseriforms; Novas (1996: appendix, character 12) characterized some Alvarezsauridae as having rectangular carpometacarpi lacking spatium; a "splintlike" spatium was attributed to *Concornis* by Sanz and Buscalioni (1992: character 3, part); Novas (1997: appendix, character 13); Novas and Puerta (1997), see identical characters in Novas (1997), in which absence of spatium is associated with elemental truncation in some Maniraptora (e.g., Ornithothoraces, *Mononykus*, and *Patagonykus*); Chiappe (2001a: appendix 1, character 103); Norell and Clarke (2001: appendix I, character 147), treated similarly by J. A. Clarke (2002: appendix I, character 147), J. A. Clarke and Norell (2002: appendix 2, character 147), and J. A. Clarke (2004: appendix 1, character 147); Chiappe (2002: appendix 20.2, character 103); Dyke and Gulas (2002: appendix 1, character 53), regarding galliforms; Zhou and Zhang (2002: appendix III, character 147); G. Mayr et al. (2003: appendix 1, character 43), indicating relation between bowing of os metacarpale III et spatium; Ji et al. (2005: supplement, part I, character 147).

1661. Corpus carpometacarpi, spatium intermetacarpale (if present), width relative to ossa metacarpalia II aut III:
a. "typical," margines parallel and proximate, width of spatium *approximately* equal to that of os metacarpale II;
b. enlarged, margines divergent distad and expanded, typically associated with divergent curvature or angulus proximalis of ossa metacarpalia II et III, and proximal segment of os metacarpale III subperpendicular with respect to os metacarpale II;
x. noncomparable (Sphenisciformes).
Note.—Treats spatium in terms of relative positions (and widths) of ossa metacarpalia; other occlusion of spatium treated elsewhere. See: Dyke et al. (2003: appendix 1, character 65), employed again by Dyke (2003: table 1).

1662. Corpus carpometacarpi, spatium intermetacarpale (if present), processus (lamina) intermetacarpalis extending caudad to facies dorsalis ossis metacarpale (III) minus to largely occlude proximal portion of spatium intermetacarpale (pons intermetacarpalis; **new term**), resulting in distinct disparity in size between ostia dorsalis (smaller) et ventralis (larger) of spatium, status et forma (**unordered**):
a. absent;
b. present, occlusion comparatively narrow, processus essentially unrefined and retaining form despite junctura metacarpale;
c. present, occlusion comparatively broad, processus laminar, accommodating fenestra proximalis symphysis (**new term**) between margo proximalis pontis et symphysis metacarpalis proximalis;
d. present, occlusion comparatively broad, processus laminar, unfenestrated proximally;
x. noncomparable (Sphenisciformes).
Note.—This character assesses partial, proximal closure of spatium intermetacarpale by pons (a variant of tuberculum insertii tendinis m. extensor carpi ulnaris), and is distinct from separately treated restriction of spatium by craniocaudal proximity or widths of ossa metacarpalis majus et minus. In at least some of the nongalliform taxa manifesting proximal occlusion (e.g., *Indicator*), the resultant difference in ostia of spatium associated with loss of m. interosseus dorsalis (spatium occupied solely by m. interosseus ventralis, tendo insertii of which passes dorsodistad from the spatium. See: Cracraft (1971a: fig. 8), regarding Coraciiformes; Rich et al. (1985: plate VI), regarding *Menura*.

Extremitas distalis carpometacarpi

1663. Extremitas distalis carpometacarpi, pars symphysialis intermetacarpalis distalis (**new term**), facies dorsalis, lamina (pons) osseum occluding distal fourth of spatium intermetacarpale, and typically perforated distad by porus pneumaticum, status:
a. absent; **b.** present;
x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—Foramen evidently part of complexus of pori pneumatici of synostosis metacarpalis distalis in Bucerotidae.

1664. Extremitas distalis carpometacarpi, margo cranialis proximal to angulus terminalis (**new term**), jugum aut septum intertendineus metacarpalia (II) majus (**new term**), status:
a. absent; **b.** present.
Note.—Typically irregular and infrequently bipartite, thin partition alternatively termed septum tendinorum mm. abductor digiti majoris et flexor digitorum profundus carpometacarpalia (**new term**). See: G. Mayr and Mourer-Chauviré (2000); G. Mayr (2004d: appendix I, character 21), referred to as "processus dentiformis"; G. Mayr (2005a: appendix 1, character 22).

1665. Extremitas distalis carpometacarpi, os metacarpale majus (II), facies craniodorsalis, impressio capitis distalis m. abductor digiti majoris (**new term**), status:
a. absent; **b.** present.
Note.—Impressio evidently related to supplementary caput m. abductor digiti majoris, synonymous with "abductor indicus brevis" of Fisher (1946: fig. 14) or "small, deep distal head . . . whose tendon fuses with the tendon of the main head . . . [of m. abductor digiti majoris]" of George and Berger (1966: 376), both reported for genera of Falconiformes (e.g., Cathartidae) and by latter for *Anser* (Anseriformes). Striking examples manifested by some large Accipitridae.

1666. Extremitas distalis carpometacarpi, os metacarpale II (majus), margo cranialis immediately proximal to facies articularis digitalis major, calcar alae distalis (**new term**), status:
a. absent;
b. present, cornuate, and covered by cornified integumentum;
x. noncomparable (Aepyornithiformes, Dinornithiformes).
Note.—See: Livezey (1986: appendix 1, character 40); Ericson (1997: table 1, character 40).

1667. Extremitas distalis carpometacarpi, pars symphysialis intermetacarpalis distalis (**new term**), facies dorsalis, sulcus interosseus dorsalis, forma (**ordered**):
a. broad, deep, bounded cranially and caudally by distally extensive cristae marginales, further accentuated by dorsally prominent facies dorsalis of os metacarpale majus;
b. narrow or moderately broad, shallow to moderately deep, and not bounded caudally by prominent crista marginalis;
x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromornithidae, *Aptornis*).
Note.—See: Lambrecht (1933); Ballmann (1969a); Livezey (1998b: appendix A, character 254), in which Otididae and some allied taxa manifested substantial variation.

1668. Extremitas distalis carpometacarpi, pars symphysialis intermetacarpalis distalis (**new term**), prominent ventral disparity in craniocaudal direction between ossa metacarpalia II et III, caused by substantially ventral position of terminus of latter relative to that of former, status:
a. absent or subtle;
b. present and marked, typically revealing part of spatium intermetacarpale distally in caudal perspective;
x. noncomparable (Aepyornithiformes, Dinornithiformes).
Note.—Apomorphic state appears to reflect distal torsion of ossa metacarpalia, e.g., acting counterclockwise to distal portions of right elements (distal perspective).

1669. Extremitas distalis carpometacarpi, pars symphysialis intermetacarpalis distalis (**new term**), facies ventralis, sulcus interosseus ventralis, forma (**unordered**):
a. comparatively long proximodistally, lacking ventral curvature;
b. comparatively short proximodistally, lacking notable ventral curvature;
c. comparatively short proximodistally, manifesting prominent ventral curvature;
x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).
Note.—Assessment of ventral curvature optimally performed in oblique craniocaudal perspective.

1670. Extremitas distalis carpometacarpi (os metacarpale majus), facies ventralis, margo cranialis (facies articularis digitalis major, vertex ventrocranialis), eminentia tendineus (**new term**), status et forma (**ordered**):
a. absent or obsolete;
b. present, moderately prominent;
c. present, very prominent;
x. noncomparable by general form (Aepyornithiformes, Dinornithiformes, Dromornithidae, *Aptornis*) or confounding with calcar (Anhimidae).
Note.—Refers to "distal process" of Stegmann (1963, 1978: fig. 3), and evidently serves (at least in part) as situs ancorae for tendo insertii m. abductor digiti majoris (Stegmann 1978: fig. 2), as well as, in many taxa, tendo insertii flexor digitorum profundus. See: Livezey (1998b: appendix A, character 255).

1671. Extremitas distalis carpometacarpi (os metacarpale majus), facies articularis digitorum major et minor, forma superficialis:

a. essentially planar, i.e., distal extents of ossa metacarpalia majus et minus approximately equal;

b. distinctly biplanar, facies articularis "two-stepped," i.e., distal extent of os metacarpale minus exceeds that of os metacarpale majus;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—Of two facies articulares, proximal articulates only with digitus major, and distal with both digiti major et minor. Alternatively, this character might be construed as structurally distinct uniosseus or biosseus articulationes metacarpophalangealis digiti majoris. See: Dyke and Gulas (2002: appendix 1, character 28), in which was polarity reversed; G. Mayr (2004d: appendix I, character 24); G. Mayr (2005a: appendix 1, character 25).

1672. Extremitas distalis carpometacarpi, facies articularis digitalis minor, forma:

a. modest in size and distal prominence, typically unilobate;

b. enlarged, distally elongate, typically bilobate.

Note.—See: G. Mayr (2004d: appendix I, character 25); G. Mayr (2005a: appendix 1, character 26).

1673. Synostoses ulno-ulnocarpale distale et ulnocarpometacarpalis dorsale, resulting in virtually unipartite segmentum antebrachio-manus (**new term**) comprising antebrachium et manus proximalis, status:

a. absent; **b.** present;

x. noncomparable by absence or radical apomorphy of skeleton alae (Aepyornithiformes, Dinornithiformes, *Aptornis*).

1674. Synostoses metacarpophalangealis digiti majoris (phalanx proximalis), status:

a. absent; **b.** present;

x. noncomparable (Dinornithiformes, *Aptornis*).

1675. Synostosis metacarpophalangealis digiti minoris, status:

a. absent; **b.** present;

x. noncomparable (Dinornithiformes).

Digiti et Phalanges Manus

Note.—The skeleton manus avium is typified by a phylogenetic trend toward reduction in numbers of digiti and of phalanges within digiti. In that taxonomic assessments show that these are related reductive trends, patterns also demonstrated that these trends occurred at different rates in different digiti and taxa and hence were not strictly redundant phylogenetically. Accordingly, the following descriptions of characters pertaining to the reduction and loss of phalanges and unguales of the digitorum manus separately (i.e., under digiti I (alularis, primus), II (majus, secundus), III (minus, tertius), IV (quartus), et V (quintus).

For references treating the debate concerning higher-order homologies of ossa metacarpalia et digiti manus avium, see: Thulborn (1984: 126–127, character 19, part); Welles (1984); Sanz and Buscalioni (1992: character 4, part); Chatterjee (1998); Padian and Chiappe (1998b: fig. 4); Chiappe et al. (1999); G. P. Wagner and Gauthier (1999). Given the generally noncontroversial evidence for the distal-to-proximal reduction and loss of phalages digitorum manus in Aves (Padian and Chiappe 1998b: fig. 4; G. P. Wagner and Gauthier 1999), each of these characters pertaining to digital reduction (paralleled largely by reductions in associated ossa metacarpalia) were treated as ordered. A similar but less-uniform commonality of digital reduction and loss among Aves and other Tetrapoda is evident (e.g., Alberch and Gale 1983; Sereno 1997; G. P. Wagner and Gauthier 1999); higher-numbered or caudalmost ("internal") digits (e.g., digiti V et IV) undergoing evolutionary reduction earlier than more-cranial (external) digits (e.g., digiti III, II, et I *in serriatum*).

Also, among Neornithes, Livezey (1994) described multiple apomorphies of the carpometacarpus and digitorum manus of *Aptornis*; with exception of the digitus alulae, evidently *Aptornis* lacked digiti manus entirely, therefore characters of the latter were treated as "noncomparable" for that single neornithine taxon. Among nonavian Theropoda, simple enumeration of digiti manus retained—e.g., Makovicky and Sues (1998: appendix 1, character 70), and Azuma and Currie (2000: appendix 1, character 76)—was refined by treatments of each digitus manus, including specification of homologues of phalanges involved and diminishment of specialization of phalanges unguales (where present).

1676. Phalanges digitorum manus, status *in toto*:

a. present; **b.** absent *in toto*.

Numerus phalangiorum digitorum manus

Note.—Numbers of digiti phalangiorum I–V plesiomorphic for Reptilia are 2-3-4-5-6 (including phalanges unguales), respectively. Reductions of digiti by means of loss of phalanges typically, if not universally, occurs from distalmost element proximad *in serriatum*.

1677. Phalanges digiti I (alularis, primus) manus, numerus modalis et forma (**unordered**):

a. two, including functional phalanx ungualis, of uniform robustness;

b. two, in which phalanx ungualis reduced, largely nonfunctional, of uniform robustness;

c. two, including phalanx ungualis, latter typically vestigia;

d. present, robust and proximally hamulate, phalanges two in number, phalanx distalis sine unguis;

e. one, phalanx vestigialis, phalanx ungualis lacking;

f. zero, phalanges alulae lacking entirely;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—The skeleton alulae of penguins is commonly considered to include an elongated, uniquely synostotic digitus alularis; examination of juveniles, however, indicates this complex comprises a uniquely elongated os metacarpale (I) alularis with digitus alularis vestigialis.

See: W. K. Parker (1888c); Romanoff (1960), using traditional enumeration of digiti manus avium; Stephan (1979); McGowan (1982: fig. 5); Thulborn (1984: 126–127, character 19, part); Novas (1992: character 8); Sanz and Buscalioni (1992: character 4, part); Baumel and Witmer (1993: 104, annotation 224); Baumel and Raikow (1993: 167, annotation 137); Chatterjee (1998); Padian and Chiappe (1998b: fig. 4); G. P. Wagner and Gauthier (1999); Ji et al. (2001), regarding unnamed dromaeosaurid NGMC 91-A; Sereno et al. (2002: fig. 8.3); Zhou and Zhang (2002: appendix III, character 151); Ji et al. (2003a: 23).

1678. Phalanges digiti II (majus, secundus) manus, numerus modalis et forma (**ordered**):

a. three, phalanges of uniform (functional) robustness, including functional phalanx ungualis;

b. three, phalanges (including unguis) of comparable functionality as indicated by robustness of elements, phalanx distalis typically cum unguis;

c. three, phalanges typically decreasing in functionality and robustness progressively distad, phalanx distalis vestigial in Neornithes;

d. two, phalanges of uniform (functional) robustness, phalanx terminalis possessing unguis vestigialis;

e. two, phalanges of uniform (functional) robustness, phalanx terminalis lacking unguis;

f. one, phalanx cum ungualis;

g. zero, digitus II (majoris) lacking entirely;

x. noncomparable, ossa alae absent or synostotic (Aepyornithiformes, Dinornithiformes).

Note.—See: R. S. Wray (1887b), regarding vestigium phalangiorum in *Struthio*; W. K. Parker (1888c, 1889a); Beddard (1898a, 1899); Lowe (1928b, 1935); Fisher (1940); Tordoff (1952); Romanoff (1960); Berger (1966); George and Berger (1966: 377); Thulborn (1984: 126–127, character 19, part); Gauthier (1986: 13, unindexed synapomorphy of Ornithurae); Sanz and Buscalioni (1992: character 4, part); Sereno and Rao (1992); Baumel and Witmer (1993: 104, annotation 224); Baumel and Raikow (1993: 167, annotation 137); Baumel and Witmer (1993), listing *Opisthocomus* and Musophagidae as having ungues alulares; Holtz (1994a: appendix 1, character 16); Livezey (1994); Chiappe et al. (1996: appendix 1, character 91); Currie and Padian (1997); Padian and Chiappe (1998b: fig. 11); Chatterjee (1998); Livezey (1998b: appendix A, character 559); Livezey (1998b: appendix A, character 235), regarding multiple apomorphies of the carpometacarpus and digiti alae of *Aptornis*; Makovicky and Sues (1998: appendix 1, character 70), in terms of number of digiti manus retained; Padian and Chiappe (1998b: fig. 4); Chiappe et al. (1999: 61–62); G. P. Wagner and Gauthier (1999); Azuma and Currie (2000: appendix 1, character 76, part); Holtz (2000 [1998]: appendix I, character 259); Chiappe (2001a: appendix 1, characters 111 and 114); Ji et al. (2001), regarding unnamed dromaeosaurid NGMC 91-A; Norell et al. (2001: appendix 1, character 151); Chiappe (2002: appendix 20.2, characters 111 and 114); J. M. Clark et al. (2002a: appendix 2.2, character 153); Sereno et al. (2002: fig. 8.3); Xu (2002: suite II, character 178); Ji et al. (2003b); Brochu (2003), regarding *Tyrannosaurus*; Ji et al. (2003a: 23); Hwang et al. (2004: supplement, character 150); Xu and Norell (2004: supplement, character 150).

1679. Phalanges digiti minus (III, tertius), numerus modalis (**ordered**):

a. four, proximalis typically shortest among included Avialae;

b. three; **c.** two; **d.** one;

e. zero, despite retention of os metacarpale III, typically vestigial;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—See: Baur (1885a), citing occurrence of "second phalanx in the third digit" of a carinate bird; R. S. Wray (1887b) regarding remnants of vestigial phalanges digiti III manus in *Struthio*; W. K. Parker (1888c); Beddard (1898a); Romanoff (1960); Currie and Padian (1997); Padian and Chiappe (1998b: fig. 11); Azuma and Currie (2000: appendix 1, character 76, part); De Klerk et al. (2000: 330, character 7); Holtz (2000 [1998]: appendix I, character 258); Zhou et al. (2000); Xu et al. (2002a: supplement, character 123); Brochu (2003), regarding *Tyrannosaurus*; Ji et al. (2003a: 23), regarding *Shenzhouraptor*; Ji et al. (2003b).

1680. Phalanges digiti IV (quartus) manus, numerus modalis et forma (**ordered**):

a. three to five; **b.** two; **c.** one;

d. zero, digitus IV absent entirely despite retention of os metacarpale IV, in some taxa vestigial;

x. noncomparable by absence of ossa alae (Dinornithiformes).

Note.—See: Romanoff (1960); Gauthier (1986: text character 46); Benton (1990a: 18); Holtz (1994a: appendix 1, character 96); Novas (1994 [1993]: appendix, character 38, appended); Chatterjee (1998); Padian and Chiappe (1998b: fig. 4); G. P. Wagner and Gauthier (1999); Holtz (2000 [1998]: appendix I, characters 256–257); Ji et al. (2003a: 23); Rauhut (2003: character 153). Theropoda purportedly synapomorphic in vestigial status or absence of digitus IV manus (Benton 1990a: 21); where vestigium remains, distalmost phalanges are uniformly sine ungues.

1681. Phalanges digiti V (quintus) manus, numerus modalis et forma (**ordered**):

a. three to six; **b.** two; **c.** one;

d. zero, digitus V absent entirely, despite retention of os metacarpale IV, in some taxa vestigial (basal Sauropodomorpha, e.g., *Riojasaurus*, *Yunnanosaurus*, *Anchisaurus*, *Thecodontosaurus*), including taxa lacking ossa metacarpalia V;

x. noncomparable by absence of ossa alae (Dinornithiformes; *Aptornis*).

Note.—See: Gauthier (1986: text character 46); Holtz (1994a: appendix 1, character 96); Novas (1994 [1993]: appendix, character 38, appended); Chatterjee (1998); Padian and Chiappe (1998b: fig. 4); Holtz (2000 [1998]: appendix I, characters 256–257); G. P. Wagner and Gauthier (1999); Ji et al. (2003a: 23); Rauhut (2003: character 153). Among Sauropodamorpha, including Theropoda, distalmost phalanges of digiti IV et V are uniformly sine ungues (Benton 1990a: 23).

Forma phalangiorum digitorum manus

1682. Phalanges digitorum I–III manus, substantial pneumatization evidenced by pori pneumatici corporalium digitorum alularis, majoris (especially phalanx proximalis), et/aut minoris, status:

a. absent; **b.** present;

x. noncomparable by absence of ossa alae (Dinornithiformes).

1683. Phalanges digitorum manus, pronounced asymmetry digitorum and maximal relative length of digitus II manus, status:

a. absent; **b.** present;

x. noncomparable by absence of ossa alae (Dinornithiformes).

Note.—See: Benton (1990a: 20).

1684. Phalanges digitorum I–III manus, digitus longitudinis maximi (**unordered**):

a. digitus III; **b.** digitus II;

c. digitus I;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromornithidae, *Aptornis*).

Note.—See: Gauthier (1986); Holtz (1994a: appendix 1, character 125); Sereno (1993); Novas (1994 [1993]: appendix, character 47); Pérez-Moreno et al. (1994: legend for fig. 3, character 21); Novas (1996: appendix, character 47); Holtz (2000 [1998]: appendix I, character 270); Maryanska et al. (2002: appendix 1, character 138); Rauhut (2003: character 154).

1685. Phalanges digitorum I–III manus, phalanx pro-ungualis (phalanges penultimates), corpus phalangis relative to other phalanges within respective digitus, length:

a. less than at least one condigital, phalanges prounguales;

b. greater than that of condigital, phalanges prounguales;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—See: Novas (1994 [1993]: appendix, character 42), limited to digitus II; Holtz (2000 [1998]: appendix I, character 271), citing Sereno and Novas (1992).

1686. Phalanges digitorum I–III manus, phalanges unguales, forma transversa (**unordered**):

a. oval, two to three times as deep as wide;

b. subtriangular, width at least as great as depth;

c. bladelike, more than three times as deep as wide;

x. noncomparable (Neornithes).

Note.—See: Sereno (1999: character 151); Azuma and Currie (2000: appendix 1, character 70); Holtz (2000 [1998]: appendix I, character 282), original states of which resequenced to permit logical ordering; Suzuki et al. (2002: character 11).

1687. Phalanges digitorum I–III manus, phalanges unguales, length (**ordered**):

a. relatively short; **b.** moderately long;

c. extremely long;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—Reflects overall size of alar ungues. See: Azuma and Currie (2000: appendix 1, character 72); Holtz (2000 [1998]: appendix I, character 283), original states of which resequenced to permit logical ordering.

1688. Phalanges digitorum I–III manus, phalanges unguales, forma et situs proximodistalis tuberculorum flexoriae (**ordered**):

a. present, curvature distinct and tuberculae flexoriae moderately distal;

b. absent, ungues with curvature obsolete or weakly developed, and tuberculae flexoriae proximal;

c. present, curvature prominent and tuberculae flexoriae significantly distal;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—See: Azuma and Currie (2000: appendix 1, character 71); Holtz (2000 [1998]: appendix I, character 284), original states of which resequenced to permit logical ordering; Norell et al. (2001: appendix 1, character 152); J. M. Clark et al. (2002a: appendix

2.2, character 154); Xu (2002: suite II, character 179); Hwang et al. (2004: supplement, character 153); Xu and Norell (2004: supplement, character 153).

1689. Phalanges digitorum I–III manus, phalanges unguales, bases phalanges, cotylae articulares, tuberculae flexoriae, status (**unordered**):
a. present, a prominent tuberositas;
b. present, a prominent tuberculum, processus aut angulus;
c. obsolete or absent entirely;
x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).
Note.—See: Stephan (1979); Pérez-Moreno et al. (1994: legend for fig. 3, character 22), with respect to "flexor tubercles of unguals"; Holtz (2000 [1998]: appendix I, character 276), in reference to "flexor tubercle of unguals" (termed "lip" by some), attributed to Pérez-Moreno et al. (1994); Norell et al. (2001: appendix 1, character 154); J. M. Clark et al. (2002a: appendix 2.2, character 154); Xu (2002: suite II, character 181); Xu et al. (2002a: supplement, character 124, part), including also differences in curvature. Also of possible interest is the proximodistal position of tuberculae flexoriae, as considered by Sereno (1999: character 152) and Suzuki et al. (2002: character 12); Rauhut (2003: character 163), in which tuberculae flexoriae were compared in size to the facies articularis proximalis phalangiorum; Hwang et al. (2004: supplement, character 151); Xu and Norell (2004: supplement, character 151).

1690. Phalanges digitorum I–III manus, phalanges unguales, bases phalanges, cotylae articulares, margines dorsales, forma:
a. relatively smooth;
b. marked by distinct rima basilaris (**new term**) or tuberculum;
x. noncomparable by absence of ungues verae (Neornithes).
Note.—If treated as comparable, Neornithes assigned to state "b." See: Currie and Russell (1988); Russell and Dong (1994a [1993a]: table 2, character 44), with respect to "small nubbin proximodorsally"; Holtz (1994a: appendix 1, character 17), in reference to "pronounced lip on dorsal edge of proximal articulation of manual ungual phalanges"; Sues (1997: appendix 1, character 35), with respect to "pronounced dorsal 'lip' on proximal articular surface"; Makovicky and Sues (1998: appendix 1, character 73); Xu et al. (1999a: characters 69–70); Azuma and Currie (2000: appendix 1, character 74); Holtz (2000 [1998]: appendix I, character 275), following Holtz (1994a, 1999); Xu et al. (2002a: supplement, character 126); Rauhut (2003: character 162).

1691. Phalanges digitorum I–III manus, phalanges unguales, corpora phalanges, facies dorsolateralis, sulcus neurovasculariorum, depth relative to sectiones plantaris et dorsalis (**new terms**), i.e., those delineated by sulcus, forma sulci dorsoplantaris:
a. sectio plantaris deeper than dorsalis, i.e., "region palmar to ungual groove wider than region dorsal to ungual groove";
b. sectio dorsalis deeper than plantaris, i.e., "palmar and dorsal regions subequal in width";
x. noncomparable by absence of ungues verae (Neornithes).
Note.—See: Azuma and Currie (2000: appendix 1, character 75); De Klerk et al. (2000: 330, character 6); Holtz (2000 [1998]: appendix I, character 277), citing Russell and Dong (1994a [1993a]).

1692. Phalanges digitorum I–III manus, phalanges sine unguales, capitulae phalanges, foveae ligamentorum collaterales, status:
a. present and prominent;
b. absent or indistinct;
x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).
Note.—See: Xu et al. (1999a: character 71).

Digitus alulae (I, primus) manus

1693. Phalanx proximalis digiti I (alulae, primus), status:
a. present; **b.** absent.
Note.—See: Poplin and Mourer-Chauviré (1985); Andors (1988).

1694. Phalanx proximalis digiti I (alulae, primus) manus, foramen neurovascularium enclosed between margo caudalis of digitus alularis (specifically caudal to synostosis metacarpo-phalangealis alularis) et (synostotic) margo cranialis of os metacarpale majus, status:
a. absent; **b.** present;
x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).
Note.—Os metacarpale alularis of palaeognathous birds and Spheniscidae are disproportionately elongate, and may necessitate the foramen whereas in other taxa the vessels pass distal to the element.

1695. Phalanx proximalis digiti I (alulae, primus) manus, facies caudalis phalangis, proximal one-half of phalanx, tuberculum insertii tendinis alulae m. flexor digitorum communis (**new term**), status:
a. absent or obsolete;
b. distinct or prominent.
Note.—Evidently related to comparatively subperpendicular angulus tendinis insertii and tension typically transmitted to tuberculum; hence comparatively variable and requiring characterization by modalities.

1696. Phalanx proximalis digiti I (alulae, primus) manus—(*i*) disproportionate robustness and marked dorsoventral compression, and (*ii*) prominent laterobasal eminentia, status:

a. absent; **b.** present;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—Bracketed taxa were coded as "unknown" for one of two diagnostic features of character. See: Russell and Dong (1994b [1993b]: troödontid character 17), citing Paul (1988) in which unguis is related in size to phalanx ungualis of digitus pedis II; Chiappe et al. (1996: appendix 1, character 80); Novas (1996: appendix, characters P6 and M13); Novas (1996: appendix, character 13); Chiappe et al. (1998: characters 59–60); Ji et al. (1998: characters 59–60); Chiappe (2001a: appendix 1, characters 109 [robustness] and 110 [tuberculum]); Sereno (2001: table 2, character 48), regarding robustness relative to that of os metacarpale II; Chiappe (2002: appendix 20.2, characters 109 [robustness] and 110 [tuberculum]).

"Prominent laterobasal eminentia" is probably synonymous with the "dorsomedial tubercle on the proximal phalanx of manual digit I" noted by Sereno (1999: character 150), Suzuki et al. (2002: character 10), and "prominent ventral projection of the proximolateral margin" of Chiappe (2002: character 110), and both terms evidently correspond to tuberculum tendinorum insertii mm. abductor et flexor digiti alularis.

1697. Phalanx proximalis digiti I (alulae, primus) manus, facies articularis, forma (planum transversus):

a. facies articularis proximalis comparatively flat, triangular in cross section, "distal ginglymus [*sic*] transversely compressed," and "extensor pit " absent;

b. facies articularis proximalis bipartite, with hamulate proximomedial processus hamulis proximomedialis (**new term**), "symmetrical distal ginglymus [*sic*]," and foveae tendinorum insertii mm. extensiorum et flexorum ("extensor ligament pit" and "flexor ligament pit") present;

x. noncomparable (Dinornithiformes, *Aptornis*).

Note.—First new term refers to "hooklike proximoventral process" in common usage in paleontological literature. See: Novas (1996: appendix, character 14); Novas (1997: appendix, character 15); Sereno (2001: table 2, character 47).

1698. Phalanx proximalis digiti alulae (I, primus), length relative to that of os metacarpale II (majus):

a. former less than or equal to that of latter;

b. former greater than that of latter;

x. noncomparable, phalanx absent (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—See: Holtz (2000 [1998]: appendix I, character 274).

1699. Phalanx ungualis digiti I (alulae, primus) manus, length relative to dorsoplantar height of cotyla articularis of same phalanx, forma:

a. former less than three times larger than latter;

b. former at least three times as great as latter;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—See: De Klerk et al. (2000: 330, character 7); Holtz (2000 [1998]: appendix I, character 279), citing Sereno et al. (1996); Xu et al. (2002a: supplement, character 124, part).

1700. Phalanx ungualis digiti I (alulae, primus) manus, facies ventro-proximalis, two foramina neurovascularia, status:

a. absent; **b.** present;

x. noncomparable (Neornithes).

Note.—See: Chiappe et al. (1998: character 61); Ji et al. (1998: supplement, character 61); Chiappe (2001a: appendix 1, character 117); Chiappe (2002: appendix 20.2, character 117).

1701. Phalanx ungualis digiti I (alulae, primus) manus, forma generalis (**unordered**):

a. "trenchant," dorsoventrally deep, facies articularis elliptical;

b. stout and robust, dorsoventrally compressed, facies articularis quadrangular;

c. diminutive, vestigial, or absent;

x. noncomparable (Dinornithiformes, *Aptornis*).

Note.—See: Novas (1996: appendix, character A5); Novas (1996: appendix, character 22); Novas (1997: appendix, character 24); Novas and Puerta (1997), identically treated by Novas (1997); Holtz (2000 [1998]: appendix I, character 280).

1702. Phalanx ungualis digiti I (alulae, primus) manus, tuberculum insertii tendinis m. adductor alulae (**new term**), status:

a. absent or diminutive;

b. present and comparatively prominent;

x. noncomparable (Dinornithiformes, *Aptornis*).

Note.—See: Livezey (1998b: appendix A, character 257). New term (formerly termed "tuberculum distocaudalis") is a variably distinct tuberculum on distocaudal portion of element. Unlike plesiomorphic homologue effecting flexion of functional unguis, tuberculum in Neornithes related to only limited, flight-related movement of digitus I manus.

1703. Phalanx ungualis digiti alulae (I, primus), length relative to phalanges unguales digitorum II–IV alae:

a. approximately equal;

b. former distinctly greater than latter.

Note.—To the extent Neornithes are comparable, group approaches state "a" most closely. See: Gauthier (1986); Novas (1994 [1993]: appendix, character 46); Forster et al. (1998: supplement, character 64); Xu et al. (1999a: character 68); Xu et al. (1999b:

character 47); Azuma and Currie (2000: appendix 1, character 73); Holtz (2000 [1998]: appendix I, character 278); Xu et al. (2000: supplement, character 34); Chiappe (2001a: appendix 1, character 112); Currie and Chen (2001: 1717); Ji et al. (2001), regarding unnamed dromaeosaurid NGMC 91-A; Norell et al. (2001: appendix 1, character 153); Chiappe (2002: appendix 20.2, character 112); J. M. Clark et al. (2002a: appendix 2.2, character 155); Vickers-Rich et al. (2002), concerning *Avimimus*; Xu (2002: suite II, character 180); Xu et al. (2002a: supplement, character 125); Hwang et al. (2004: supplement, character 152); Xu and Norell (2004: supplement, character 152).

1704. Phalanges digiti alulae (I, primus), phalanx ungualis, length relative to that of os radius:

a. unguis less than one-half length of radius;

b. unguis more than two-thirds length of radius.

Note.—See: Sereno et al. (1998); Rauhut (2003: character 161). Represents an alternative index to relative enlargement of the alular unguis than effected by preceding character.

1705. Phalanx proximalis digiti I (alulae, primus), length relative to os metacarpale I:

a. less than or equal to latter;

b. at least as great;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromaiidae, Casuariidae, *Apteryx*, *Aptornis*).

Note.—Length of latter measured in parallel to axes majores of ossa metacarpalia II et III. See: Sereno et al. (1993: legend for fig. 3a); Novas (1994 [1993]: appendix, character 31).

1706. Phalanges digiti alulae (I, primus), length relative to homologous points on phalanges proximalis et intermedia digiti majoris (II) (**ordered**):

a. former approximately opposite midpoint of phalanx intermedia (II-2);

b. former approximately opposite midpoint of phalanx proximalis (II-1);

c. former substantially shorter than latter, in articulatio former extends approximately to midpoint of os metacarpale majus (II);

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—Assessments made with digiti in articulation. See: Holtz (2000 [1998]: appendix I, character 273).

Digitus majoris (II, secundus) manus

1707. Phalanges proximalis et intermedia digiti II (majus, secundus) manus, forma corporis (planum transversus), especially regarding dorsoventral compression, forma (**unordered**):

a. subcylindrical to subtriangular;

b. distinctly dorsoventrally compressed, but retaining pila cranialis or related differential robustness;

c. strongly dorsoventrally flattened and craniocaudally expanded, lacking pila cranialis;

x. noncomparable (Dinornithiformes, *Aptornis*).

Note.—See: Stephan (1979); Gauthier (1986: 13, unindexed synapomorphy of Ornithurae), regarding phalanx distalis aut intermedia; Chiappe et al. (1996: appendix 1, character 99); Hughes (2000: appendix 2, character 125), after Seibel (1988: character PH 1); Chiappe (2001a: appendix 1, character 115); Norell and Clarke (2001: appendix I, character 150), Chiappe (2002: appendix 20.2, character 115); J. A. Clarke (2002: appendix I, character 150); J. A. Clarke and Norell (2002: appendix 2, character 150); Zhou and Zhang (2002: appendix III, characters 150 and 152); J. A. Clarke (2004: appendix 1, character 150); Ji et al. (2005: supplement, part I, character 150).

1708. Phalanx proximalis digiti II (majus, secundus) manus, facies dorsalis, margo caudalis, invaginatio caudoproximalis (**new term**) approximately aligned with pila obliqua fossae (**new term**), status:

a. absent; **b.** present;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—Invaginatio approximately occupies proximal area of subfossa.

1709. Phalanx proximalis digiti II (majus, secundus) manus, extremitas proximalis phalangealis, margo cranialis, facies articularis metacarpalis, tuberculum articularis metacarpalis (**new term**), status et forma (**ordered**):

a. absent, facies articularis planar;

b. present, variably prominent tumulus or tuberculum;

c. present, uniquely elongated, medially concave processus, continuous proximally with facies articularis metacarpalis;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—Serves as situs ancorae insertii mm. flexores digitorum superficialis et profundus. See: Stegmann (1978), for general myological relationships; Manegold et al. (2004: character 2), for Piciformes; G. Mayr et al. (2003: fig. 2; appendix 1, character 49), regarding state “c”; G. Mayr (2004d: appendix I, character 26); G. Mayr (2005a: appendix 1, character 27).

1710. Phalanx proximalis digiti II (majus, secundus) manus, facies ventralis, extremitas distalis phalangis, sulcus tendineus phalangis (**new term**), status:

a. absent; **b.** present;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—After Manegold et al. (2004: character 7) for Bucconidae and Galbulidae, in which he considered that canalis enclosed tendines insertii mm. flexores digitorum superficialis et profundus.

1711. Phalanx proximalis digiti II (majus, secundus) manus, facies articularis metacarpalis, dorsoventral bilobation (proximal perspective) comprising cotyla ventralis et tuberculum dorsalis tendinis (**new term**), status:

a. absent; **b.** present;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—Tuberculum dorsalis tendinis evidently serves as situs tendinis insertii m. abductor digiti majoris.

1712. Phalanx proximalis digiti II (majus, secundus) manus, margo caudalis phalangis (**new term**), orientation of axis marginis caudalis phalangis relative to axis marginis cranialis phalangis (**new term**), forma (**unordered**):

a. shallowly concave or linear;

b. slightly convex;

c. angular, proximodistally divergent;

d. moderately or strongly convex;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromaiidae, Casuariidae, *Apteryx*, *Aptornis*).

Note.—See: J. A. Clarke and Chiappe (2001: character 54).

1713. Phalanx proximalis digiti II (majus, secundus) manus, margo cranialis phalangis (**new term**), pila cranialis phalangis, status:

a. absent, margo cranialis not differentiated or more robust than complement of phalanx;

b. present, margo cranialis well differentiated and distinctly more robust than corpus phalangis et margo caudalis, pila typically manifesting torsion about axis majoris;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—See: Manegold et al. (2004: character 3).

1714. Phalanx proximalis digiti II (majus, secundus) manus, (especially phalanx proximalis), margo cranialis phalangis (**new term**), pila cranialis phalangis, forma:

a. essentially planar or subtly convex;

b. distinctly concave, resulting in sulcus on facies cranialis pilae;

x. noncomparable (ratites).

Note.—See: G. Mayr and Clarke (2003: appendix A, character 89), pertaining to narrow, elongate phalanx in some taxa (Podicipedidae, Phoenicopteridae).

1715. Phalanx proximalis digiti II (majus, secundus) manus, corpus phalangis, fossa dorsalis phalangis, translucentia(e) aut fenestra(e) ovalis(es) (**new term**), status, typus et numerus (**ordered**):

a. absent or obsolete;

b. present, single or (more frequently) paired, clearly emarginated translucentia ovales phalangis;

c. present, singular, pars caudodistalis fossae dorsalis phalangis, essentially circular, typically positioned *in articulatio* (dorsal perspective) between tendines insertii mm. interossea dorsalis et ventralis;

d. present, paired fenestrae, pars caudodistalis fossae dorsalis phalangis, separated by pila obliqua fossae;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromaiidae, Casuariidae, *Apteryx*, Dromornithidae, *Aptornis*).

Note.—New feature refers to translucent, ovale lamina sine perforata et/aut fenestra(e) phalangis, which typically comprises two fenestrae partitioned by pila obliqua fossae (**new term**). See: Stegmann (1963: figs. 7–9) for illustrations; Strauch (1978: character 49), reanalyzed by Björklund (1994: appendix) and Chu (1995); Zusi and Bentz (1984: fig. 16a); Chu (1998: appendix 1, character 104); G. Mayr (2002a: appendix 1, character 21, part), with respect to Caprimulgiformes; G. Mayr (2003c: appendix, character 22); G. Mayr (2005b: appendix A, character 38).

1716. Phalanx proximalis digiti II (majus, secundus) manus (typically fossa dorsalis), foramina pneumatica, status:

a. absent; **b.** present;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

1717. Phalanx proximalis digiti II (majus, secundus) manus, facies et fossa dorsales, pila obliqua fossae (**new term**), status:

a. absent; **b.** present;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Sphenisciformes, *Aptornis*).

Note.—See: G. Mayr (2002a: appendix 1, character 21, part), with respect to Caprimulgiformes; G. Mayr et al. (2003: appendix 1, character 47); G. Mayr (2005b: appendix A, character 38). Evidently a highly consistent synapomorphy for neognathous Neornithes, typically dividing fossa dorsalis into subfossae dorsales proximocaudalis et distocranialis phalangis (**new terms**).

1718. Phalanx proximalis digiti II (majus, secundus) manus, margo cranialis, dorsoventral expansion resulting in lamina cranialis phalangis (**new term**), status:

a. absent; **b.** present, variably concave;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—Lamina may be homologous to prominently expanded pila cranialis, typically distinguished by dorsoventral width approximating craniocaudal width of fossa dorsalis phalangis.

1719. Phalanx proximalis digiti II (majus, secundus) manus, fossa ventralis, status et forma:

a. absent, obsolete or irregularly, often subtly, contoured;

b. present, ellipsoidal;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—Presence of fossa principally determined by sharp prominence of delimiting rimae or pilae.

1720. Phalanx proximalis digiti II (majus, secundus) manus, margo caudalis, pila caudalis phalangis (**new term**), status:

a. present, at least proximally, thereby augmenting distinctness of fossa;

b. absent entirely, resulting in caudally undistinguished fossa dorsalis phalangis;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

1721. Phalanx proximalis digiti II (majus, secundus) manus, extremitas distalis phalangis, margo caudalis, tuberculum insertii tendo m. interosseus ventralis (**new term**), status:

a. absent or rudimentary; **b.** present;

x. noncomparable (Dinornithiformes, *Aptornis*).

Note.—Tuberculum in question serves as angulus for tendo insertii m. interosseus ventralis, termed by Stegmann (1963, 1965, 1978) as "processus internus indicus," the musculus inserting by tendo on terminus of phalanx distalis digiti majoris. See: Russell and Dong (1994 [1993]); Livezey (1998b: appendix A, character 258), regarding distal extent of "processus distocaudalis"—angular eminentia at vertex distocaudalis phalangis—relative to facies articularis phalangis; Holtz (2000 [1998]: appendix I, character 281), regarding "nubbin" proximodistally; G. Mayr (2002a: appendix 1, character 22), with respect to Caprimulgiformes; J. A. Clarke and Chiappe (2001: character 53); Norell and Clarke (2001: appendix I, character 152), treated similarly by J. A. Clarke (2002: appendix I, character 152), J. A. Clarke and Norell (2002: appendix 2, character 152), and J. A. Clarke (2004: appendix 1, character 152), in reference to processus on "posterodistal edge"; G. Mayr (2003a: appendix I, character 35); G. Mayr et al. (2003: appendix 1, character 48); J. A. Clarke (2004: fig. 4.9); G. Mayr and Ericson (2004: appendix I, character 62); G. Mayr (2005b: appendix A, character 39); Ji et al. (2005: supplement, part I, character 152).

1722. Phalanx proximalis digiti II (majus, secundus) manus, extremitas distalis phalangis, margo caudalis, tuberculum insertii tendinis m. interosseus ventralis (**new term**), forma apicalis (**unordered**):

a. acuminate—includes tubercular or obsolete conditions;

b. carinate—cum jugum aut lobus caudalis (**new term**);

c. hamulate—cum hamulus caudalis (**new term**);

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—Feature for which form is given actually encompasses more surface than that accommodating insertio tendinis, in some taxa supporting in part ligamenta aut aponeuroses interphalangeales. See: Stegmann (1963), who referred this feature to situs ancorae tendinis insertii m. interosseus ventralis; Livezey (1998b: appendix A, character 259).

1723. Phalanx distalis digiti II (majus, secundus) manus, facies dorsalis, fossa dorsalis, forma:

a. variable but not conspicuously deep throughout;

b. notably deep, concave, from basis through terminus distalis;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Sphenisciformes, *Aptornis*).

1724. Phalanges proximalis et prounguralis digiti II (majoris, secundus), relative lengths:

a. phalanx penultimatus shorter than phalanx proximalis;

b. phalanx penultimatus longer phalanx proximalis;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromornithidae, *Aptornis*).

Note.—See: Chiappe (2001a: appendix 1, character 116); Norell and Clarke (2001: appendix I, character 151), treated similarly by J. A. Clarke (2002: appendix I, character 151), J. A. Clarke and Norell (2002: appendix 2, character 151), and J. A. Clarke (2004: appendix 1, character 151); Chiappe (2002: appendix 20.2, character 116); Chiappe and Walker (2002: appendix 11.1, character 25); Zhou and Zhang (2002: appendix III, character 151); Rauhut (2003: character 159); Ji et al. (2005: supplement, part I, character 151).

1725. Phalanx ungualis digiti (majoris, secundus) II, unguis, status et forma (**ordered**):

a. present, robust and (if present) larger than phalanx ungualis alularis;

b. present, but vestigial and (if present) distinctly smaller than phalanx ungualis alularis;

c. absent;

x. noncomparable (Dinornithiformes).

Note.—In captive individuals of *Dromaius*, the unguis digiti majoris can attain exceptional lengths.

Digitus minoris (III, tertius) manus

1726. Phalanges digiti minus (III, tertius), phalanx proximalis, extremitas proximalis digiti, vertex proximocaudalis, situs tendinis insertii m. extensor digiti minoris manus, forma:

a. tuberculum, extending distinctly but at most moderately proximad to facies articularis digiti;

b. processus, approaching proximad or reaching coplanarity with symphysis distalis intermetacarpalis;

x. noncomparable (ratites, Dromornithidae).

Note.—See: Lowe (1933: fig. 15), regarding hyperapomorphic state in Sphenisciformes; S. L. Olson and Hasegawa (1979, 1985, 1996); Stephan (1979); S. L. Olson (1980).

1727. Phalanges proximalis et intermedia digiti III (minoris, tertius), combined length of first and second phalanges relative to that of phalanx distalis (tertius), forma:

a. former greater than latter;

b. former less than latter;

x. noncomparable by absence of (at least) phalanges distales (Neornithes).

Note.—See: Gauthier (1986: text character 62); Pérez-Moreno et al. (1994: legend for fig. 3, character 20); Russell and Dong (1994b [1993b]: list A, character 10); Makovicky and Sues (1998: appendix 1, character 72); Holtz (2000 [1998]: appendix I, character 272); Chiappe (2001a: appendix 1, character 113); Maryanska et al. (2002: appendix 1, character 139).

1728. Phalanx proximalis digiti III (minoris, tertius), length of former relative to combined lengths of other phalanges digiti III, forma:

a. former subequal to or longer than latter;

b. former significantly shorter than latter;

x. noncomparable by absence of all but phalanx proximalis (Neornithes).

Note.—See: Chiappe (2002: appendix 20.2, character 113).

1729. Phalanx proximalis digiti III (minoris, tertius), facies corporis dorsalis, jugum ligamentosus (**new term**), status:

a. absent or obsolete; **b.** present;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—Jugum oriented along axis majoris phalangis, aligned with ligamenta et aponeuroses metacarpo-phalangeales et interphalangeales.

1730. Phalanx proximalis digiti III (minoris, tertius), foramina (pori) pneumatica, status:

a. absent; **b.** present;

x. noncomparable by absence digitus III (Aepyornithiformes, Dinornithiformes, Dromaiidae, Casuariidae, *Apteryx*, *Aptornis*).

1731. Phalanx proximalis digiti III (minoris, tertius), processus flexorius, ventral prominence, status (**ordered**):

a. absent; **b.** weakly developed;

c. distinct to prominent, typically rendering margo caudalis phalangis triangular in profile;

x. noncomparable by absence digitus III (Aepyornithiformes, Dinornithiformes, Dromaiidae, Casuariidae, *Apteryx*, *Aptornis*).

Note.—Processus homologous to tuberculum insertii tendinis m. flexor digiti minoris (**new term**). See: Stegmann (1965) for tendines et ligamenta stabilizing digitus III; Sereno (1999: character 149). Also possibly relevant are Sereno (1999: character 148) and Suzuki et al. (2002: character 8) regarding possibly related, unconventionally termed feature "flexor depression proximal to the distal condyles on the manual proximal phalanges" primarily related to facies ventralis of phalanx proximalis alulae.

1732. Phalanges proximalis (primus) et intermedius (secundus) et proungualis (tertius) digiti majoris (III, tertius), relative lengths (**ordered**):

a. penultimatus no longer than either intermedius aut proximalis;

b. penultimatus longer than either intermedius aut proximalis;

c. penultimatus longer than both intermedius et proximalis;

x. noncomparable (Aves).

Note.—See: Gauthier (1986); Rauhut (2003: character 160).

1733. Phalanges proximalis digiti III (minoris, tertius), length relative to that of phalanx proximalis digiti II (majus, secundus):

a. former approximately equal to latter;

b. former less than latter;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

1734. Phalanges digitorum II et III in articulatio, apex phalangis (proximalis) digiti III, opposite articulatio interphalangealis phalangiorum proximalis et distalis digiti II, situs relativum (**ordered**):

a. proximal; **b.** opposite; **c.** distal.

1735. Phalanges digitorum II et III in articulatio, phalanges proximales digitorum II et III, conformation of spatium interdigitalis as subelliptical fenestra interdigitalis manus (**new term**), status:

a. absent, spatium fissuriform;

b. present, spatium broad, subelliptical.

Note.—Fenestra typically covered by translucent membrana and bordered in part by ligamenta interphalangealis digiti majoris, collaterale caudale, et accessoria alae, and creating distinctive bifenestrate aspect in combination with spatium intermetacarpalis (dorsal or ventral perspectives).

Juncturae Alae

Note.—In birds (excepting Dinornithiformes), juncturae cubiti comprise the distal articulationes synoviales humeroulnaris et humeroradialis, and the lesser articulatio radioulnaris proximalis. Distally, the antebrachium participates in articulationes ulnocarpalis et radiocarpalis. In addition, the antebrachium is involved with several other minor contacts: juncturae radio-radiocarpo-ulnaris, ulno-ulnocarpo-radialis, ulno-ulnocarpo-radialis, radio-ulnaris proximalis, et radio-radiocarpo-ulnaris. Within the carpus (wrist), multiple articulationes occur: articulationes intercarpales carpo-carpometacarpales. Distad, juncturae continue with juncturae (synostoses in Aves) carpometacarpales, intermetacarpalis proximalis, et intermetacarpalis distalis. Distalmost juncturae comprise: articulationes metacarpophalangeales digitorum alulae, majoris, et minoris, as well as varying numbers of articulationes interphalangeales for the digiti alae—I–III (Aves) or I–IV or V (basal Theropoda)—which manifest two compounding patterns of reduction within crown Theropoda, by caudo-cranial loss of digiti and proximo-distal reduction within digiti.

1736. Articulationes humero-ulnaris, humeroradialis, radio-ulnaris proximalis, et radio-ulnaris distalis and resultant alar adductability, typus:

a. fully functional, permitting adduction of ala;

b. functionally limited by ligamenta, precluding "typical" adduction of ala, the appendage remaining largely extended;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—See: S. L. Olson and Hasegawa (1979, 1985, 1996); Stephan (1979); S. L. Olson (1980).

1737. Omni-synostosis antebrachii et manus, associated with profound apomorphy related to comparatively ancient flightlessness and giantism in a cursorial bird—synostoses humero-ulnaris humeroradialis, intercarpales, ulnocarpalis, radiocarpalis, intermetacarpalis, carpometacarpales, carpocarpometacarpales, metacarpophalangeales, et interphalangeales—in combination with multiple other qualitative apomorphies—e.g., occlusion of spatium interosseus antebrachii, spatium intermetacarpale, trochlea carpalis, processus pisiformis, et processus extensorius—related to flightlessness, status:

a. absent; **b.** present;

x. noncomparable (Dinornithiformes).

Note.—Only *Aptornis* approaches this level of apomorphy, and there it is limited to the manus (especially carpometacarpus et digitus alularis), although both evidently are the result of early and marked paedomorphosis. Landmarks in evidence as vestigial are a depressio proximalis on facies dorsalis of extremitas proximalis (corresponding to spatium interosseus antebrachii), shallow and broad distal sulci on both facies lateralis et medialis of distal half (marking spatium intermetacarpale), and a distinct eminentia at the midpoint of margo cranialis of the complex (evidently the vestigium of processus alularis carpometacarpi). See corresponding reductive character of the humerus.

1738. Juncturae radio-ulnares proximalis et distalis, typae modales:

a. both juncturae proximalis et distalis are articulationes, i.e., comparatively "loosely joined";

b. one or both juncturae proximalis et distalis are syndesmoses, i.e., comparatively "tightly joined";

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—See: Bledsoe (1988: appendix, character 27), discounted by K. Lee et al. (1997: appendix 2) for ratites; Pérez-Moreno et al. (1994: legend for fig. 3, character 17); Livezey (1996a: appendix 1, characters 52 and 54), regarding "exostosis" or distal synostosis radio-ulnaris in some flightless anatids; Holtz (2000 [1998]: appendix I, character 250), concerning degree of "conjoined" articulationes.

1739. Juncturae cubiti, trochlea humero-ulnaris—partes humeralis proprius et accessoria ulnaris (**new terms**)—variation associated with mm. expansor secundariorum et flexor (meta)carpi ulnaris, status et typus (**unordered**):

a. trochlea absent, or if present, comprising only pars ulnaris as origo m. expansor secundariorum, m. flexor (meta)carpi ulnaris reduced to tendo;

b. trochlea present, comprising partes humeralis proprius, humeralis accessoria, et ulnaris;

c. trochlea present, comprising partes humeralis proprius et ulnaris, associated with reduction of m. expansor secundariorum to tendo;

d. trochlea present, comprising partes humeralis proprius, humeralis accessoria, et ulnaris, but origo tendinis m. expansor secundariorum comparatively caudodistal and, together with pars ulnaris, guides tendo m. flexor (meta)carpi ulnaris, typically associated with diminishment of partes trochlearum humeralis proprius et (rarely) accessoria;

e. trochlea present, comprising only pars humeralis proprius (*Hemiprocne comata*), humeralis accessoria (*Cypseloides niger*, *Apus pallidus*), aut ulnaris, the last united with a neomorphous fascia ligamentosa cum sesamoideum origii m. extensor metacarpi ulnaris and passing around margo caudalis ulnae to attach with vestigium of trochlea humeroulnaris;

x. noncomparable (Dinornithiformes, Dromornithidae).

Note.—See: Shufeldt (1890); Stephan (1979); Baumel and Raikow (1993: annotation 110). Scoring largely after Bentz and Zusi (1982).

1740. Articulatio omalis (cavitas glenoidalis)—juncturae cubiti (articulationes humero-ulnaris et humeroradialis), et juncturae carpi et manus (articulationes intercarpales, ulnocarpalis, et radiocarpalis)—permitting of rotation of membri thoracici and adduction and appression of ossa alae against corpus (e.g., flight and closure of wings), status:

a. absent; **b.** present.

Note.—See: Cracraft (1986: appendix, character 73); Cracraft (1988: series I, character 12); Sereno et al. (2002), regarding *Sinornis*. Also see characters of articulatio omalis et cavitas glenoidalis pertaining to capacity for aerial flight (Sereno and Rao 1992; Sereno 1997, 1999).

1741. Synostosis intercarpalia of ossa carpi distalia I et II, status:

a. absent; **b.** present;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—See: Holtz (2000 [1998]: appendix I, character 254), in reference to union of distal carpals, exclusive of involvement with ossa metacarpalia.

1742. Articulationes (synostoses) intercarpalia of ossa carpi distalia I et II, ambitus distalis articulationis:

a. limited to extremitates proximales metacarpale II;

b. extended by appression through semiossis proximalis ossis metacarpale II;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—See: Gauthier (1986: text character 44); Holtz (1994a: appendix 1, character 95); Sues (1997: appendix 1, character 33); J. D. Harris (1998: appendix 2, character 97); Xu et al. (1999a: character 65); Currie and Carpenter (2000: appendix 1, character 76); Chiappe (2001a: appendix 1, character 107); Chure (2001); Rauhut (2003: character 148).

1743. Synostosis carpometacarpi involving os carpi distalis "scapholunare" (semilunate), status et forma (**ordered**):

a. absent, forming articulatio scapholunarometacarpalis;

b. present, forming incomplete (i.e., suturae discernable) synostosis scapholunaro-metacarpalis, or requiring protracted period to achieve;

c. present, forming complete (i.e., suturae indiscernable) synostosis scapholunaro-metacarpalis.

Note.—See: Chiappe (2002: appendix 20.2, character 101, part).

1744. Juncturae (synostosis) carpometacarpi, articulationes (synostoses) carpometacarpi between os carpi distalis "scapholunare" (semilunate) et os metacarpale I (alularis, primus), typus:

a. former articulates with entire facies proximalis of latter;

b. former articulates with less than one-half facies proximalis of latter;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—A fundamental difference between ratites and other Neornithes is the symmetrical union of ossa carpi distalia composing the definitive trochlea carpalis in the former, whereas in the latter taxa the ossa forming the bases for facies articularis ulnocarpalis and facies articularis radiocarpalis are significantly proximodistally misaligned.

See: Norell and Clarke (2001: appendix I, character 140), treated similarly by J. A. Clarke (2002: appendix I, character 140), J. A. Clarke and Norell (2002: appendix 2, character 140), and J. A. Clarke (2004: appendix 1, character 140); Ji et al. (2005: supplement, part I, character 140).

1745. Juncturae carpi et manus, juncturae (synostosis) carpo-carpometacarpales, articulationes (synostoses) between os carpi distalis ("scapholunare" or semilunate carpal) et ossa metacarpalia I et/aut II, typus et forma (**ordered**):

a. os carpi distale ("block 1") articulates only with os metacarpale I, proximalmost basis, forming articulatio carpo-metacarpalis scapholunaro-alularis (**new term**), whereas ("block II") covers extremitas proximalis of os metacarpale II;

b. ossa carpi distale ("block I") articulates with os metacarpale I, extremitas proximalis, and *ventrally* with os metacarpale II;

c. ossa carpi distalia ("block I") articulates with os metacarpale I, extremitas proximalis, and *both* dorsally and ventrally with os metacarpale II.

Note.—See: Chiappe (1996b: character 54); Holtz (2000 [1998]: appendix I, character 253); Chiappe (2001a: appendix 1, character 101); Norell et al. (2001: appendix 1, character 148); Chiappe (2002: appendix 20.2, character 101, part); J. M. Clark et al. (2002a: appendix 2.2, character 150); Xu (2002: suite II, character 175); Xu et al. (2002a: supplement, character 119), in which an admission is made that ontogenetic information is required for interpretation of the composition of the "semilunate carpale of birds" by one (os carpi distale) or two ossa carpalia distales. In addition, Russell and Dong (1994a [1993a]: table 2, character 38) cited variation in dorsoventral overlap between ossa carpalia distales and os metacarpale II. Ji et al. (2003a: 23) concluded that os scapholunare articulates with a "small part" of extremitas proximales metacarpale I and the entire extremitates proximales metacarpalia II et III in *Shenzhouraptor*; Hwang et al. (2004: supplement, character 147); Xu and Norell (2004: supplement, character 147).

1746. Articulationes proximalia metacarpalia of ossa metacarpalia IV et V with respect to proximal segments of ossa metacarpalia I–III, status et forma (**unordered**):

a. ossa metacarpalia IV et V present, and "lying on palmar surfaces" of ossa metacarpalia I–III;

b. ossa metacarpalia IV et V present, and "overlap bases" of ossa metacarpalia I–III;

c. os metacarpale IV vestigial and marginally palmar;

x. noncomparable, ossa metacarpalia IV et/aut V absent (Neornithes).

Note.—See: Sereno et al. (1993: legend for fig. 3a); Novas (1994 [1993]: appendix, character 30).

1747. Synchon-synostoses intermetacarpales (**new term**), especially spatium intermetacarpale, status et typus (**unordered**):

a. absent, synostoses intermetacarpalia lacking;

b. partial, synostosis intermetacarpalis proximalis lacking or incomplete, but synostosis intermetacarpalis distalis complete;

c. partial, synostosis intermetacarpalis proximalis complete, synostosis intermetacarpalis distalis incomplete in that sutura remains discernable, region having aspect of deep fissura;

d. partial, synostosis intermetacarpalis proximalis present but synostosis intermetacarpalis distalis lacking, ossa metacarpalia II et III separate distally;

e. present, comprising ossa metacarpale alulare, metacarpale majus, and metacarpale minus, with synostoses intermetacarpales proximalis et distalis complete, enclosing spatium intermetacarpale;

f. vestigial, ossa metacarpale majus et minus truncated distally, synostosis metacarpalis distalis and extremitas distalis carpometacarpi present and occluding spatium entirely;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—Maturity of skeletons crucial (Romanoff 1960; Hinchliffe 1985), as embryonic *Gallus* lack both synchon-synostoses intermetacarpalia (T. J. Parker 1891; Lowe 1928b). See: Ostrom (1976a); L. D. Martin and Tate (1976); Hogg (1982); Thulborn (1984: 126–127, character 18); Cracraft (1986: appendix, character 13); Bledsoe (1988: appendix, character 32, part), discounted by K. Lee et al. (1997: appendix 2) for ratites; Cracraft (1988: series III, character 3); Houde (1988: table 27, character 38); Sanz and Buscalioni (1992: character 3, part); Sereno and Rao (1992); Chiappe and Calvo (1994: appendix I, character 43); Chiappe (1995a: legend for fig. 1); Chiappe (1995b: character 43); Elzanowski (1995: character C2); Sanz et al. (1995, 1997: character 41); Chiappe (1996b: character 40); Chiappe et al. (1996: appendix 1, character 39); Hou et al. (1996: character 7); Novas (1996: appendix, character 45); Novas (1997: appendix, character 12); Novas and Puerta (1997), identically by Novas (1997); Chiappe et al. (1998: character 54); Forster et al. (1998: supplement, character 60); Padian and Chiappe (1998b); Chatterjee (1999: appendix II, character 64); Holtz (2000 [1998]: appendix I, character 252); Chiappe (2001a: appendix 1, characters 101–102); J. A. Clarke and Chiappe (2001: character 36), for basal carinates; Ji et al. (2001), regarding dromaeosaurid NGMC 91-A; Norell and Clarke (2001: appendix I, character 139); Sereno (2001: table 1, character 4), regarding Alvarezsauridae; Chiappe (2002: appendix 20.2, characters 101–103); Maryanska et al. (2002: appendix 1, character 136); Sereno et al. (2002), regarding *Sinornis*; Xu et al. (2002a: supplement, character 120); Zhou and Zhang (2002: appendix III, character 139).

1748. Digiti I–III manus, extremitates distales, facies dorsales, articulationes metacarpophalangeales, hyperextensibility and associated prominence of foveae ligamentorum collateralium ("extensor pits"), forma:

a. not "hyperextensible," with reduced or obsolete "extensor pits";

b. "hyperextensible," with deep "extensor pits";

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—See: Sereno et al. (1993); Novas (1997: appendix, character 15), Novas and Puerta (1997), employed identically by Novas (1997), with respect to facies articularis and foveae of phalanx proximalis digiti II; Holtz (2000 [1998]: appendix I, character 269), citing Pérez-Moreno et al. (1994); Rauhut (2003: character 155).

1749. Articulatio metacarpophalangealis alulae, typus (**unordered**):

a. articulatio sellaris, involving labrum distalis (**new term**) on terminus distalis of os metacarpale alularis (I);

b. articulatio plana, involving pluteus distalis (**new term**) on terminus distalis of os metacarpale alularis (I);

c. synostosis;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—See: J. A. Clarke and Chiappe (2001: character 46); Norell and Clarke (2001: appendix I, character 144), treated similarly by J. A. Clarke (2002: appendix I, character 144), J. A. Clarke and Norell (2002: appendix 2, character 144), and J. A. Clarke (2004: appendix 1, character 144); Zhou and Zhang (2002: appendix III, character 144), contrasting "gynglimoid" *vs.* "shelf." Baumel and Raikow (1993: annotation 131), stated that articulatio metacarpophalangealis alulae apomorphically is a synostosis (cf. *Spheniscus*); a modification of digitus alulae may be involved, perhaps elongation of os metacarpale I; Ji et al. (2005: supplement, part I, character 144).

1750. Articulatio metacarpophalangealis alulae, approximate position with respect to facies cranialis ossis metacarpale II (in repose), angulus (**ordered**):

a. parallel (approximating 0°), alula essentially parallel to ossa metacarpalia, associated with facies articularis phalangealis perpendicular to axis majoris phalangis alularis;

b. diagonal (approximating 45°), alula approaching diagonality with respect to ossa metacarpalia, associated with facies articularis phalangealis spheroidal and subdiagonal to axis majoris phalangis alularis;

c. perpendicular (approximating 90°), alula approaching perpendicularity with respect to ossa metacarpalia, associated with facies articularis phalangealis approximately diagonal to axis majoris phalangis alularis;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromaiidae, Casuariidae, *Apteryx*).

1751. Synostosis metacarpophalangealis alulae cranialis, status:

a. absent; **b.** present;

x. noncomparable (Aepyornithiformes, Dinornithiformes, Dromornithidae).

Note.—Synostosis is compound—synostosis digitus alularis cum ossa metacarpalia alulae (facies articularis phalangealis) et majus (margo cranialis). See: S. L. Olson and Hasegawa (1979, 1985, 1996); Stephan (1979); S. L. Olson (1980).

1752. Junctura metacarpophalangealis digiti majoris, status et typus (**unordered**):

a. articulatio condylaris;

b. synostosis, phalanx proximalis distinct but significantly truncated;

c. synostosis, phalanx proximalis vestigial or indiscernable;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

1753. Junctura metacarpophalangealis digiti minoris, status et typus (**ordered**):

a. articulatio condylaris;

b. synostosis, phalanx proximalis distinct but significantly truncated;

c. synostosis, phalanx proximalis vestigial or indiscernable;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

1754. Articulatio interphalangealis lateralis manus, status (**unordered**):

a. present, elements attached by ligamentum interosseum;

b. absent, phalanges digiti minoris united by synostosis to phalanges digiti majoris;

c. absent, phalanges digiti minoris evidently lost;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—See: Pelissier (1923).

1755. Synostosis metacarpophalangealis alulae, in combination with other synostoses metacarpophalangeales and phalangis alularis, status vestigialis (**unordered**):

a. absent, despite retention of both phalanges alulae in many taxa;

b. present;

c. present, shared by synostosis metacarpophalangealis alularis involving both ossa metacarpalia alulare et majus;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—See: C. W. Parsons (1934) regarding ontogeny; S. L. Olson and Hasegawa (1979, 1985, 1996); Stephan (1979); S. L. Olson (1980).

1756. Junctura interphalangealis (proximalis) digiti majoris manus, typus (**unordered**):

a. articulatio trochlearis;

b. articulatio (synovialis) subspheroidal aut tubercular;

c. articulatio (synovialis) plana;

d. synchondrosis;

x. noncomparable (Aepyornithiformes, Dinornithiformes, *Aptornis*).

Note.—In reference to condyli distales manus, plesiomorphic form of which resembling those of pes.

Ossa Cinguli Membri Pelvici

Partes Pelvici et Os Coxae

Note.—See: du Toit (1912–1913) and Boas (1934) for classical reviews; Romer (1923a) regarding ilii of Dinosauria; Boas (1934), Hutchinson (2001a) for issues of general anatomical nomenclature and taxonomic variation; Archey (1941) and Oliver (1949) regarding Dinornithiformes; Andrews (1897) and Lowe (1930) regarding *Aepyornis*. Development and comparisons with dinosaurs provided by A. D. Walker (1977, 1980). A notable departure from the nomenclature of Baumel and Witmer (1993) involved the delimitation of the portions of the ossa pelvici that border the acetabulum (i.e., os coxae). For each—ossa ilium, ischium, et pubis—partes acetabulares refer to those portions that collectively compose the rima acetabularis (**new term**), each of which include segments in articulation with the two components adjacent to it—e.g., pars acetabularis ilii comprises pedunculus articularis ischii (**new term**) et pedunculus articularis pubis (**new term**), each with respective facies articularis as well as the semicircular section of the rima acetabularis contributed by that element. E.g., the latter component of os ilium includes incisura acetabularis ilii (**new term**).

Regarding myological homologies of the pelvis, see figures 6.14–6.17 of Vanden Berge and Zweers (1993). Given that significant structural details of the definitive pelvis of birds derive from membrana ossificantes and other components distinguishable from the ossa cinguli membri pelvici—e.g., membrana iliocaudalis ossificans forming part of the caudalmost part of the ilioischial complex (arthrologia annotation 185)—some potentially informative characters were not assessable using skeletons of adults.

Geometrica pelvici

1757. Angulus synsacro-pubica (**new term**), typus aut forma (**ordered**):

a. cranioventral, i.e., propubic (**new term**) condition;

b. approximately perpendicular, but includes modest caudal component, i.e., mesopubic (**new term**) condition;

c. ventrocaudal, i.e., pro-opisthopubic (**new term**) condition;

d. caudal, i.e., eu-opisthopubic (**new term**) or opisthopubic *sensu stricto*.

Note.—Angulus defined by axis majoris pubicus relative to axis vertebralis sacrales manifests strong correlation between developmental changes and taxonomic differences in Aves. Some distantly related Dinosauria (notably Ornithischia) also possessed pubic positions similar to those found in modern birds (i.e., state phylogenetically plesiomorphic to state "a" among Theropoda is ostensibly referable to state "c" here), whereas state "a" pertains to Crocodylia.

See: Ostrom (1976a); Barsbold (1979), emphasizing "opisthopubic" state; Gauthier (1986); Cracraft (1986: appendix, characters 18 and 35); Cracraft (1988: series I, character 5; series II, character 8); Benton (1990a: 25) listed opisthopubic condition as synapomorphic of Ornithischia, convergent with that of some crown Theropoda; Sanz and Bonaparte (1992: character 16); Sereno and Rao (1992); Chiappe and Calvo (1994: appendix I, characters 47 and 55); Russell and Dong (1994a [1993a]: table 2, character 50); Russell and Dong (1994b [1993b]: troödontid character 18, part); Holtz (1994a: appendix 1, character 31); Chiappe (1995a: legend for fig. 1); Chiappe (1995b: characters 47 and 55); Currie (1995: appendix, character 25); Sanz et al. (1995, 1997: characters 45 and 53); Chiappe (1996b: character 44); Chiappe et al. (1996: appendix 1, character 43); Hou et al. (1996: legend for fig. 3, "opisthopubic" condition); Novas (1996: appendix, character M14); Novas (1996: appendix, character 52); Carroll (1997: 312); Norell and Makovicky (1997); Novas (1997: appendix, character 53); Novas and Puerta (1997), see identical characters in Novas (1997); Sues (1997: appendix 1, character 39); Chiappe et al. (1998: character 63); Forster et al. (1998: supplement, character 78); Hutchinson and Chiappe (1998: fig. 2); Ji et al. (1998: supplement, character 63); Makovicky and Sues (1998: appendix 1, character 80); Chatterjee (1999: appendix II, character 73, and "not included" character 19); Xu et al. (1999a: 51); Xu et al. (1999b: character 59); Holtz (2000 [1998]: appendix I, character 309); Xu et al. (2000: supplement, character 44); Zhou and Wang (2000); Zhou et al. (2000); Chiappe (2001a: appendix 1, character 122); Currie and Chen (2001); Hutchinson (2001a: appendix 1, character 17); Norell and Clarke (2001: appendix I, character 156), treated similarly by J. A. Clarke (2002: appendix I, character 157), J. A. Clarke and Norell (2002: appendix 2, character 157), and J. A. Clarke (2004: appendix 1, character 157); Norell et al. (2001: appendix 1, character 176); Chiappe (2002: appendix 20.2, character 122); J. M. Clark et al. (2002a: appendix 2.2, character 178); Maryanska et al. (2002: appendix 1, character 165); Sereno et al. (2002), regarding *Sinornis*; Xu (2002: suite II, character 198); Xu et al. (2002a: supplement, character 143), in which four states were recognized; Zhou and Zhang (2002: appendix III, character 153); Rauhut (2003: character 167); Xu et al. (2003); Hwang et al. (2004: supplement, character 175); Xu and Norell (2004: supplement, character 175); Ji et al. (2005: supplement, part I, character 156).

Related studies are: Hutchinson and Gatesy (2000) regarding locomotion of archosaurs; Carrier and Farmer (2000) regarding role of pelvis in respiration among archosaurs; Hutchinson (2001a: figs. 8 and 11) for continuum of states.

Ossa Coxae

Note.—A number of characters pertain to features of the "pelvis" *sensu lato*—a structural complex comprising ossa ilia, ischia, et pubici—together variably joined with the columna vertebralis (synsacrum). Such features are not readily assignable to any single element, and are treated below.

1758. Synsacrum et ala preacetabularis ilii, facies ventralis, comparatively extreme truncation of synsacrum et dorsal ilia cranial to intersectio craniomedialis of crista iliaca obliqua et synsacrum, vertebrae thoracicae synsacri, status:

a. absent;

b. present, limiting vertebrae in series to two or three in number;

x. noncomparable (palaeognathous Neornithes).

Note.—Considered only superficially similar to trivertebral synsacri at basal Archosauromorpha.

1759. Synsacrum et ala postacetabularis ilii, margo caudalis, incisura (invaginatio) suturae iliosynsacralis (**new term**), status:

a. variably conspicuous and penetrating craniad to point parallel to margo caudalis foraminis ilioischiadica;

b. absent or rudimentary.

Note.—New feature refers to invagination of ilium, margo dorsomedialis, at extremitas caudalis pelvici, at sutura iliosynsacralis.

1760. Synsacrum et ala postacetabularis ilii, facies dorsalis, sutura vestigialia iliosynsacralis (dorsal perspective), status (**ordered**):

a. present; **b.** absent.

1761. Ala (pars) postacetabularis ilii, facies dorsalis, synsacrum, elements immediately caudal to acetabula and adjacent to vertebrae thoracicae, depressio iliosynsacralis dorsalis (**new term**), status (**ordered**):

a. absent;

b. present, forming lateromedially narrow depressio along midline of synsacrum, and including comparatively ventral, planar state of crista spinosa synsacri;

c. present, partitioned medially by elevated crista spinosa synsacri, forming bilateral pair of sulcuslike depressiones in regio.

Note.—See: Livezey (1998b: appendix A, character 281).

1762. Acetabulum, craniocaudal width relative to that of os ilium, corpus ilii, pars acetabularis ilii, pila articularis ischii (**new term**), forma:

a. width of latter less than diameter of former;

b. width of latter greater than diameter of former.

Note.—See: Gauthier (1986: text character 78); Chiappe and Calvo (1994: appendix I, character 46); Chiappe et al. (1996: appendix 1, character 42); Novas (1996: appendix, character 23); Forster et al. (1998: supplement, character 76); Xu et al. (1999a: character 47); Xu et al. (1999b: character 58); Sereno (2000: table 4, character 6); Xu et al. (2000: supplement, character 42), regarding the relative width of the "pubic peduncle on ilium." Related metric of relative acetabular diameter is by ratio comparison with the length of the ilium: Chiappe (1995a: legend for fig. 1); Chiappe (1995b: character 46); Sanz et al. (1995, 1997: character 44); Chiappe (1996b: character 43); Chiappe et al. (1996: appendix 1, character 42); Forster et al. (1998: supplement, character 73, modified); Xu et al. (1999b: character 55, modified); Chiappe (2001a: appendix 1, character 120); Chiappe (2002: appendix 20.2, character 120).

1763. Acetabulum, differential in dorsoventral diameter (height) relative to craniocaudal (width) diameter (**ordered**):

a. former approximately 27–33% of latter;

b. former approximately 50% of latter;

c. former approximately 100% of latter, i.e., foramen approximately circular.

Note.—See: Sereno and Novas (1992); Novas (1994 [1993]: appendix, character 49); Holtz (2000 [1998]: appendix I, character 301).

1764. Acetabulum (lateral perspective), partes acetabulares ilii et pubici, rima acetabularis, incisura in which processus costalis of one of the caudalmost vertebrae thoracicae synsacri extends, status:

a. absent, rima acetabularis entire;

b. present.

1765. Acetabulum, hiatus rimae ilio-pubica preacetabularis (**new term**), status:

a. absent, rima complete, suborbiculate;

b. present, rima incomplete and interrupted by prominent fissura.

Note.—Term rima employed loosely here in that functional acetabulum varies with respect to included elements among taxa. However, regardless of elemental composition or form (e.g., foraminate or occluded, deep cavitas or shallow impressio), a variably prominent rima acetabularis (**new term**) is evident among Archosauromorpha (Romer 1956). Hypothetical losses of critical portion of rima acetabularis—evidently pars acetabularis ossis pubici—requires minimal change if initial condition approximated by that manifested by *Protoceratops* and *Triceratops* (Romer 1956: figs. 157E–F).

1766. Acetabulum, position immediately lateral or lateroventral to columna synsacralis, a result of bilateral compression of ossa coxae, status:

a. absent; **b.** present.

Note.—See: Cracraft (1974: 503, character 14) for ratites; Cracraft (1982: series 1, character 6) for extremely derived foot-propelled diving birds; Houde (1988: table 27, characters 42–43); G. Mayr and Clarke (2003: appendix A, character 90). Presents a "slim-hipped" *Gestalt*, evidently a refinement for streamlining in some foot-propelled diving birds or centering of pelvic appendages directly beneath the body in some massive, cursorial birds.

1767. Acetabulum, rima acetabularis (**new term**), pars ventrocranialis (evidently deriving from pubis, pars acetabularis, incisura acetabularis), foramen pneumaticum (communicating with foramen in tuberculum preacetabularis), status:

a. absent; **b.** present.

1768. Acetabulum, foramen acetabuli, status:

a. absent, i.e., medially closed;

b. present, i.e., largely to fully open.

Note.—Absence of foramen in Crocodylomorpha confusing in that lamina against which caput femoris articulates is to a great extent os ilium—as opposed to the triosseous nature in Euryapsida, Synapsida, and most Archosauria—the hiatus ilio-pubicus cranioventral to it not being homologous to the foramen acetabuli (Romer 1956).

See: Romer (1956: fig. 155); Benton and Clark (1988: appendix 1, character 16); Novas (1992: character 9); Novas (1994 [1993]: appendix, character 16); Sereno and Arcucci (1994 [1993]: fig. 1).

1769. Acetabulum, foramen acetabuli, diameter relative to that of acetabulum, margines laterales, forma:

a. foramen distinctly smaller than externum of acetabulum;

b. foramen subequal in diameter to that of externum of acetabulum.

Note.—State "a" reflects broad facies articularis on rima dorsocranialis or ventrocranialis acetabularis.

1770. Acetabulum, foramen acetabuli (craniolateral perspective), internum rimae, forma:

a. virtually circular;

b. weakly bilobate or irregularly subrectangular, foramen interrupted by inward intrusions, typically cranial and caudal, of the rima.

1771. Acetabulum, foramen acetabuli (lateral perspective), central position within fossa acetabuli, situs:

a. essentially encompasses entire fossa or central portion;

b. distinctly occupies portion caudal to center of fossa.

1772. Acetabulum, foramen acetabuli, orientation (angulus) of vector through acetabulae (**ordered**):

a. perpendicular to axis majoris synsacri;

b. moderately caudally angled such that vector transacetabularis intersects facies lateralis synsacri immediately caudal to rima caudalis of foramen acetabuli;

c. conspicuously caudally angled such that vector transacetabularis intersects facies lateralis synsacri at least one acetabular diameter caudal to rima caudalis of foramen acetabuli, and that processes transverses et costales of vertebrae acetabulares instead of facies lateralis synsacri.

1773. Acetabulum, foramen acetabuli, bilateral compression and dorsal position relative to synsacrum—sectio II of Boas (1934)—in combination creating dorsally deep bilateral recessi—here termed recessus acetabulo-synsacralis (**new term**)—visible through acetabulae (lateral perspective) and/or between ossa coxae et synsacrum (ventral perspective), status:

a. absent; **b.** present.

1774. Processus antitrochantericus, inclusion of os ischium (in addition to os ilium), status:

a. absent or small; **b.** present and large.

Note.—See: Rowe and Gauthier (1990); Holtz (1994a: appendix 1, character 34); Holtz (2000 [1998]: appendix I, character 321).

1775. Processus antitrochantericus, prominence relative to pelvis et acetabulum, status et forma (**ordered**):

a. absent; **b.** present, abbreviate;

c. present, elongate.

Note.—See: Ostrom (1976a); Cracraft (1986: appendix, character 7); Gauthier (1986: 13, unindexed synapomorphy of Ornithurae); Cracraft (1988: series II, character 2); Siegel-Causey (1988: character 111); Baumel and Witmer (1993: annotation 255); Perle et al. (1993); Chiappe and Calvo (1994: appendix I, character 48); Chiappe (1995b: character 48); Elzanowski (1995: character C3); Sanz et al. (1995, 1997: character 46); Chiappe (1996b: character 45); Chiappe et al. (1996: appendix 1, character 44); Novas (1996: appendix, character 50); Novas (1997: appendix, character 51); Novas and Puerta (1997), identically characterized by Novas (1997); Chiappe et al. (1998: character 64); Forster et al. (1998: supplement, character 74); Ji et al. (1998: supplement, character 64); Livezey (1998b: appendix A, character 266); Chatterjee (1999: appendix II, character 67, modified); Holtz (2000 [1998]: appendix I, character 303); Chiappe (2001a: appendix 1, character 123); Norell et al. (2001: appendix 1, character 163); Sereno (2001: table 1, character 5), regarding Alvarezsauridae; Chiappe (2002: appendix 20.2, character 123); J. M. Clark et al. (2002a: appendix 2.2, character 165); Maryanska et al. (2002: appendix 1, characters 156 and 163); Xu (2002: suite II, character 186); Xu et al. (2002a: supplement, character 131); Hwang et al. (2004: supplement, character 162); Xu and Norell (2004: supplement, character 162).

1776. Processus antitrochantericus, orientation relative to acetabulum, forma:

a. directly caudad; **b.** dorsocaudad.

Note.—See: Norell and Clarke (2001: appendix I, character 157), treated similarly by J. A. Clarke (2002: appendix I, character 158), J. A. Clarke and Norell (2002: appendix 2, character 158), and J. A. Clarke (2004: appendix 1, character 158); Zhou and Zhang (2002: appendix III, character 157); Ji et al. (2005: supplement, part I, character 157).

1777. Processus antitrochantericus, facies mediocaudalis (contra-articularis) antitrochantericus, fovea (pori aut recessus) pneumatica(us) antitrochantericus (**new term**), status:

a. absent; **b.** present.

Note.—See: Livezey (1998b: appendix A, character 267); Dyke et al. (2003: appendix 1, character 75).

1778. Sulcus antitrochantericus (corpus ilii), status et forma (**ordered**):

a. absent or obsolete;

b. present, distinct, but comparatively shallow and caudally abbreviated;

c. present, conspicuous, and deep (typically cum concavitas ventral to angulus craniolateralis ilii or encompassing entire area between processus trochantericus et crista spinosa synsacri) and often caudally extensive.

Note.—To variable extent, sulcus presents aspect of a continuation of the fossa iliaca dorsalis dorsocaudad to processus antitrochantericus.

1779. Sulcus antitrochantericus (corpus ilii), caudodorsal extremity of sulcus, perforation by large foramen pneumaticum, status:
a. absent; **b.** present.

1780. Sulcus antitrochantericus (corpus ilii), occlusion by distinct jugum—jugum supra-antitrochantericus (**new term**)—between crista dorsolateralis ilii and processus antitrochantericus, status:
a. absent; **b.** present.

1781. Tuberculum supra-antitrochantericus (**new term**), status:
a. absent; **b.** present;
x. noncomparable (Dinornithiformes).
Note.—Aspect probably homologous to prominent, cranially positioned vertex of crista dorsolateralis.

1782. Concavitas (sulcus) infracristalis (facies lateralis), comparative depth (**ordered**), forma:
a. obsolete; **b.** moderate;
c. substantial, typically including significantly overhanging, often lateroventrally slanting crista dorsolateralis ilii;
x. noncomparable (palaeognathous Neornithes).
Note.—Multiple components of concavity render problematic some assessments.

1783. Processus obturatum, foramen obturatum, status et typus (**unordered**):
a. present, typus pubici—a circumosseus foramen in margo ventralis (obturatoria) pubici immediately caudal to acetabulum;
b. present, typus ischii—a circumosseus foramen in margo ventralis (obturatoria) ischii immediately caudal to acetabulum;
c. absent, failure of tuberculum ligamentosum aut ligamentum ischiopubica ossificans effecting a margo caudalis despite presence of an incisura obturatum in ossa ischii et/aut pubis;
d. present, typus ischiopubici—tuberculum ligamentosum aut ligamentum ischiopubica ossificans completing septum caudalis and delimiting a foramen obturatum involving incisurae obturatici ischii et pubici.
Note.—See: Payne and Risley (1976: character 31), regarding "ischiopubic symphysis" and delimitation of obturator foramen among Ardeidae; Strauch (1978: character 59), reanalyzed by Björklund (1994: appendix) and Chu (1995); Cracraft (1986: appendix, character 34); Cracraft (1988: series IV, character 10); Cracraft and Mindell (1989: table 1, character 10); Barsbold and Maryanska (1990: fig. 18.2E), illustrating exceptionally distal processus obturatorius ischii in *Segnosaurus*; Rowe and Gauthier (1990: fig. 5.7); Weishampel and Witmer (1990: fig. 19.4); Holtz (1994a: appendix 1, characters 91 and 94); Sereno et al. (1996: footnote 45, characters 12 [ischium] and 61 [pubis]); K. Carpenter (1997: fig. 6); Ericson (1997: table 1, character 30); K. Lee et al. (1997: appendix 1, character 24); Norell and Makovicky (1997); J. D. Harris (1998: appendix 2, character 114); Sereno et al. (1998: footnote 22, character 45); Currie and Carpenter (2000: appendix 1, character 91); Holtz (2000 [1998]: appendix I, character 307), limited strictly to presence or absence of foramen; Hughes (2000: appendix 2, character 94), after Seibel (1988: character PE 8); J. A. Clarke and Chiappe (2001: character 68); Livezey (1998b: appendix A, characters 260 and 294); J. A. Clarke and Chiappe (2001: characters 68–69); Cracraft and Clarke (2001: appendix 2, character 25), including extensive discussion of variation among avialian theropods; Norell and J. A. Clarke (2001: appendix I, character 164), treated similarly by J. A. Clarke (2002: appendix I, character 165), J. A. Clarke and Norell (2002: appendix 2, character 165), and J. A. Clarke (2004: appendix 1, character 165); Norell et al. (2001: appendix 1, characters 169 [foramen] and 170 [incisura]); J. A. Clarke (2002: appendix I, character 156), J. A. Clarke and Norell (2002: appendix 2, character 156), and J. A. Clarke (2004: appendix 1, character 156), in terms of "dorsal process" of ischium contacting ilium; J. M. Clark et al. (2002a: appendix 2.2, characters 171 [foramen] and 172 [incisura]); Elzanowski (2002: fig. 6.4); Xu (2002: suite II, characters 192 [foramen] and 193 [incisura]); Xu et al. (2002a: supplement, character 138), in which only a binary treatment of "obturator notch" in unspecified bone was provided; G. Mayr et al. (2003: appendix 1, character 55, part); Rauhut (2003: character 180), regarding foramen obturatum pubici; Hwang et al. (2004: characters 168–169); G. Mayr (2004d: appendix I, character 29); Novas et al. (2004: appendix, character 45); Xu and Norell (2004: supplement, characters 168–169); G. Mayr (2005a: appendix 1, character 30); Ji et al. (2005: supplement, part I, character 164).

Conversion of the incisura obturatorius (**new term**) into a fenestra among most or all avialians is effected union of several elements, most variable of which being partial or complete closure of margo (incisura) foraminis ilioischiadici caudally by variably interrupted ligamentum ischiopubicum ossificans from processus obturatorius ischii to margo dorsalis pubis (Hutchinson 2001a: character 14). Other delimiting features include: margo dorsalis pubis (ventrally) and margo obturatoria ischii (dorsally). Note at least partial correlation between this character and the orientation of the pubis with respect to the axis vertebralis (Hutchinson 2001a: fig. 8).

1784. Fenestra ischiopubica, facies ventralis, significantly lateral convexity and lateral position of scapus pubis relative to lateral concavity and medial position of ala ischii (ventral perspective), resulting in broad exposure of fenestra, status:

a. absent; **b.** present.

1785. Ilium et (to lesser degree) ischium, facies lateralis, depressio supra-obturatorum (**new term**), comparative distinctness and pneumaticity, status:

a. indistinct, at most a subtly delimited subtriangular regio, apneumatic;

b. distinct, a deep, sharply demarcated, frequently pneumatic, triangular sulcoid depressio immediately dorsal to margo obturatoria et foramen obturatum (apparently principally or wholly on ilium), subtending margo caudoventralis of facies articularis of processus antitrochantericus, on facies lateralis of margo caudalis of rima acetabularis, and positioned immediately cranial to margo cranialis of foramen (incisura) ilioischiadicum.

1786. Corpus pubis immediately distal to pars acetabularis, fenestra subobturatorius (**new term**), status:

a. absent; **b.** present.

Note.—See: Gauthier (1986); Holtz (1994a: appendix 1, character 1); Rowe (1989); Rowe and Gauthier (1990); J. D. Harris (1998: appendix 2, character 114); Currie and Carpenter (2000: appendix 1, character 91); Holtz (2000 [1998]: appendix I, character 308), in reference to perforation of "pubic plate" by a "pubic fenestra below the obturator foramen"; Rauhut (2003: character 181).

1787. Spatium ischiopubica (lateral perspective), status et forma (**unordered**):

a. wide (divergent) incisura—delimited by widely divergent ala postacetabulares alae ischii et pubici;

b. intermediate incisura—by absence of caudal completion of membrana ischiopubica ossificans, craniocaudally of moderately deep, subuniform width;

c. narrow incisura—by absence of caudal completion of membrana ischiopubica ossificans, of narrow shape with subparallel margines;

d. wide fenestra—by presence of membrana ischiopubica ossificans, dorsoventrally deep, semiellipsoidal in shape;

e. narrow fenestra—by presence of membrana ischiopubica ossificans, dorsoventrally narrow with subparallel margines dorsalis et ventralis or triangular outline, and terminated comparatively craniad on ala ischii;

f. absent—replaced by synchondrosis ischiopubica by variable combination of membrana ischiopubica ossificans and proximity of ischium et pubis.

Note.—See: Weishampel et al. (1990); Novas (1994 [1993]: fig. 5); Livezey (1998b: appendix A, character 260); Chiappe and Witmer (2002).

1788. Regio postacetabularis (**new term**), ala ischii proximalis et scapus pubis proximalis, comparative robustness of former to latter, magnitudo (**ordered**):

a. broad; **b.** approximately equal;

c. narrow.

Note.—See: Sereno et al. (1994); Holtz (2000 [1998]: appendix I, character 319).

1789. Foramen ilioischiadicum (including synchondrosis ilioischiadica caudalis), status definitivum:

a. absent, spatium an incisura with margo caudalis not closed by tuberculum or membrana ilioischiadica ossificans;

b. present, margo caudalis of spatium closed by membrana ilioischiadica ossificans.

Note.—Ontogenetic changes in partes caudales ilii et ischii indicate that reversals in states among Neornithes represent paedomorphosis. Caudal closure of the incisura to form a foramen is effected by the ossification of the cartilago ilioischiadica; the caudal majority of the spatium (whether incisura or fenestra) is spanned by the membrana ilioischiadica (exclusive of Galliformes), to which musculi are attached on lateral (superficial) and medial (deep) surfaces and traversed cranially by nervi and tubae vascularia. Caudal synchondrosis of the foramen ilioischiadicum, as well as other juncturae ossis coxae, occur comparatively late in skeletal ontogeny (Glutz von Blotzheim 1958: figs. 40–41), evidently predisposing related features to intraspecific variation. Similarity of states in juvenile Neornithes and adult ratites—e.g., Dinornithiformes (Archey 1941: pl. 15) and *Aepyornis* (Andrews 1897: 248) suggest confounding of plesiomorphic with paedomorphic states.

See: Andrews (1897: fig. 2) and Lowe (1930: pl. XVI), regarding *Aepyornis*; Cracraft (1974: 503, character 15; 505, character 3); Thulborn (1984: 126–127, character 15); Cracraft (1985: character 26); S. L. Olson (1985); Houde (1988: table 27, character 44); Cracraft and Mindell (1989: table 1, character 20); and Kurochkin (1995b: table 1, character 18) for ratites; Cracraft (1982: series 3, character 6) for Hesperornithiformes; Cracraft (1986: appendix, character 33); Livezey (1996a: appendix 1, character 62); Livezey (1997a: appendix 1, character 78; *corrigenda*, Livezey 1998a); Rotthowe and Starck (1998: appendix, character 4); Chatterjee (1999: appendix II, character 68, revised); J. A. Clarke and Chiappe (2001: character 69); Cracraft and Clarke (2001: appendix 2, character 27); Norell and Clarke (2001: appendix I, character 154), for occlusion of "ilioishiatic [*sic*] fenestra"; Zhou and Zhang (2002: appendix III, character 154); G. Mayr and Clarke (2003: appendix A, character 94), who considered state for Rheidae not homologous with those of other palaeognathous taxa, citing K. Lee et al. (1997); G. Mayr et al. (2003: appendix 1, character 55); Dyke and van Tuinen (2004: appendix 1, character 67); G. Mayr (2004d: appendix I, character 27); G. Mayr (2005a: appendix 1, character 28).

1790. Foramen ilioischiadicum (if caudally delimited), craniocaudal extent within concavitas infracristalis, status definitivum (**ordered**):

a. encompasses at least cranial one-half of concavitas caudal to acetabulum;

b. limited to cranial one-half but exceeding one-third of concavitas caudal to acetabulum;

c. limited to cranial one-third or less of concavitas caudal to acetabulum;

x. noncomparable by hiatus caudalis fenestrae (nonavialian Therapoda; palaeognathous Neornithes).

Note.—With respect to the relative measurement, note that the complement of the foramen within the concavitas infracristalis is the lamina infracristalis. See: Cracraft (1974: 505, character 3); Cracraft (1988: series VIII, character 3); see also Cracraft (1988: series XI, character 3) concerning unspecified “lengthy fusion of ilium and ischium”; G. Mayr (2004a: appendix 1, character 47, part).

1791. Foramen ilioischiadicum (if caudally delimited), forma definitiva (**ordered**):

a. “ellipsoidal-planar”—with pronounced axis majoris craniocaudad in orientation;

b. “subcircular-planar” or orbiculate—with weakly defined axis majoris (if discernable) craniocaudad in orientation;

c. “subcircular-caudodorsal”—with variably pronounced axis majoris having cranial terminus distinctly dorsal to caudal terminus;

d. “subcircular-caudoventral”—with variably pronounced axis majoris having cranial terminus distinctly ventral to caudal terminus;

x. noncomparable by absence of delimiting membrana ilioischiadica ossificans (nonavialian Therapoda, palaeognathous Neornithes).

Note.—See: Ligon (1967: fig. 2, table 3); Livezey (1998b: appendix A, character 261).

1792. Foramen ilioischiadicum, margo caudalis, primary compositional element of margo caudalis osseum, typus (**ordered**):

a. membrana ilioischiadica ossificans;

b. significant partial contribution by processus dorsalis ischii;

c. entirely os ischium, ala ischii, processus dorsalis;

x. noncomparable by absence of closure by membrana ilioischiadica ossificans (nonavialian Theropoda; palaeognathous Neornithes).

Note.—Processus dorsalis alae ischii variably developed among Mesozoic avialians (Chiappe and Walker 2002: 254–255). Examination of juveniles revealed that galliform taxa uniquely and uniformly occluded the caudal terminus of the foramen ilioischiadicum by a caudodorsal expansion of extremitas caudalis of ala ischii, with prominent margo dorsalis ischii virtually exclusively achieving closure of margo caudalis foraminis with ala postacetabularis ilii. See: Houde (1988: table 27, character 45).

1793. Fossa renalis (par[te]s unspecified), status et forma (**unordered**):

a. absent; **b.** present, variably shallow;

c. present, deep.

Note.—Status a *Gestalt* presented by the variable combination of delimiting ventral features (e.g., processes costales of vertebrae synsacrales, crista iliaca obliqua, crista iliaca intermedia, recesses caudalis fossae, et pila postrenalis). Critical to ascertain whether paleontological citations confused fossa renalis with recessus iliacus. See: Radu (1975); Andors (1992: table 2, character 36); Chatterjee (1995: character 14, part); Chatterjee (1999: appendix II, character 72); Norell and Clarke (2001: appendix I, character 162), treated similarly by J. A. Clarke (2002: appendix I, character 163), J. A. Clarke and Norell (2002: appendix 2, character 163), and J. A. Clarke (2004: appendix 1, character 163); Vickers-Rich et al. (2002), concerning *Avimimus*; Zhou and Zhang (2002: appendix III, character 162); Ji et al. (2005: supplement, part I, character 162).

1794. Fossa renalis, virtual partitioning of partes ischiadica (cranialis) et pudenda (caudalis) by processes costales of vertebrae acetabulares synsacri et crista iliaca intermedia (ventral perspective), status:

a. present, effecting transverse dorsal partition of majority of lateral expanse of fossa;

b. obsolete, fossa craniocaudally continuous and largely unipartite;

x. noncomparable by absence of fossa renalis, at least pars pudenda (ratites, Gaviiformes, Podicipediformes).

Note.—See also assessment of prominent processes costales of vertebrae acetabulares synsacri.

1795. Fossa renalis, pars ischiadica fossae, status et forma (**ordered**):

a. absent;

b. present, rudimentary or vestigial, processes costales of caudalmost vertebrae thoracicae synsacri not markedly ventral to corpora of vertebrae eusacrales, and/or cristae iliaca obliqua (laterally) et iliaca intermedia (caudally) only indistinctly demarcate the limits of subfossa;

c. present, expansive, processes costales of caudalmost vertebrae thoracicae synsacri markedly ventral to corpora of vertebrae eusacrales, and/or cristae iliaca obliqua (laterally) et iliaca intermedia (caudally) distinctly demarcate the limits of subfossa.

Note.—See: Radu (1975).

1796. Fossa renalis, pars ischiadica fossae, vertex caudolateralis (craniolateral to corpus ilii, crista iliaca intermedia, if present), depressio, recessus, aut fovea (typically enclosing pori pneumatici), status et forma (**unordered**):

a. absent;

b. present, as depressio aut recessus;

c. present, as fovea;

x. noncomparable by absence of crista intermedia (ratites, Dromornithidae, *Aptornis*).

Note.—Presumably homologous pori pneumatici occur in at least *Fregata* lacking a recessus or fovea in this *situs*.

1797. Fossa renalis, pars pudenda fossae, position lateroventral to processes costales et transverses of vertebrae caudales stabiles, approximately bisected craniocaudad by sutura iliosynsacralis, status:

a. absent, either pars pudenda only vaguely suggested or situated lateral to synsacrum;

b. present.

1798. Fossa renalis, pars pudenda fossae, craniolateral vertex (i.e., cranial terminus of recessus iliacus caudolateral to corpus ilii, crista iliaca intermedia, if present), ovoid depressio (enclosing pori pneumatici) aut fovea, status (**unordered**):

a. absent;

b. present, as depressio aut recessus;

c. present, as fovea;

x. noncomparable (most ratites).

Note.—See: Radu (1975); Baumel and Witmer (1993: Osteologia, annotation 237); Livezey (1998b: appendix A, character 264).

1799. Fossa renalis, recessus caudalis fossae, status:

a. absent; **b.** present;

x. noncomparable (palaeognathous Neornithes).

Note.—See: Strauch (1978: character 54), reanalyzed by Björklund (1994: appendix) and Chu (1995); Livezey (1986: appendix 1, character 120); Livezey (1989: table 1, character 120); Andors (1992: table 2, character 38); Livezey (1996a: appendix 1, character 63); Ericson (1997: table 1, character 31; table 2, character 24); Livezey (1997a: appendix 1, character 79; *corrigenda*, Livezey 1998a); Chu (1998: appendix 1, character 106); G. Mayr and Clarke (2003: appendix A, character 95), exceptional treatment of *Balaeniceps* and Otididae excluded herein; Dyke and van Tuinen (2004: appendix 1, character 68); G. Mayr (2004a: appendix 1, character 50).

1800. Fossa renalis, recessus caudalis fossae, enclosed pori aut foramina pneumatica, status aut numerus modalis (**unordered**):

a. absent, devoid of pori aut foramina;

b. present, comparatively few, minute pori pneumatici;

c. present, comparatively many pori and/or large formina pneumatica;

x. noncomparable where recessus absent or obsolescent (see status).

Note.—See: Holman (1961, 1964); Strauch (1978: character 55), reanalyzed by Björklund (1994: appendix) and Chu (1995); Chu (1998: appendix 1, character 106). Ala (pars) postacetabularis ilii, facies ventralis, spina dorsolateralis ilii.

1801. Fossa renalis, recessus caudalis fossae (if present), depth as reflected by number of vertebrae caudales stabiles interposed between bilateral recessi and distinctly differentiated (e.g., thickened, ventrally displaced crista caudalis fossae renalis) as medial supports for lamina ventralis of same, numerus vertebralia (**ordered**):

a. zero; **b.** one; **c.** two; **d.** three;

x. noncomparable where recessus absent.

Note.—Imprecision incorporated in this character by multiple manifestations of differentiation of vertebrae in question. See: Chu (1998: appendix 1, character 106); Livezey (1998b: appendix A, character 125), under vertebrae and essentially redundant.

1802. Fossa renalis, recessus caudalis fossae, craniocaudal length of internum (margo cranialis of which is crista caudalis fossae renalis) relative to craniocaudal width of lamina infracristalis, status et forma (**ordered**):

a. absent, *sensu* lacking measurable internum;

b. present, depth of recessus comparatively shallow, craniocaudal internal depth less than one-fourth of craniocaudal width of lamina infracristalis;

c. present, depth of recessus comparatively moderate, craniocaudal internal depth between one-fourth and one-half of craniocaudal width of lamina infracristalis;

d. present, depth of recessus comparatively great, craniocaudal internal depth greater than one-half of craniocaudal width of lamina infracristalis.

Note.—See: Lowe (1925b); Hesse (1990) used this term to refer to incisura marginis caudalis; Chu (1998: appendix 1, character 106); Livezey (1998b: appendix A, character 263); Hughes (2000: appendix 2, character 93), after Seibel (1988: character PE 20).

1803. Fossa (marginis pelvici) postrenalis (**new term**), recessus marginis ventralis (**new term**)—a small recessus on facies ventralis of ala postacetabularis ilii et ischium, immediately caudal to pila renalis and enclosing several pori pneumatici—status:

a. absent; **b.** present.

Note.—Ericson (1997: table 1, character 32), noted "a distinct, deep, pneumatic depression . . . medio-posteriorly on ilium" in Otididae and Eurypygidae, with limited pneumaticity noted also in Scolopacidae. This character may refer to aberrations of the fossa iliocaudalis or recessus postrenalis.

1804. Fossa (marginis pelvici) postrenalis (**new term**), craniocaudal expanse approximating that of partes ischiadica et pudenda propriae of fossa renalis, status modalis:

a. absent; **b.** present.

Note.—Appears as extension of fossa renalis caudal to pila postrenalis aut fossa renalis, recessus caudalis fossae.

1805. Incisura caudalis pelvis, lateromedial width (defined as that between processes margines caudales) relative to that of extremitas caudalis synsacri, forma (**ordered**):

a. obsolete, delimiting processes almost articulate medially, incisura essentially comprising width of extremitas caudalis synsacri and bilateral processes margines caudales, in which incisura at terminus caudalis of sutura iliosynsacralis obsolete;

b. limited to moderate, width of incisura between once and twice that of extremitas caudalis synsacri;

c. expansive, width of incisura at least twice that of extremitas caudalis synsacri;

x. noncomparable because of form of margo caudalis pelvici (*Aepyornis*, Dinornithiformes).

Note.—Precision compromised in some taxa because of conformation of processes margines caudales. See: G. Mayr (2003b: appendix I, character 13), in which lateromedial width of pelvis was assessed across the processes antitrochanterici.

1806. Incisura marginis caudalis, (dorsoventral) height relative to diameter foraminis acetabulae (**ordered**):

a. absent or obsolete, lamina infracristalis et margo dorsalis ilii lacking defined incisura;

b. present, narrow, maximal dorsoventral height no greater than diameter of foramen acetabuli;

c. present, wide, maximal dorsoventral height greater than diameter of foramen acetabuli.

Note.—Height assessed relative to diameter of foramen acetabuli; imprecision resulted in some taxa from ill-defined margines incisurae. See: Hesse (1990), who united *Eurypyga*, *Rhynochetos*, and *Messelornis* (but not *Aptornis*) by apparently same character, under term "recessus iliacus"; Livezey (1998b: appendix A, character 265); G. Mayr and Ericson (2004: appendix I, character 69).

1807. Incisura marginis caudalis, marked cranial depth delimiting ossa ilii et ischii as comparatively narrow alae for considerable extents, status:

a. absent; **b.** present;

x. noncomparable (palaeognathous Neornithes).

Note.—Depth of Rhamphastidae confounded by conformational details; Fregatidae, Anhingidae, Phalacrocoracidae, and Sulidae are superficially similar but largely reflect caudal elongation of spina marginis caudalis. Position at junctura ilioischiadica precludes character comprising variations of margo (incisura) foraminis ilioischiadici. See: Cracraft (1971a) for states of Brachpteraciidae and Leptosomatidae.

1808. Processus marginis caudalis, status et forma (**unordered**):

a. absent or obsolete;

b. present, but of limited prominence, often manifested as rounded eminentia;

c. present, prominent, but imbedded as pila within membrana ossificans;

x. noncomparable palaeognathous Neornithes).

Note.—This processus, if present, is positioned (lateral perspective) between the dorsalmost spina dorsolateralis ilii and the ventralmost processus terminalis ischii, and often appears proximate to or coincident with synchondrosis ilioischiadica and to be of bi-elemental composition. See: Ericson (1997: table 1, character 33).

1809. Tuberculum preacetabulare (processus pectinealis), os principalis:

a. os pubis; **b.** os ilium;

x. noncomparable (Dinornithiformes, *Aptornis*).

Note.—Tuberculum aut processus serves as ancora caudale of ligamentum inguinale. Regardless of derivation, structure evidently represents same landmark—caudal attachment of ligamentum inguinale and cranial attachment being margo lateralis of ala (pars) preacetabularis ilii—which forms a lacuna neurovascularia for the plexus lumbralis of nervi synsacrales, and arteria et vena iliacae externae—therefore the relative contributions of these adjacent, synostotic ossa coxae ventrocranial to the acetabulum may not bear on the issue of homology.

1810. Tuberculum preacetabulare (processus pectinealis), status et forma (**ordered**):

a. absent or obsolete;

b. small tuberculum, torus, or area rugositas;

c. elongate processus, terminus ventral to margo dorsalis acetabulae.

Note.—See: Bledsoe (1988: appendix, character 41), discounted by K. Lee et al. (1997: appendix 2) for ratites; Andors (1992: table 2, character 40); Livezey (1997a: appendix 1, character 82; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, character 270); J. D. Harris (1998: appendix 2, character 102) and Currie and Carpenter (2000: appendix 1, character 81), in reference to "hooklike ventral process on anteroventral margin forming preacetabular notch"; J. A. Wilson and Sereno (1998: appendix, character 99), with respect to relative prominence among Sauropoda; Hughes (2000: appendix 2, characters 86–87), after Seibel (1988: characters PE 5 and PE 10); Dyke (2001b: appendix 1, character 82); Hutchinson (2001a: appendix 1, character 16), in reference to "pubic tubercle"; Norell and Clarke (2001: appendix I, character 158), treated similarly by J. A.

Clarke (2002: appendix I, character 159), J. A. Clarke and Norell (2002: appendix 2, character 159), and J. A. Clarke (2004: appendix 1, character 159); Maryanska et al. (2002: appendix 1, characters 152–153); Zhou and Zhang (2002: appendix III, character 158); Dyke et al. (2003: appendix 1, character 68); G. Mayr and Clarke (2003: appendix A, character 93); G. Mayr et al. (2003: appendix 1, character 53); Dyke and van Tuinen (2004: appendix 1, character 66); G. Mayr (2004a: appendix 1, character 49); G. Mayr and Ericson (2004: appendix I, character 67); Ji et al. (2005: supplement, part I, character 158).

Tyrannosauridae, Troödontidae, *Deinonychus*, Alvarezsauridae, *Archaeopteryx*, *Confuciusornis*, Enantiornithes, Hesperornithiformes, *Ichthyornis*, Neornithes were characterized by a cranially oriented processus or crista, presumably pubic in derivation, the latter especially likely where associated by cranioventral retroversion of the ossa pubis (relative to the ossa ilii).

1811. Tuberculum preacetabulare (processus pectinealis), "preacetabular process," facies dorsalis, margo cranialis, forma:

a. smooth; **b.** notched.

Note.—See: Holtz (2000 [1998]: appendix I, character 294), citing Sereno et al. (1996).

1812. Tuberculum preacetabulare (processus pectinealis), recessus pneumaticus ventralis, status:

a. absent; **b.** present.

Ilium

1813. Craniocaudal length of os ilium *in toto* relative to proximodistal length of femur, magnitudo (**unordered**):

a. former significantly shorter than latter;

b. former approximately equal in length to latter;

c. former significantly longer than latter.

Note.—See: Holtz (2000 [1998]: appendix I, character 302); Maryanska et al. (2002: appendix 1, character 164).

Ala (pars) preacetabularis ilii

Note.—Alleged variation in caudal extent of ala (pars) preacetabularis ilii and associated articulation with caudal vertebrae eusacrales synsacri found to be unreliable (cf. Hesperornithiformes, ratites, and Gaviiformes).

See: Cracraft (1985: character 27); Gauthier (1986: 13, unindexed synapomorphy of Ornithurae); Gauthier (1986: 14, unindexed synapomorphy of Aves); Chatterjee (1995: character 14, part); Elzanowski (1995: character N5); Sereno (1999: character 153); Maryanska et al. (2002: appendix 1, character 151); Suzuki et al. (2002: character 13).

1814. Ala (pars) preacetabularis ilii, facies dorsalis, margo dorsomedialis, cristae iliacae dorsales, synostosis dorsomedialis forming carina iliacae dorsales (**new term**), status et forma (**unordered**):

a. present, carina distinct and synostotic;

b. present, rudimentary or vestigial, cristae dorsally prominent and approach medially, but clearly separated from crista spinosa synsacri by variably narrow but distinct sulci iliosynsacrales;

c. absent, cristae limited to ventral lamina not approaching medially, typically exposing fenestrae intertransverariae.

Note.—Development of the carina characterized here is associated closely with that treating the sulcus aut canalis iliosynsacrales, and related as well to bilateral compression of alae preacetabulares iliorum. See: Cracraft (1988: series XI, character 4); Elzanowski (1995: 38, unindexed); Azuma and Currie (2000: appendix 1, character 60).

1815. Ala (pars) preacetabularis ilii, dorsalis, fossa iliaca dorsalis, inclusion of one or two bilaterally symmetrical, elliptical fenestrae ventrolateral to the crista spinosa synsacri, status:

a. absent; **b.** present.

1816. Ala (pars) preacetabularis ilii, facies dorsalis, fossa iliaca dorsalis, inclusion of one to several circular fenestrae ventrolateral to the crista spinosa synsacri and enclosed completely within ilia, status:

a. absent; **b.** present.

1817. Ala (pars) preacetabularis ilii, facies dorsalis, regio ilii craniodorsal to acetabulae, inclusion of irregular fenestra, status:

a. absent; **b.** present.

1818. Ala (pars) preacetabularis ilii, facies dorsalis, margo lateralis, ventrolateral profile (lateral perspective), forma:

a. monotonically concave, essentially linear, or convex;

b. interrupted by variably marked serratia or eminentia.

Note.—Uncertain whether eminentia in question are lateral lamina related to articulationes iliocostales, or impressiones ligamentum iliopubica (Hutchinson 2001a; Carrano and Hutchinson 2002), although an attempt to exclude cases in which irregularities were limited features attributed to the impressio m. pubo-ischio-femoralis internus ("preacetabular fossa" or "cuppedicus fossa" of Hutchinson 2001a) and the small tuberculum that commonly marks margo cranialis of this impressio, treated elsewhere.

1819. Ala (pars) preacetabularis ilii, facies dorsalis, margo medialis et crista iliaca dorsalis, bilateral compression, medial proximity, elevation, and synostosis between cranial vertebrae sacrales, cristae spinosae (**unordered**):

a. margines et cristae synostotic;

b. cristae articulate without synostosis, excluding limited interpolation of trabeculae osseae;

c. cristae do not articulate, but remain straight, elevated, and medially appressed;

d. cristae do not articulate, remain straight, but are not elevated and do not approach medially.

Note.—See: Holtz (1994a: appendix 1, character 70); Livezey (1998b: appendix A, character 275); Holtz (2000 [1998]: appendix I, character 287); Hughes (2000: appendix 2, character 82), after Seibel (1988: character PE 18); G. Mayr (2004d: appendix I, character 28), regarding obsolescence of middle segment of crista; G. Mayr (2005a: appendix 1, character 29).

1820. Ala (pars) preacetabularis ilii, facies dorsalis, margo cranialis, multilobate, semilaminate subdivisions, defining a composite ala approximately perpendicular to crista spinosa synsacri, status:

a. absent; **b.** present.

1821. Ala (pars) preacetabularis ilii, facies lateralis, recessus pneumaticus preacetabularis lateralis (**new term**), status:

a. absent; **b.** present.

Note.—Recessus presents diversity of pneumaticity and expanse.

1822. Ala (pars) preacetabularis ilii, facies dorsalis, crista iliaca lateralis, craniolateral expansion of vertices producing broad, rectangular or cranially directly spinous aspect to ilii (dorsal perspective), status:

a. absent; **b.** present;

x. noncomparable (*Menura*).

Note.—See: Xu (2002: suite I, character 59), regarding "sharp" angles in Dromaeosauridae and *Archaeopteryx*.

1823. Ala (pars) preacetabularis ilii, with respect to planum transversum synsacri, angulus (**unordered**):

a. subvertical, wherein alae approach perpendicularity with respect to planum transversum synsacri, i.e., margines dorsales approximately strictly dorsal to margines laterales;

b. oblique, wherein alae approximate subdiagonality with respect to planum transversum synsacri, i.e., slope obliquely with margines dorsales mediodorsal to margines laterales;

c. subhorizontal, where alae approximate coplanarity with planum transversum synsacri, i.e., margines dorsales approximately strictly medial to margines laterales.

Note.—See: Cracraft (1985: character 25); Cracraft (1988: series VIII, character 8); Chu (1998: appendix 1, character 105), concerning relative breadth of ala (pars) preacetabularis ilii, Livezey (1998b: appendix A, character 278); Xu (2002: suite I, character 59). Curvature of alae necessitated reference to planum maximally descriptive of the actually curved surface for some assessments.

1824. Ala (pars) preacetabularis ilii, facies dorsalis, margo cranialis (dorsal perspective), dorsal coverage of synsacrum, forma (**ordered**):

a. subobsolete, synsacrum apparently exposed throughout;

b. incomplete or reduced, margo cranialis caudal to first (cranialmost) vertebra thoracica synsacralis (first element in sectio I of Boas 1934), exposing corpus vertebrae and dorsal fenestra intertransversaria;

c. extensive to complete, with synsacrum concealed by ala (pars) preacetabularis ilii.

Note.—See: S. F. Simpson and Cracraft (1981: character 4); Hughes (2000: appendix 2, characters 83–85), after Seibel (1988: characters PE 21–23); Zhou and Zhang (2002: appendix III, character 160).

1825. Ala (pars) preacetabularis ilii, facies dorsalis, margo cranialis, rounded indentations, status:

a. absent; **b.** present.

Note.—See: Livezey (1998b: appendix A, character 272).

1826. Ala (pars) preacetabularis ilii, facies dorsalis, margines (plicae) dorsales immediately cranial to margo cranialis of acetabulum, conformation as *squared* angulae supra-synsacrales (**new term**), status:

a. absent; **b.** present.

1827. Ala (pars) preacetabularis ilii, facies dorsalis, tuberculum origii m. iliotrochantericus medius (primordial position relative to margo ilii obscured by adjacent membrana iliosynsacralis ossificans), status:

a. absent; **b.** present.

1828. Ala (pars) preacetabularis ilii, facies dorsalis, extremitas cranialis alae, lamina ellipsoidalis lateralis (**new term**), status:

a. absent; **b.** present.

Note.—Feature refers to ellipsoid flangelike expansion of margo craniolateralis of ala preacetabularis ilii.

1829. Ala (pars) preacetabularis ilii, facies dorsalis, margo cranialis et crista lateralis, processus craniolateralis (**new term**), or vertex of margo cranialis et margo lateralis of ala (pars) preacetabularis ilii, forma (**unordered**):

a. rounded or straight;

b. strongly curved; **c.** acuminate;

d. elongated, laterally prominent, abrupt, angular flange;

e. dorsocaudally oriented, tuberculate eminentia.

Note.—See: S. L. Olson and Hasegawa (1979, 1985, 1996); Stephan (1979); S. L. Olson (1980); Livezey (1998b: appendix A, character 273); J. A. Wilson and Sereno (1998: appendix, character 45), concerning shape among Sauropoda; Norell et al. (2001: appendix 1, characters 155–157); J. M. Clark et al. (2002a: appendix 2.2, characters 157–159); Xu (2002: suite II, characters 182–249); Xu et al. (2002a: supplement, character 194); Hwang et al. (2004: characters 154–156); Xu and Norell (2004: supplement, characters 154–156).

1830. Ala (pars) preacetabularis ilii, facies dorsalis, margines cranialis et lateralis, conspicuous lateroangular expansions, status et forma (**ordered**):

a. absent;

b. present, simple unilaminate expansion without cranially oriented tuberculum on margo cranialis of margines dorsales iliorum;

c. present, comparatively elaborate bilaminate expansion including cranially oriented tuberculum on margo cranialis of margines dorsales iliorum.

1831. Ala (pars) preacetabularis ilii, facies dorsalis, bidimensional character of surface (lateral perspective), forma superficialis:

a. concave;

b. moderately convex to subplanar.

1832. Ala (pars) preacetabularis ilii, margo cranialis, spina supra-transversalis vertebrae (**new term**), status:

a. absent;

b. present, bilaterally symmetrical spinae emerging perpendicularly and dorsal to processes transverses synsacri;

x. noncomparable (Pelecanidae).

Note.—These spina represent the caudal remnants of ligamenta ossificantes intertransversalia which are synostotically united with the extremitas cranialis synsacri caudally; in the case of *Pelecanus*, these ligamenta provide support for dorsum of the articulatio notariosynsacralis unique to the Pelecanidae. Easily confused with spinae et eminentiae marginis ilii (e.g., *Dromas*).

1833. Ala (pars) preacetabularis ilii, fossa iliaca dorsalis, subpart corresponding to impressio m. pubo-ischio-femoralis internus (synonymous with dorsolaterally shifted m. iliofemoralis internus, formerly referred to as "m. cuppedicus"), status et forma (**unordered**):

a. absent or rudimentary, among Neornithes represented by impressio or small tuberculum cranial to acetabulum on ala preacetabularis ilii, margo lateralis;

b. present, shallow or moderately deep, without dorsal lamina extending laterad to subtending concavitas;

c. present, deep and ventrally concave.

Note.—See: Chiappe and Calvo (1994: appendix I, character 50); Chiappe (1995b: character 50); Sanz et al. (1995, 1997: character 48); Chiappe (1996b: character 46); Chiappe et al. (1996: appendix 1, character 45); Novas (1996: appendix, character 25); Sereno et al. (1996: footnote 45, character 29); Norell and Makovicky (1997); Novas (1997: appendix, character 27), including details of shape; Novas and Puerta (1997), see identical characters in Novas (1997); Chiappe et al. (1998: character 65); Ji et al. (1998: supplement, character 65); Forster et al. (1998: supplement, character 90); Makovicky and Sues (1998: appendix 1, character 77); Xu et al. (1999a: character 44), with respect to "Iliac fossa for m. cuppedicus"; Holtz (2000 [1998]: appendix I, characters 288 [presence] and 289 [breadth]); Hutchinson (2001a), regarding "reptilian" and "avian" synonyms for muscle formerly named m. cuppedicus; Norell and Clarke (2001: appendix I, character 163), treated similarly by J. A. Clarke (2002: appendix I, character 164), J. A. Clarke and Norell (2002: appendix 2, character 164), and J. A. Clarke (2004: appendix 1, character 164); Norell et al. (2001: appendix 1, character 165); J. M. Clark et al. (2002a: appendix 2.2, character 167); Maryanska et al. (2002: appendix 1, character 154); Xu (2002: suite I, character 88 [part]; suite II, character 188); Xu et al. (2002a: supplement, character 133), whose rather different treatments necessitated the parallel codings (a', b', c'); Zhou and Zhang (2002: appendix III, character 163); Hwang et al. (2004: supplement, character 164); Xu and Norell (2004: supplement, character 164); Ji et al. (2005: supplement, part I, character 163).

Also see: Livezey (1986: appendix 1, character 113); Livezey (1996b: appendix 1, character 34). In many nonavian theropods, the "fossa for m. cuppedicus" is an impressio of origo located on facies ventralis of ala (pars) preacetabularis ilii, the homologous feature becomes progressively restricted, synonymously referred to as the impressio of origo of m. iliofemoralis internus in Aves, to a small, largely lateral depressio immediately cranial to the acetabulum (J. R. Hutchinson, pers. comm.).

1834. Ala (pars) preacetabularis ilii, fossa iliaca dorsalis, subpart corresponding to impressio m. pubo-ischio-femoralis internus (synonymous with m. iliofemoralis internus, formerly "m. cuppedicus"), caudal extent relative to acetabulum et os ilium, pars acetabularis, pila articularis pubici (**new term**), forma:

a. extending caudad to point dorsal to margo cranialis of acetabulum;

b. extending only caudad to terminus cranialis of os pubis, pars acetabularis;

x. noncomparable (Neornithes).

Note.—New term synonymous with traditional paleontological term "pubic peduncle," and character involves traditionally named feature "*cuppedicus* fossa." See: Norell et al. (2001: appendix 1, character 164); J. M. Clark et al. (2002a: appendix 2.2, character 166); Xu (2002: suite I, character 88 [part]; suite II, character 187); Xu et al. (2002a: supplement, character 132); Hwang et al. (2004: supplement, character 163); Xu and Norell (2004: supplement, character 163).

1835. Ala (pars) preacetabularis ilii, fossa iliaca dorsalis, subpart corresponding to Hutchinson (2001a: appendix 1, character 6, and table 3: entry C2), "preacetabular fossa," status (**unordered**):
a. absent;
b. present but reduced onto margo lateralis of crista iliaca;
c. present and large.
Note.—See: Hutchinson (2001a: appendix 1, character 6), in which state "d" was defined but not represented within matrix given; Carrano and Hutchinson (2002).

1836. Ala (pars) preacetabularis ilii—"brevis fossa" or "brevis shelf" (impressio m. caudofemoralis brevis of nonavian Reptilia = impressio m. caudofemoralis pars pelvica of Aves)—status et forma (**ordered**):
a. present, restricted, "shelflike," with margines subparallel, distal end narrow;
b. present, strongly expanded caudally, "deeply concave with lateral overhang";
c. vestigial or absent.
Note.—The "brevis shelf" or "brevis fossa"—serving as origo m. caudofemoralis pars pelvica (Hutchinson 2001a)—is synapomorphic of Dinosauria (Novas 1996) and a pronounced, caudal form is purportedly synapomorphic of Theropoda (Benton 1990a: 21). Typically positioned on facies ventralis ilii, caudal to the acetabulum, and slanted medially, progressively shifted in location to the facies laterodorsalis of ala postacetabularis ilii, including in *Archaeopteryx* (Hutchinson 2001a).

See: Molnar et al. (1990); Novas (1992: character 15); Sereno et al. (1993: legend for fig. 3a); Chiappe and Calvo (1994: appendix I, character 49); Novas (1994 [1993]: appendix, character 17); Russell and Dong (1994a [1993a]: table 2, character 49); Russell and Dong (1994b [1993b]: troödontid character 19); Chiappe (1995b: character 49); Sanz et al. (1995, 1997: character 47); Chiappe (1996b: character 46); Chiappe et al. (1996: appendix 1, character 67); Norell and Makovicky (1997); Novas (1996: appendix, character 27); Novas (1997: appendix, character 29); Novas and Puerta (1997), identically treated by Novas (1997); Chiappe et al. (1998: character 66, modified); Forster et al. (1998: supplement, character 87, modified); Ji et al. (1998: supplement, character 66, modified); Makovicky and Sues (1998: appendix 1, character 76); Xu et al. (1999a: character 50); Xu et al. (1999b: character 66, modified); Holtz (2000 [1998]: appendix I, characters 290–291); Xu et al. (2000: supplement, character 50, modified) with respect to "iliac brevis fossa"; Chiappe (2001a: appendix 1, character 124); (Hutchinson 2001a: character 5); Norell et al. (2001: appendix 1, character 162); Chiappe (2002: appendix 20.2, character 124); J. M. Clark et al. (2002a: appendix 2.2, character 164); Maryanska et al. (2002: appendix 1, character 162); Xu (2002: suite II, character 185); Xu et al. (2002a: supplement, character 130); Rauhut (2003: character 176); Hwang et al. (2004: supplement, character 161); Novas et al. (2004: appendix, character 27); Makovicky and Norell (2004: character 214); Xu and Norell (2004: supplement, characters 161 and 214).

1837. Ala (pars) preacetabularis ilii, facies dorsalis, margines medialis et lateralis (dorsal perspective), throughout expanse from extremitas cranialis caudad to processus antitrochantericus, forma alae (**ordered**):
a. distinctly convex, craniocaudally aligned margo lateralis;
b. essentially linear, craniocaudally aligned margo lateralis;
c. deeply concave, craniocaudally curved margo lateralis.
Note.—See: Pycraft (1903d: figs. 46–48); Hughes (2000: appendix 2, characters 83–85), after Seibel (1988: characters PE 21–23).

1838. Ala (pars) preacetabularis ilii, facies dorsalis, crista iliaca lateralis, curvature or hamulate profile, status:
a. weak, margo essentially straight or subtly curved;
b. moderate, vertex craniolateralis hamulate.
Note.—See: Cracraft (1985: character 28); Maryanska et al. (2002: appendix 1, character 155); Xu et al. (2002a: supplement, character 127); Rauhut (2003: characters 168 [hamulation] and 173 [curvature]).

1839. Ala (pars) preacetabularis ilii, length relative to os ilium, ala (pars) postacetabularis ilii et pila articularis pubici ("pubic peduncle" of ilium), and correlated with length of synsacrum, forma (**ordered**):
a. "brachyiliacic"—length of former subequal to that of latter, not well expanded dorsoventrally;
b. "iliacic"—intermediate to brachyiliacic and dolichoiliacic conditions, including ancillary emphasis on relative lengths of alae ilii;
c. "dolichoiliacic"—length of former substantially greater (roughly twice) that of latter, well expanded dorsoventrally.
Note.—Initial coding followed Xu et al. (2000) and Holtz (2000 [1998]), Forster et al. (1998), Hutchinson (2001a), and Rauhut (2003); states based on

multiple criteria of length of ala (pars) preacetabularis ilii into a single, ordered, three-state character.

See: Mivart (1877: 2); T. J. Parker (1891); Boas (1934: fig. 4); Oliver (1949); Tarsitano and Hecht (1980); Cracraft (1982: series 4, character 2); Cracraft (1985: character 50); Bledsoe (1988: appendix, character 37); Cracraft (1988: series II, character 2); Cracraft (1988: series XI, character 2); Currie and Russell (1988); Holtz (1994a: appendix 1, character 53); K. Lee et al. (1997: appendix 1, character 21); Norell and Makovicky (1997); Sues (1997: appendix 1, character 37); Forster et al. (1998: supplement, character 71); Chatterjee (1999: appendix II, character 65, modified); Xu et al. (1999a: characters 48–49); Xu et al. (1999b: character 53); Holtz (2000 [1998]: appendix I, characters 286 and 293); Chiappe (2001a: appendix 1, character 119); Hutchinson (2001a: appendix 1, character 2); Norell et al. (2001: appendix 1, character 156); J. M. Clark et al. (2002a: appendix 2.2, character 158); Xu (2002: suite II, character 246); Xu et al. (2002a: supplement, character 39); Chiappe (2002: appendix 20.2, character 119); Xu et al. (2002a: supplement, character 191), who divided states using criterion of two-thirds of length; Rauhut (2003: characters 166 and 169); Hwang et al. (2004: supplement, character 155); G. Mayr and Ericson (2004: appendix I, character 63, part); Xu and Norell (2004: supplement, character 155).

1840. Ala (pars) preacetabularis ilii, dorsoventral height relative to that of ala (pars) postacetabularis ilii (exclusive of "ventral expansion"):

a. former approximately as high as latter;

b. former significantly higher than latter.

Note.—See: Makovicky and Sues (1998); Rauhut (2003: character 170).

Corpus (pars acetabularis) ilii

Note.—Pars acetabularis ilii (**new term**) includes incisura acetabularis ilii of the *Nomina* (Baumel et al. 1993) as margo acetabularis et pilae articulares et ischialis et pubici (**new terms**). The latter traditionally were referred to as "pubic peduncle [of ilium]" and "ischial peduncle [of ilium]."

1841. Pars acetabularis ilii (margo medialis), crista iliaca dorsalis, jugum (tuberculum) supra-trochantericus, status et forma (**unordered**):

a. absent;

b. present, as mere jugum or variably distinct angulus;

c. present, as well-developed tuberculum, spina, or jugum, dorsal or slightly caudal to processus trochanteris.

Note.—Apomorphic state synonymous evidently with the processus supratrochantericus of J. R. Hutchinson (2001a: appendix 1, character 3), and corresponds to the "tuberculum on dorsal margin ilium above caudal acetabulum (?)" noted by Forster et al. (1998). J. R. Hutchinson (pers. comm.) described the transformation of the "supracetabular process" as one beginning with (*i*) a primary state of a laterally extensive ala (e.g., *Dilophosaurus*), through (*ii*) a reduced crista or jugum (e.g., Tetanurae), to (*iii*) a small linea (Velociraptorinae, Tyrannosauridae), and finally (*iv*) indistinguishable incorporation into rima acetabularis (Aves).

See: Payne and Risley (1976: character 27), regarding angularity of "iliac crest dorsal to acetabulum" among Ardeidae; Strauch (1978: character 60), re-analyzed by Björklund (1994: appendix) and Chu (1995); Andors (1992: table 2, character 37); Russell and Dong (1994a [1993a]: table 2, character 48); Chiappe et al. (1996: appendix 1, character 72), in regard to "supracetabular lip"; Novas (1996: appendix, character 4); Novas (1996: appendix, character 26); Novas (1997: appendix, characters 4 [presence] and 28 [craniocaudal extent]); and Novas and Puerta (1997: see identical characters in Novas 1997), in regard to "supracetabular crest"; Chiappe et al. (1998: character 68); Forster et al. (1998: supplement, character 75); Ji et al. (1998: supplement, character 68); Xu et al. (1999a: character 45), with respect to "presence"; Xu et al. (1999b: character 56); Holtz (2000 [1998]: appendix I, character 299), with respect to "supracetabular crest"; Sereno (2000: table 4, character 6), with respect to overall breadth; Xu et al. (2000: supplement, character 41); Chiappe (2001a: appendix 1, characters 126–127); Norell et al. (2001: appendix 1, character 158); Chiappe (2002: appendix 20.2, characters 126–127); J. M. Clark et al. (2002a: appendix 2.2, character 160); Maryanska et al. (2002: appendix 1, character 157); Xu (2002: suite II, character 250); Xu et al. (2002a: supplement, characters 195 and 205), former with respect to supracetabular crest"; Hwang et al. (2004: supplement, character 157); Xu and Norell (2004: supplement, character 157), in reference to "supraacetabular 'hood.'"

1842. Pars acetabularis ilii, facies dorsalis, angulus (tuberculum) supra-trochantericus ilii (**new term**), recessus pneumaticus enclosing pori pneumatici under margo ventralis angulae, status:

a. absent; **b.** present.

1843. Pars acetabularis ilii, facies lateralis, recessus preacetabularis pneumaticus ilii (**new term**), status et forma (**unordered**):

a. absent;

b. present, perforated by pori pneumatici;

c. present, perforated by pori pneumatici et single, irregular margined, moderately large foramen pneumaticum.

Note.—See: Livezey (1998b: appendix A, character 269).

1844. Pars acetabularis ilii, facies caudomedialis, recessus postacetabularis pneumaticus ilii (**new term**), status:

a. absent; **b.** present.

1845. Pars acetabularis ilii, interacetabular width relative to synsacral length, magnitudo (**ordered**):

a. great, exceeds one-half synsacral length;

b. moderate, one-half to one-third synsacral length;

c. small, approximately one-fourth synsacral length;

d. extremely small, approximately one-sixth synsacral length.

Note.—See: Livezey (1998b: appendix A, character 274); G. Mayr and Clarke (2003: appendix A, character 90). Currie and Chen (2001) reported that in *Sinosauropteryx* and most Theropoda the ilia extended over five vertebrae sacrales. Related alternative metric is a ratio of *minimal* transverse widths of pelvis across acetabulae and processes antitrochantericae: Hughes (2000: appendix 2, character 81), after Seibel (1988: character PE 15); G. Mayr (2003b: appendix I, character 13); G. Mayr et al. (2003: appendix 1, character 50); G. Mayr (2004a: appendix 1, character 47, part). *Megalapteryx* shows variation in range of alae preacetabulares iliorum from almost equality to twice the length of alae postacetabulares.

1846. Pars acetabularis ilii, facies cranialis (lateral perspective), forma marginalis:

a. straight or convex; **b.** concave.

Note.—See: Rauhut (2003: character 179).

1847. Pars acetabularis ilii, orientation relative to axis vertebralis, forma:

a. ventral or caudoventral; **b.** cranioventral.

Note.—Related in part to "retroversion" of os pubis relative to the axis majoris of the columna vertebralis (synsacralis). See: Gauthier (1986: text character 78); Currie (1995: appendix, character 25); Novas (1996: appendix, character 24); Chiappe et al. (1998: character 67); Ji et al. (1998: supplement, character 67), regarding orientation of "pubic pedicel"; Chiappe (2001a: appendix 1, character 125); Chiappe (2002: appendix 20.2, character 125).

1848. Pars acetabularis ilii, pila articularis pubici ("pubic peduncle of ilium"), relative mediolateral and craniocaudal extents (lateral perspective):

a. more mediolateral than craniocaudal, roughly triangular;

b. more craniocaudal than mediolateral, elongate and narrow.

Note.—See: Sereno et al. (1994); Novas (1997: appendix, characters 25–26), regarding craniocaudal width and ventral prominence, respectively; Novas and Puerta (1997), see identical characters in Novas (1997); J. D. Harris (1998: appendix 2, character 106); J. A. Wilson and Sereno (1998: appendix, character 7), regarding prominence among Sauropoda; Azuma and Currie (2000: appendix 1, character 61); Currie and Carpenter (2000: appendix 1, character 84); Holtz (2000 [1998]: appendix I, character 305), regarding relative proportions within the "pubic peduncle of ilium"; Maryanska et al. (2002: appendix 1, character 160); Rauhut (2003: character 175).

1849. Pars acetabularis ilii, facies articularis acetabulae, principal orientation and related status of abrupt angulus ("kink"), forma:

a. cranioventral, lacking angulus;

b. essentially cranial, possessing pronounced angulus.

Note.—See: Rauhut (2003: character 178).

1850. Pars acetabularis ilii, ventral extent relative to that of pila articularis pubici ("pubic peduncle on ilium"), forma:

a. approximately equal;

b. former ventral to latter.

Note.—See: Gauthier (1986: text character 78); Russell and Dong (1994b [1993b]: list B, character 11); Currie (1995: appendix, character 25); Sereno et al. (1996: footnote 45, character 30); Xu et al. (1999a: character 46) and Xu et al. (1999b: character 57), regarding the ventral extent of the "pubic peduncle on ilium"; Holtz (2000 [1998]: appendix I, character 306); Maryanska et al. (2002: appendix 1, characters 158–159).

1851. Pars acetabularis ilii, facies dorsalis, margo dorsomedialis ilii, orbiculate fenestrae paired with adjacent, medial fenestrae intertransversae synsacrales, status:

a. absent; **b.** present.

1852. Pars acetabularis et ala postacetabularis ilii, facies ventralis, crista iliaca obliqua, caudal distinctness relative to (*i*) acetabulum, (*ii*) recessus caudalis fossae, et (*iii*) crista caudalis fossae renalis, forma (**ordered**):

a. crista iliaca obliqua remaining strongly differentiated caudad to medial inflection to sutura iliosynsacralis, effectively continuous with crista caudalis fossae renalis;

b. crista iliaca obliqua becoming indistinct cranial to recessus caudalis fossae or margo foraminis ilioischiadica caudalis, typically appearing to continue caudad as pila ischiadica;

c. crista iliaca obliqua becoming indistinct opposite or immediately caudal to acetabulum;

d. crista iliaca obliqua absent or obsolete throughout;

x. noncomparable (palaeognathous Neornithes).

Note.—Cranial distinctness of crista iliaca obliqua closely related to that of pila ilioischiadica.

1853. Pars acetabularis ilii et corpus ischii, facies medialis, pila ilioischiadica (medial perspective), robustness and definition, caudal extent as structurally defined relative to (*i*) foramen (incisura) ilioischiadica, (*ii*) pila postrenalis, and (*iii*) processus terminalis ischii, forma:

a. distinct caudad essentially throughout or at least to basis of processus terminalis ischii;

b. indistinct caudal to pila postrenalis;

x. noncomparable (palaeognathous Neornithes).

Note.—Essentially pila ilioischiadica becomes well defined medially immediately ventral to the acetabulum, variation in caudal extent exists and can pose challenges of assignments to state.

1854. Pars acetabularis ilii, facies ventralis, crista iliaca intermedia, status et forma (**unordered**):

a. absent or obsolete;

b. distinct, sublaminar;

c. prominent, laminar;

x. noncomparable (most palaeognathous Neornithes).

Note.—See: Strauch (1978: characters 50–52), reanalyzed by Björklund (1994: appendix) and Chu (1995); also Strauch (1985: character 15), in reference to "synsacral strut." See Livezey (1998b: appendix A, character 268), regarding dorsoventral position of terminus of crista iliaca intermedia on facies lateralis of fossa renalis.

Ala (pars) postacetabularis ilii

1855. Ala (pars) postacetabularis ilii, planum dorsalis postsynsacralis (**new term**), typically with pori pneumatici in facies ventralis, essentially a laminar expanse caudal to the crista iliaca caudalis, status:

a. planum absent, precluding pori aut foramina;

b. planum present, pori aut foramina present.

1856. Ala (pars) postacetabularis ilii, "depth" relative to that of pars acetabularis ilii, forma:

a. former more than 50% of latter, "squared off";

b. former less than 50% of latter, and caudally conformed as low, acuminate processus.

Note.—See: Ostrom (1976a); Gauthier (1986); Holtz (1994a: appendix 1, character 45); Russell and Dong (1994a [1993a]: table 2, character 47); Russell and Dong (1994b [1993b]: list B, character 10); Novas (1997); Forster et al. (1998: supplement, character 72); Xu et al. (1999a: character 41); Xu et al. (1999b: character 54); Holtz (2000 [1998]: appendix I, character 296, essentially duplicated by character 297), who referred to Russell and Dong (1994a [1993a]); Xu et al. (2000: supplement, character 40); Chiappe (2001a: appendix 1, character 121); Chiappe (2002: appendix 20.2, character 121); Xu et al. (2002a: supplement, character 128), who restricted assessments to shape of terminus.

1857. Ala (pars) postacetabularis ilii, facies dorsalis, sharp ventral curvature caudal to foramen ilioischiadicum, status:

a. absent; **b.** present.

Note.—See: Cracraft (1988: series XIV, character 5). Illustrated by Shufeldt (1909: figs. 47 and 54). Alternative reference to this character would be corpus ilii (lateral perspective), angulus peri-acetabularis iliosynsacralis (**new term**), indexed by angulus defined by alae preacetabularis et postacetabularis ilii (lateral perspective) with acetabulum defining the vertex of the angulus.

1858. Ala (pars) postacetabularis ilii, facies dorsalis, fossa iliocaudalis, relative extent:

a. regio immediately cranial to margo caudalis pelvici;

b. much of an expanded facies dorsalis of ala postacetabularis ilii;

x. noncomparable (most ratites).

Note.—See: Ericson (1997: table 1, character 32), noted "a distinct, deep, pneumatic depression- . . . medio-posteriorly on ilium" in Otididae and Eurypygidae, with limited pneumaticity noted also in Scolopacidae; Livezey (1998b: appendix A, character 279).

1859. Ala (pars) postacetabularis ilii facies dorsalis, fossa iliocaudalis, depth so great as to render margo caudalis of ala postacetabularis ilii dorsally recurved, status:

a. absent; **b.** present.

Note.—See: Livezey (1998b: appendix A, character 280).

1860. Ala (pars) postacetabularis ilii, facies dorsalis, extreme bilateral compression of elements resulting in pars caudalis pelvici being lateromedially narrower than ala (pars) preacetabularis ilii, status:

a. absent; **b.** present.

1861. Ala (pars) postacetabularis ilii, facies dorsalis (lateralis), linea origii aponeurosi m. iliotibialis, angulus:

a. sloping obliquely dorsocaudad;

b. approximately coincident with crista dorsolateralis ilii.

1862. Ala (pars) postacetabularis ilii, facies dorsalis, crista iliaca dorsolateralis, vertex (angulus) caudolateralis ilii (**new term**), forma:

a. indistinct or (curvi)linear extension of crista caudad (lacking vertex) only present, or crista and vertex completely absent;

b. moderately distinct angulus or laterally prominent, ventrally concave crista;

x. noncomparable (most ratites).

Note.—See: Livezey (1998b: appendix A, character 285); Hughes (2000: appendix 2, character 88), after Seibel (1988: character PE 10), regarding crista iliaca dorsolateralis; Norell et al. (2001: appendix 1, character 159), in reference to "tuber along dorsal edge of ilium"; J. M. Clark et al. (2002a: appendix 2.2, character 163); Xu (2002: suite II, character 260); G. Mayr and Ericson (2004: appendix I, character 64), likened to "process of iliac crest" of Bock and McEvey (1969a: fig. 22A); Hwang et al. (2004: supplement, character 160); Xu and Norell (2004: supplement, character 160).

1863. Ala (pars) postacetabularis ilii, crista dorsolateralis ilii, pronounced ventral curvature to approach or contact processus terminalis ischii, status et forma (**unordered**):
a. absent; **b.** present, approaching only;
c. present, contacting.
Note.—See: Payne and Risley (1976: character 28), regarding profile of "posterior iliac crest" among Ardeidae.

1864. Ala (pars) postacetabularis ilii, facies dorsalis, crista iliaca dorsolateralis, vertex craniolateralis (**new term**) craniocaudalis relative to processus antitrochantericus, situs (**ordered**):
a. caudodorsal; **b.** dorsal;
c. craniodorsal;
x. noncomparable (*Apteryx*, *Fregata*, *Phaethon*).
Note.—Many difficult assessments resulted from poorly defined vertices craniolaterales. See: Andrews (1897: fig. 2), regarding *Aepyornis*; Hughes (2000: appendix 2, characters 91–92), after Seibel (1988: characters PE 17 and 24); Livezey (1998b: appendix A, character 282).

1865. Ala (pars) postacetabularis ilii, margo lateralis, crista iliaca dorsolateralis, vertex craniolateralis (see above), tuberculum craniolateralis (**new term**), status:
a. absent; **b.** present.
Note.—See: Livezey (1997a: appendix 1, character 84; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, character 283); Dyke (2001b: appendix 1, character 84); G. Mayr et al. (2003: appendix 1, character 54).

1866. Ala (pars) postacetabularis ilii, margo lateralis, crista iliaca dorsolateralis, angulus intermedius, status:
a. absent or obsolete;
b. distinct or prominent.
Note.—Angularity craniocaudally intermediate to vertices craniolateralis et caudolateralis on crista iliaca dorsolateralis.

1867. Ala (pars) postacetabularis ilii, facies lateralis, crista iliaca dorsolateralis, prominence and shape of which, in combination with bilateral compression of alae iliorum, produces a prominent, "diamond-shaped" transversely oriented eminentia dorsal to and approximately laterally as prominent as the processus antitrochantericus, status:
a. absent; **b.** present.

1868. Ala (pars) postacetabularis ilii, facies dorsalis, spina dorsolateralis ilii, caudal extent relative to that of ala ischii, processus terminalis ischii, forma (**ordered**):
a. former greater than latter;
b. former subequal to latter;
c. former distinctly but not substantially shorter than latter;
d. former substantially shorter than latter, difference approximately shorter than latter by twice the craniocaudal depth of the incisura marginis caudalis.
Note.—Spina dorsolateralis ilii is a feature of a single osseus element, os ilium; processus marginis caudalis is derived from both ossa ilii et ischii, and for this reason and the limited taxonomic distribution of the latter that processus terminalis ischii was selected as a standard for relative caudal extent. See: Marsh (1880: pl. XI); Strauch (1978: character 58), reanalyzed by Björklund (1994: appendix) and Chu (1995); and Strauch (1985: character 16), in reference to "posterior projection of the ilium" and "ischial angle," respectively; Hughes (2000: appendix 2, character 89), after Seibel (1988: character PE 12), with respect to simple "posterior extent" of spina in cuculiforms.

1869. Ala (pars) postacetabularis ilii, crista iliaca dorsolateralis, spina dorsolateralis ilii, ventral curvature, status:
a. absent; **b.** present.

1870. Ala (pars) postacetabularis ilii, facies dorsalis, crista iliaca dorsolateralis, spina dorsolateralis ilii, comparative prominence (dorsal perspective), forma:
a. virtually indistinct to moderately distinguished;
b. prominent, caudally directed spinae, typically bordering laterally and in parallel.
Note.—See: Lebedinsky (1913); Cracraft (1985: character 24); Livezey (1986: appendix 1, character 118); Livezey (1989: table 1, character 118); Livezey (1996a: appendix 1, character 64); Ericson (1997: table 2, character 23); Livezey (1997a: appendix 1, character 83; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, character 284), in which the Alcidae were assessed to be variable, and the Pedionomidae as weakly differentiated; G. Mayr et al. (2003: appendix 1, character 51).

1871. Ala (pars) postacetabularis ilii, crista iliaca dorsolateralis, spina dorsolateralis ilii, pronounced medial orientation, status:
a. absent; **b.** present.
Note.—See: Livezey (1998b: appendix A, characters 288–289).

1872. Ala (pars) postacetabularis ilii, crista iliaca dorsolateralis, spina dorsolateralis ilii, dorsal recurvature, status:

a. absent, spina typically coplanar with facies dorsalis;

b. present.

Note.—See: Livezey (1998b: appendix A, character 290).

1873. Ala (pars) postacetabularis ilii, crista iliaca dorsolateralis, spina dorsolateralis ilii, laterodorsal curvature—in combination with exceptional elongation, narrowly separated medial positions, and cristula lateralis spinae (treated elsewhere)—status:

a. absent; **b.** present.

1874. Ala (pars) postacetabularis ilii, crista iliaca dorsolateralis, spina dorsolateralis ilii, extension of crista caudad to produce cristula on facies lateralis of spina to form cristula lateralis spinae ilii (**new term**), status:

a. absent; **b.** present.

1875. Ala (pars) postacetabularis ilii, margo lateralis, crista iliaca dorsolateralis, angulus caudolateralis (**new term**), marked elongation, providing primary component of junctura (pila) ilioischiadica caudalis (if present), status:

a. absent; **b.** present.

Note.—New term refers to variably angular eminentia at margo caudolateralis ilii. See: Livezey (1998b: appendix A, character 285).

1876. Ala (pars) postacetabularis ilii, facies lateralis, margo lateralis, crista iliaca dorsolateralis, angulus caudolateralis (where present), adornment by prominent eminentia et/aut ventrally concave crista (lateral perspective), status:

a. absent;

b. present, typically manifested by well-developed concavitas infracristalis.

Note.—See: Livezey (1998b: appendix A, character 286); G. Mayr et al. (2003: appendix 1, character 52).

1877. Ala (pars) postacetabularis ilii, margo lateralis, crista iliaca dorsolateralis, between angulus caudolateralis (where present) and processus dorsolateralis, forma:

a. essentially straight or slightly concave;

b. deeply concave, giving angulus caudolateralis the appearance of a caudally prominent processus.

Note.—See: Livezey (1998b: appendix A, character 287).

1878. Ala (pars) postacetabularis ilii, orientation relative to columna vertebralis (dorsal perspective):

a. dorsoventrad, alae essentially parallel;

b. mediolaterad, alae diverge caudad.

Note.—See: Marsh (1880: pl. XI); Azuma and Currie (2000: appendix 1, character 60); Norell and Clarke (2001: appendix I, character 161), treated similarly by J. A. Clarke (2002: appendix I, character 162), J. A. Clarke and Norell (2002: appendix 2, character 162), and J. A. Clarke (2004: appendix 1, character 162); Norell et al. (2001: appendix 1, character 161); J. M. Clark et al. (2002a: appendix 2.2, character 162); Xu (2002: suite II, character 184); Xu et al. (2002a: supplement, character 129); Hwang et al. (2004: supplement, character 159); Xu and Norell (2004: supplement, character 159); Ji et al. (2005: supplement, part I, character 161).

1879. Ala (pars) postacetabularis ilii, orientation et forma marginalis (lateral perspective):

a. dorsally prominent, rectangular;

b. sloping ventrad.

Note.—See: Gauthier (1986); Rauhut (2003: character 174).

1880. Ala (pars) postacetabularis ilii, facies lateralis, lamina infracristalis ilii, concavitas infracristalis, status et forma (**ordered**):

a. absent or barely discernable;

b. distinct, shallow to moderately deep;

c. conspicuous, extremely deep, typically extending from dorsum of foramen ilioischiadicum caudad to margo caudalis pelvici;

x. noncomparable (ratites).

Note.—See: Baumel and Witmer (1993: annotation 251).

1881. Ala (pars) postacetabularis ilii, facies lateralis (lateral perspective), lamina infracristalis ilii, margo foraminis ilioischiadici (exclusive of vestigia of membrana ossificans ilioischiadica, if present), status et forma (**unordered**):

a. absent, lamina infracristalis lacking;

b. present, delimiting a subangular, significantly caudally attenuated margo;

c. present, delimiting a shallow (axis minoris less than one-half axis majoris) elliptical to circular margo;

d. present, delimiting a deep (axis minoris at least one-half axis majoris) elliptical to circular margo.

Note.—See: Elzanowski (1995: character O7), apparently in reference to “distal forking” of margo foraminis ilioischiadici.

1882. Ala (pars) postacetabularis ilii, facies lateralis, lamina infracristalis ilii, margo foraminis (incisura) ilioischiadici, craniocaudal extent (lateral perspective) relative to recessus caudalis fossae (if present), situs:

a. cranial, concealing internum of recessus caudalis fossae;

b. caudal, exposing internum of recessus caudalis fossae;

x. noncomparable in taxa lacking recessus or lamina infracristalis ilii.

Note.—See: Kurochkin (1995b: table 1, character 21), pertaining to presence or absence of "margo foraminis ilioischiadici."

1883. Ala (pars) postacetabularis ilii, facies ventralis, facies renalis ilii, forma superficialis:

a. concave, sloping uniformly with adjacent facies ventralis ilii, delimiting comparatively shallow fossa renalis, recessus caudalis fossae;

b. flat or convex, deviating from slope of adjacent facies ventralis ilii, delimiting comparatively dorsoventrally deep fossa renalis recessus caudalis fossae;

x. noncomparable in taxa lacking recessus or lamina infracristalis ilii.

Note.—See: Livezey (1998b: appendix A, character 293); Chu (1998: appendix 1, character 106); G. Mayr and Ericson (2004: appendix I, character 70).

1884. Ala (pars) postacetabularis ilii, facies dorsalis, crista iliaca dorsolateralis, angulus craniolateralis (**new term**), dorsal extremity adorned with crescentiform or subangular plica craniolateralis (**new term**), status:

a. absent; **b.** present.

1885. Alae (partes) preacetabulares et postacetabulares ilii, distinct thickening of ossa through investment by os spongiosum, status:

a. absent; **b.** present.

1886. Ala (partes) preacetabularis et postacetabularis ilii, facies dorsalis, comparative dorsoventral breadth, magnitudo:

a. small; **b.** large.

Note.—See: Gauthier (1986); Russell and Dong (1994a [1993a]: table 2, character 45); Holtz (1994a: appendix 1, character 22); Kurochkin (1995b: table 1, character 19); Makovicky and Sues (1998: appendix 1, character 75), with respect to comparative depths; Holtz (2000 [1998]: appendix I, character 292), with respect to relative lengths, regarding dorsoventral expansion; Xu et al. (2002a: supplement, character 129).

1887. Alae (partes) preacetabulares et postacetabulares ilii, facies dorsalis, lamina iliaca supracetabularis (**new term**)—"supracetabular shelf"—status:

a. absent; **b.** present.

Note.—See: Rowe and Gauthier (1990); Holtz (2000 [1998]: appendix I, character 300), for "supracetabular shelf."

1888. Alae (partes) preacetabulares et postacetabulares ilii, facies dorsalis, cristae iliacae dorsolaterales, vertex craniomedialis cristae (**new term**) relative to axis transacetabularis, situs craniocaudalis (**unordered**):

a. "hypercranial," such that cristae extend without intersection with margo cranialis of ala preacetabularis ilii;

b. moderately cranial;

c. approximately equal;

d. distinctly caudal;

x. noncomparable (*Apteryx*).

Note.—See: Strauch (1978: character 57), reanalyzed by Björklund (1994: appendix) and Chu (1995), treated angulus between margines laterales ilii et synsacri; Livezey (1986: appendix 1, character 119); Livezey (1995a: appendix 1, character 8); Livezey (1995c: appendix II, character 24), in reference to "anterior terminus of shield."

1889. Alae (partes) preacetabulares et postacetabulares ilii, facies dorsalis supracetabularis, jugum septalis fossae origii mm. iliofemorales—craniad, pars externum craniad and caudad, generalis caudad (**new terms**)—status:

a. absent; **b.** present.

Note.—Myological homology of feature based on Carrano and Hutchinson (2002, fig. 4), based on *Tyrannosaurus*. See: Molnar et al. (1990); Russell and Dong (1994a [1993a]: table 2, character 46); J. D. Harris (1998: appendix 2, character 103); Currie and Carpenter (2000: appendix 1, character 82); Holtz (2000 [1998]: appendix I, character 295); Maryanska et al. (2002: appendix 1, character 161); Rauhut (2003: character 172).

1890. Alae preacetabulares et postacetabulares ilii, facies dorsalis, relative craniocaudal lengths, indexed by ratio of length of former divided by length of latter (**ordered**):

a. ala preacetabularis distinctly greater in craniocaudal length than ala postacetabularis, ratio significantly greater than unity;

b. ala preacetabularis approximately equal in craniocaudal length to ala postacetabularis, ratio approximately unity;

c. ala preacetabularis less in craniocaudal length than ala postacetabularis, ratio significantly less than unity.

1891. Alae (partes) preacetabulares et postacetabulares ilii, facies dorsalis, crista iliaca dorsolateralis, extreme, semicircular lateral impressiones of ala postacetabularis ilii, status:

a. absent; **b.** present.

Note.—See: Hughes (2000: appendix 2, character 90), after Seibel (1988: character PE 13). Relative lengths of sections of crista defined by Seibel (1988: fig. 4)—sections "B" (between spina dorsolateralis et angulus caudolateralis) and "C" (between angulae caudolaterales et craniolaterales—are not applicable consistently across Aves.

1892. Ala (pars) postacetabularis ilii et ala postacetabularis ischii, facies lateralis, margines caudales, caudal extent of ala ilii relative to that of ala ischii, forma:

a. former not distinctly cranial, collectively defining an obliquely sloping margo caudalis of pelvis exclusive of spina dorsolateralis ilii and incisura marginis caudalis, if present;

b. former distinctly cranial, characterized by distinct angular indentation proximate to the terminus caudalis of sutura ilioischiadica;

x. noncomparable (palaeognathous Neornithes).

Note.—See: Livezey (1986: appendix 1, character 114); Livezey (1989: table 1, character 114); Livezey (1996a: appendix 1, character 65); Ericson (1997: table 2, character 22). See juvenile pelvis for accipitrid *Haliaetus leucocephalus* (USNM 611757).

1893. Ala (pars) postacetabularis ilii et ala postacetabularis ischii, facies lateralis, margines caudales, spina dorsolateralis ilii et processus marginis caudalis, investment of both within common membrana ossificans closing incisura marginis caudalis, status:

a. absent; **b.** present;

x. noncomparable (Dinornithiformes).

Note.—In some cases, it is problematic to distinguish this apomorphy from taxa in which one or more of included features are lacking but that possess simply curving or "entire" margines caudales pelvici.

1894. Extremitates postacetabulares ischii et pubici, dorsoventral expansion of angulus (exclusive of membrana ilioischiadica ossificans) relative to axis majoris synsacri and associated expansion of incisura ilioischiadica (**unordered**):

a. present, pronounced, angulus subdiagonal;

b. present, magnitude intermediate;

c. absent, extremitates postacetabulares ischii et pubici subparallel with extremitas postacetabularis ilii.

Note.—See: Archey (1941: pl. 9).

Ischium

Corpus ischii

Note.—Os ischium, pars acetabularis ischii, pilae articulares ilialis et pubici (**new terms**) correspond to the two segments of the acetabular basis of os ischium that articulate with ossa ilii et pubis, partes acetabularis, respectively, and include intervening incisura acetabularis ischii.

1895. Corpus ischii, pars acetabularis ischii, facies synchondrosis ischiopubica caudalis (**new term**), forma (**unordered**):

a. width essentially uniform with that of corpus ischii, facies equivalent to terminus of corpus ischii;

b. facies elongate and comprising margo ventralis of caudally arcuate corpus ischii, resulting in considerably elongate (wide) synchondrosis;

c. markedly expanded (rostro)caudally, significantly widening synchondrosis.

Note.—Although synchondrosis obscures juncturae, apomorphy "b" reflects caudal curvature of uniform corpus ischii, whereas apomorphy "c" implies presence of expanded terminus ischii or "ischial boot." See: Kuroda (1954: fig. 32); Novas et al. (2004: appendix, character 30).

1896. Corpus ischii, bases ischii et pubis, facies caudomedialis immediately dorsocranial to synchondrosis ischiopubica et foramen obturatum, recessus pneumaticus, status modalis:

a. absent; **b.** present.

Note.—See: Norell et al. (2001: appendix 1, character 169); J. M. Clark et al. (2002a: appendix 2.2, character 171); Xu (2002: suite II, character 192); Hwang et al. (2004: supplement, character 168); Xu and Norell (2004: supplement, character 168).

1897. Corpus ischii, pars acetabularis ischii, pilae articulares ischii et pubici iliorum, facies synchondroses ilioischiadica et ischiopubica (**new terms**), status:

a. well developed, a dorsoventrally deep shelf;

b. comparatively reduced, narrow.

Note.—See: Sereno et al. (1994); Novas (1996: appendix, character M16), with respect to "ischial articular surfaces for ilium and pubis." Sereno and Arcucci (1994 [1993]: appendix, character 5) encoded variation in pila articularis ischialis ilii "ischial peduncle on ilium" among basal Dinosauria; Holtz (2000 [1998]: appendix I, character 318).

1898. Corpus ischii, pars acetabularis ischii, facies ventralis, extreme bilateral compression with elements separated medially by one or two, disproportionately broad processes transverses of corresponding number of associated, caudalmost vertebrae thoracicae synsacrales, status et forma (**unordered**):

a. absent;

b. present, separation involves single modified vertebra;

c. present, separation involves two modified vertebrae.

Note.—Condition described here is distinct from the bilateral compression and medial struts affecting the ilia of some diving taxa (e.g., Podicipediformes, Gaviiformes).

1899. Scapus ischii, facies (perspective) lateralis, forma dorsoventralis (**unordered**):

a. present, margo ventralis ischii concave, corpus decurved;

b. obsolete, corpus ischii essentially linear;

c. present, margo ventralis ischii convex, corpus recurved.

Note.—See: Livezey (1998b: appendix A, character 271); Norell et al. (2001: appendix 1, character 167, in part); J. M. Clark et al. (2002a: appendix 2.2, character 169, in part); Xu (2002: suite II, character 190, in part); Xu et al. (2002a: supplement, character 135). Assessments primarily based on margo ventralis, typically revealed as margo dorsalis of the fenestra (incisura) ischiopubica, and secondarily by the general form of the corpus ischii as discernable within the ilio-ischial complex post synostosis (including attempting to minimize obfuscation by membrana ischiopubica ossificans), often using the pila ilioischiadica as one important indicator of orientation; Hwang et al. (2004: supplement, character 166); Xu and Norell (2004: supplement, character 166).

1900. Scapus ischii (sectiones cranialis et intermedius), forma in planum transversus (**ordered**):

a. columnar, cross section (sub)circular;

b. hemicylindrical, cross section planar laterally;

c. laminar, cross section mediolaterally compressed.

Note.—See: Gauthier (1986: 12, unindexed synapomorphy of Avialae); Sereno and Rao (1992); Novas (1994 [1993]: appendix, character 32); Forster et al. (1998: supplement, character 86); Xu et al. (1999a: character 52); Xu et al. (1999b: character 65); Xu et al. (2000: supplement, character 49); Sereno et al. (2002), regarding *Sinornis*; G. Mayr and Ericson (2004: appendix I, character 65); Novas et al. (2004: appendix, character 31).

1901. Scapus ischii et scapus pubis (lateral perspective), caudal extent of os pubis relative to os ischium:

a. absent or negligible, elements of approximately equal caudal extent;

b. present, caudal extent of pubis roughly 25–50% greater (rarely more) than that of ischium;

c. present, caudal extent of pubis roughly 75–100% greater than that of ischium.

Note.—Pronounced curvature of ossa pubici can confound assessments. See: Chiappe et al. (1999); Currie and Chen (2001); J. A. Clarke (2004).

1902. Scapus ischii, length relative to that of os pubis, forma (**ordered**):

a. former three-fourths or more of latter;

b. former between two-thirds and three-fourths of latter;

c. former two-thirds or less of latter;

x. noncomparable (Dromornithidae).

Note.—See: Ostrom (1976a); Gauthier (1986: text character 80); Sereno (1991a: appendix, ingroup-clades character 13); Russell and Dong (1994b [1993b]: list B, character 13); Chiappe et al. (1996: appendix 1, character 69); Novas (1996: appendix, character 55); Novas (1997: appendix, character 56), relating length of ischium to both pubis and femur; Novas and Puerta (1997), see identical characters in Novas (1997); Sues (1997: appendix 1, character 41); Chiappe et al. (1998: character 70); Ji et al. (1998: supplement, character 70); Forster et al. (1998: supplement, character 79); J. D. Harris (1998: appendix 2, character 117), using ischium/pubis criterion of two-thirds; Makovicky and Sues (1998: appendix 1, character 84); J. A. Wilson and Sereno (1998: appendix, character 8), in reference to Sauropoda; Xu et al. (1999a: character 54); Xu et al. (1999b: character 60); Azuma and Currie (2000: appendix 1, character 64); Currie and Carpenter (2000: appendix 1, character 94), using ischium/pubis criterion of two-thirds; Holtz (2000 [1998]: appendix I, character 320); Xu et al. (2000: supplement, character 45); Chiappe (2001a: appendix 1, character 130); Hutchinson (2001a: appendix 1, character 24); Norell et al. (2001: appendix 1, character 173); Sereno (2001: table 1, character 14), regarding Alvarezsauridae; Chiappe (2002: appendix 20.2, character 130); J. M. Clark et al. (2002a: appendix 2.2, character 174); Maryanska et al. (2002: appendix 1, character 172); Xu (2002: suite I, character 91; suite II, character 195); Xu et al. (2002a: supplement, character 140); Rauhut (2003: character 191); Hwang et al. (2004: supplement, character 171); Xu and Norell (2004: supplement, character 171).

1903. Corpus ischii, margo ventralis, angulus (tuberculum) postobturatorius (**new term**), if present, facies lateralis tuberculae, recessus pneumaticus, status:

a. absent; **b.** present.

Note.—Possibly atavistic vestigium of totipubic foramen obturatorum. See: Holtz (2000 [1998]: appendix I, character 324).

1904. Corpus ischii, facies lateralis, margo dorsalis (pubica), distinct ventral curvature or angulation toward synlateral os pubis, status et forma (**ordered**):

a. absent, ala approximately linear or only slightly curved;

b. present, ala distinctly but comparatively gradually, monotonically curved, and typically extended ventrocaudad to unite by synchondrosis ischiopubica along margo ventralis of processus terminalis ischii;

c. present, ala sharply angled ventrad at approximate midpoint, and typically extended ventrocaudad to unite by synchondrosis ischiopubica along margo ventralis or caudalis of processus terminalis ischii.

Note.—See: Kuroda (1954: figs. 31–32).

1905. Corpus ischii, facies lateralis, margo caudalis, angulus caudalis ischii (**new term**), status:

a. absent; **b.** present.

Note.—Feature is marginal, triangular prominence of ischium, which typically is immediately dorsal to synostosis ischiopubica.

1906. Corpus ischii, facies lateralis, pronounced expansion of margo dorsalis so as to encompass entirely the synchondrosis ilioischiadica forming margo caudalis foraminis ilioischiadica and resultant lamina infracristalis (if present), status:

a. absent, lamina infracristalis typically involving membrana ilioischiadica ossificans and approximately equal contributions from ossa ilium et ischium;

b. present, lamina infracristalis composed essentially by terminal flaring of ischium, typically discernable only in juvenile specimens;

x. noncomparable because foramen ilioischiadicum incomplete (palaeognathous Neornithes).

Note.—Typically determinable only by examination of juvenile specimens. See: W. K. Parker (1891a: pls. 22–25).

1907. Corpus ischii, facies dorsalis, abrupt narrowing at approximate midpoint, producing distinct, marginal convexity, status:

a. absent; **b.** present;

x. noncomparable (*Aptornis*).

Note.—Kuroda (1954: figs. 31–32).

1908. Corpus ischii, facies lateralis, processus obturatorius, status et forma (**unordered**):

a. present, conjoined with processus articularis pubicus;

b. present, rectangular or trapezoidal;

c. present, peaked, and broadly triangular;

d. vestigial or absent.

Note.—Note that present character treats presence and conformation of processus *per se*, whereas following characters treat details of form cranial and caudal to processus, craniocaudal position of processus, or conformational details of processus. See: Gauthier (1986: text character 47), in which confusion as to element involved (ilium or ischium) was involved; Russell and Dong (1994a [1993a]: table 2, character 52), attributed to os ischium; Russell and Dong (1994b [1993b]: list B, character 14); Holtz (1994a: appendix 1, character 94); Holtz (1994a: appendix 1, character 80); Novas (1996: appendix, character 54); Sereno et al. (1996: footnote 45, character 60); Novas (1997: appendix, character 55); Novas and Puerta (1997), identically treated by Novas (1997); Chiappe et al. (1998: character 71); J. D. Harris (1998: appendix 2, characters 114 [status] and 116 [shape]); Ji et al. (1998: supplement, character 71); Forster et al. (1998: supplement, character 81, as given above); Makovicky and Sues (1998: appendix 1, character 81); Xu et al. (1999b: character 61, modified); Chatterjee (1999: appendix II, character 73, in part); Azuma and Currie (2000: appendix 1, characters 91 [status] and 93 [shape]); Holtz (2000 [1998]: appendix I, character 322); Chiappe (2001a: appendix 1, character 131); Hutchinson (2001a: appendix 1, characters 15 and 22, differently delimited, and treating position and extent separately, difficult to compare); Chiappe (2002: appendix 20.2, character 131); Maryanska et al. (2002: appendix 1, character 170); Xu et al. (2002a: supplement, character 137), regarding the junctura between processus obturatorius et os pubis; Zhou and Zhang (2002: appendix III, character 164).

1909. Corpus ischii, margo ventralis, processus obturatorius, pars caudalis processi (**new term**), incisura distalis between processus and corpus ischii, status:

a. absent or obsolete, a corollary of which is a triangular aspect for the processus obturatum in lateral perspective;

b. present, a conspicuous angulus, modest tuberculum or cranioventrally oriented, acuminate, hamulate processus, often in ischia rotated ventrad from ilia and precluding the closure of incisura foraminis obturatorii and formation of a foramen obturatum or part of complete partition.

Note.—See: Hou et al. (1996: characters 22 and 32); Sereno et al. (1996), regarding “triangular” conformation of the processus; Rauhut (2003: character 190), in terms of the partially formative incisura. See previous character regarding a proximal incisura bordering the processus obturatum.

1910. Corpus ischii, margo ventralis, processus obturatorius, margo cranialis processi (**new term**), incisura between pars acetabularis ischii et processus obturatum, forma:

a. uniform, features “confluent”;

b. processus offset by incisura or “distinct notch.”

Note.—See: Rauhut (2003: character 188), regarding “obturator process on ischium . . . offset from pubic peduncle by a distinct notch.”

1911. Corpus ischii, facies lateralis, processus obturatorius, status et situs (craniocaudalis) proximodistalis (**ordered**):

a. conjoined with processus articularis pubici, “obturator flange” of Charig and Milner (1997), proximal in position;

b. separate, proximal in position;

c. separate, distal in position;

d. absent, corpus ischii sublinear from incisura obturatorum to terminus.

Note.—See: Gauthier (1986: text character 81); Novas (1992: character 10); Holtz (1994a: appendix 1, character 33); Novas (1994 [1993]: appendix, character 18); Charig and Milner (1997), in reference to “obturator flange”; Sues (1997: appendix 1, character 40); Forster et al. (1998: supplement, character 82, modified); J. D. Harris (1998: appendix 2, character 115); Makovicky and Sues (1998: appendix 1, character 83); Xu et al. (1999a: character 53); Xu et al. (1999b: character 62, modified); Currie and Carpenter (2000: appendix 1, character 92); Holtz (2000 [1998]: appendix I, characters 323–324); Norell et al. (2000: appendix 1, character 32); Xu et al. (2000: supplement, character 46); Hutchinson (2001a: appendix 1, character 15, in part); Norell et al. (2001: appendix 1, character 168); J. M. Clark et al. (2002a:

appendix 2.2, character 170); Maryanska et al. (2002: appendix 1, character 170); Xu (2002: suite I, character 92; suite II, character 191); Xu et al. (2002a: supplement, character 136); Rauhut (2003: character 189); Hwang et al. (2004: supplement, character 167); Xu and Norell (2004: supplement, character 167).

1912. Ala ischii, processus terminalis ischii, expansion, status:

a. absent, essentially uniform with ala ischii;
b. present.

Note.—See: Mivart (1877: figs. 13 and 22); Oliver (1949: figs. 90 and 104); Cracraft (1974: fig. 9); D. Smith and Galton (1990), Holtz (1994a: appendix 1, character 43); Sereno and Rao (1992: 845), who described the os ischium of *Sinornis* as "blade-shaped rather than strap-shaped"; Novas (1994 [1993]: appendix, character 50); K. Lee et al. (1997: appendix 1, character 22); J. D. Harris (1998: appendix 2, character 96); Livezey (1998b: appendix A, character 296); Azuma and Currie (2000: appendix 1, character 63); Currie and Carpenter (2000: appendix 1, character 96); Holtz (2000 [1998]: appendix I, character 327); Norell et al. (2001: appendix 1, character 175); J. M. Clark et al. (2002a: appendix 2.2, character 176); Maryanska et al. (2002: appendix 1, character 171); Sereno et al. (2002), regarding *Sinornis*; Xu (2002: suite II, character 197); Xu et al. (2002a: supplement, characters 134 and 142), pertaining to state "c" above (perhaps "b" and "c" equivalent); Dyke et al. (2003: appendix 1, character 72), employed again by Dyke (2003: table 1), in reference to rounded or acuminate terminus ischii in galliforms; Rauhut (2003: characters 192–193); Hwang et al. (2004: supplement, character 173); Xu and Norell (2004: supplement, character 173).

1913. Ala ischii, margo ventralis (pubica) ischii, processus terminalis ischii, a cranially oriented hamulus, status:

a. absent; **b.** present;
x. noncomparable (palaeognathous Neornithes).

Note.—See: Ericson (1997: table 2, character 25), in reference to acuminate extremity of margo articularis ischii abutting os pubis.

1914. Ala ischii, processus terminalis ischii, caudal extent relative to that of ala postacetabularis ilii (**ordered**):

a. substantially or only moderately greater in caudal extent than ala postacetabularis ilii, margo lateralis, crista iliaca dorsolateralis, processus (spina) dorsolateralis ilii, creating typical oblique margo pelvici;
b. approximately equal in caudal extent, resulting in approximately rectangular margo in lateral perspective;
c. conspicuously less in caudal extent than ala postacetabularis ilii, margo lateralis, crista iliaca dorsolateralis, processus (spina) dorsolateralis ilii.

Note.—See: Cracraft (1974: 503–504, 508); Bledsoe (1988: appendix, character 38); K. Lee et al. (1997: appendix 1, character 23), segregating synchondroses et symphyses; Chu (1998: appendix 1, character 108); Livezey (1998b: appendix A, character 295); Norell et al. (2001: appendix 1, character 160); J. M. Clark et al. (2002a: appendix 2.2, character 161); Xu (2002: suite II, character 183); G. Mayr and Ericson (2004: appendix I, character 71); Hwang et al. (2004: supplement, character 158); Xu and Norell (2004: supplement, character 158).

1915. Ala ischii, caudal extent relative to that of scapus (corpus) pubis (**ordered**):

a. less; **b.** approximately equal;
c. distinctly greater.

1916. Ala ischii, processus terminalis ischii, margo caudalis, incisura terminalis ischii (**new term**), status:

a. absent;
b. present, margo caudalis enclosing shallow fossa.

Note.—See: Zhou and Zhang (2002: appendix III, character 155).

1917. Ala ischii, corpus (pars caudalis) et processus terminalis ischii, pronounced ventral angling bringing acuminate terminus into close dorsal proximity of apex pubis with which it is subequal in caudal extent from sutura ischiopubica, status:

a. absent; **b.** present.

Note.—See: Livezey (1998b: appendix A, character 297). To avoid redundancy of encoded information, taxa having crescentic corpora ischii were excluded from this apomorphic state, the latter being treated *sensu stricto*.

1918. Ala ischii, processus terminalis ischii, pronounced ventral expansion, resulting in ventral orientation of os pubis and dorsoventrally deep pelvis at margo caudalis, status:

a. absent; **b.** present.

Note.—See: Livezey (1998b: appendix A, characters 296 and 298).

1919. Ala ischii, processus terminalis ischii, pronounced caudal extent while maintaining comparatively deep ala, ultimately effecting articulatio ischiopubica by shallow angulus and involving margo ventralis alae, status:

a. absent; **b.** present.

1920. Ala ischii, processus terminalis ischii, prominent ventral curvature, resulting in subperpendicular articulatio ischiopubica limited to terminus processi ischii, without associated derivation of os pubis, status:

a. absent; **b.** present.

Note.—See: G. Mayr (2004d: appendix I, character 29, revised); G. Mayr (2005a: appendix 1, character 30).

1921. Ala ischii, impressio muscularis cranialis (**new term**), status:

a. absent; **b.** present.

Note.—See: Holtz (1994a: appendix 1, character 71); Holtz (2000 [1998]: appendix I, character 326), regarding "semicircular scar on anterior of ischium, just distal to iliac process"; Norell et al. (2002: appendix 1, character 171); J. M. Clark et al. (2002a: appendix 2.2, character 173); Xu (2002: suite II, character 194); Hwang et al. (2004: supplement, character 170); Xu and Norell (2004: supplement, character 170).

1922. Ala ischii, sulcus obturatorius, prominence as reflected by craniocaudal extent, distinctness, and laterodorsal support by membrana ossificans attached to margo ventralis of ala ischii, forma (**ordered**):

a. obsolete, spatium for musculus concerned provided by medially convex ischium et laterally convex pubis;

b. discernable but limited in structural delimitation;

c. distinctly, but not exceptionally manifested;

d. conspicuously determinate of margo ventralis ischii, effecting either a demarcated laminar surface or deep sulcus laterally augmented by comparatively extensive membrana ischiopubica ossificans.

Note.—This sulcus represents margo dorsalis of the impressio m. obturatorius medialis, also supported dorsally by membrana ischiopubica et facies medialis pubica.

1923. Ala ischii, notably pila ischiadica, marked, distinct ventral bowing (correlated with approach to sutura ischiopubica caudalis), status:

a. absent; **b.** present.

Note.—See: Maryanska et al. (2002: appendix 1, character 169).

1924. Ossa ischii et pubis, wide medial separation, status:

a. present, reflected by comparatively broad interacetabular width;

b. absent, reflected by comparatively narrow interacetabular width.

Note.—See: Gauthier (1986: 13, unindexed synapomorphy of Ornithurae).

Pubis

Basis pubis

Note.—Os pubis, pars acetabularis pubis, pilae articulares iliorum et ischiorum (**new terms**), correspond to the two segments of the basis acetabularis ossis pubis that articulate with ossa ilii et pubis, partes acetabulares, respectively, and includes intervening incisura acetabularis pubis.

1925. Pila articularis ischialis (**new term**), forma transversa (**unordered**):

a. essentially circular;

b. bilaterally compressed with reniform terminus proximalis.

Note.—Termed "pubic peduncle" in traditional works. See: Gauthier (1986: 14, unindexed synapomorphy of Aves), in reference to "thin conformation"; Barsbold et al. (1990); Sereno and Rao (1992); Chiappe and Calvo (1994: appendix I, character 53); Chiappe (1995b: character 53); Sanz et al. (1995, 1997: character 51); Chiappe (1996b: character 49); Chiappe et al. (1996: appendix 1, character 48); Chiappe et al. (1998: character 76), including compression of scapus and "kidney-shaped proximal end"; Ji et al. (1998: supplement, character 76); Forster et al. (1998: supplement, character 86); Makovicky and Sues (1998: appendix 1, character 79), with respect to state "c" in which element appears "anteriorly convex in lateral view"; Chiappe (2001a: appendix 1, character 135); Norell and Clarke (2001: appendix I, character 165), treated similarly by J. A. Clarke (2002: appendix I, character 166), J. A. Clarke and Norell (2002: appendix 2, character 166), and J. A. Clarke (2004: appendix 1, character 166); Chiappe (2002: appendix 20.2, character 135); Sereno et al. (2002), regarding *Sinornis*; Zhou and Zhang (2002: appendix III, character 165); Ji et al. (2005: supplement, part I, character 165).

1926. Pilae articulares ischialis et pubici iliorum (**new term**), length relative to that of pars acetabularis ischii (lateral perspective):

a. pila articularis pubica subequal in length to pila articularis ischii;

b. pila articularis pubica significantly longer than pila articularis ischii, latter tapering ventrad and lacking distinct facies articularis.

Note.—See: Rauhut (2003: character 177), described in terms of "pubic peduncle" and "ischial peduncle," in which reference to pars acetabularis ilii that supports facies articularis ischii.

Scapus (corpus) pubis

1927. Scapus (corpus) pubis, pars acetabularis (basis) pubis, facies synchondrosis ischiopubica (**new term**), forma in planum transversus (**unordered**):

a. subcircular, angular-cylindrical;

b. bilaterally compressed, laminar.

Note.—See: Sereno et al. (1996); Chiappe et al. (1998: character 73); Ji et al. (1998: supplement, character 73); Azuma and Currie (2000: appendix 1, character 94); Chiappe (2001a: appendix 1, character

133); Chiappe (2002: appendix 20.2, character 133); Sereno et al. (2002), regarding *Sinornis*.

1928. Scapus (corpus) pubis, exclusive of marked departures in apex pubis (lateral perspective), margo dorsalis, forma dorsoventralis (**unordered**):

a. decurved, margo dorsalis convex;

b. essentially straight or sigmoid (latter typically recurved craniad and decurved caudad), approximately aligned with axis majoris of apex pubis;

c. slightly but distinctly recurved, margo dorsalis moderately concave;

d. conspicuously recurved, margo dorsalis deeply concave.

Note.—See: Livezey (1986: appendix 1, character 115); Livezey (1996a: appendix 1, character 66); Maryanska et al. (2002: appendix 1, character 166), with respect to straight *vs*. concave cranially. Source of error is warping of pubis related to preparation of skeletal specimens.

1929. Scapus (corpus) pubis, incisura (foramen) obturatorium pubici (**new term**)—passage for mm. obturatorii entirely within os pubis, status:

a. present;

b. absent, either by way of failure to complete closure of incisura or involvement of os ischium.

Note.—See: Holtz (1994a: appendix 1, character 91); Sereno et al. (1996); J. D. Harris (1998: appendix 2, character 108); Currie and Carpenter (2000: appendix 1, character 85).

1930. Scapus (corpus) pubis (lateral perspective), margo dorsalis, processus (tuberculum) obturatorius or completion of caudal closure of foramen obturatum ischiopubicum (**new term**), status et forma (**unordered**):

a. absent or obsolete;

b. distinct tuberculum;

c. tuberculum included within margo caudalis foraminis.

Note.—See: Gauthier (1986: 13, unindexed synapomorphy of Ornithurae), regarding proximal position of "prepubic process"; Carroll (1997: 312).

1931. Scapus (corpus) pubis (dorsal perspective), pars intermedia (i.e., between tuberculum obturatorius cranially and processus terminalis ischii caudally), facies lateralis, forma lateromedialis (**ordered**):

a. concave; **b.** straight;

c. slightly to moderately convex laterally;

d. strongly convex laterally, apices typically closely approaching or contacting caudomedially.

Note.—See: Livezey (1998b: appendix A, character 299).

1932. Scapus (corpus) pubis (dorsal perspective), pars intermedia, forma:

a. variably robust;

b. flexible, filamentous, extremely reduced in diameter.

1933. Scapus (corpus) pubis (lateral perspective), pars cranialis (especially ventral to acetabulum) filamentous, abruptly deepening dorsoventrad at middle of corpus to distinctly laminar form immediately cranial to pars caudalis et apex, status:

a. absent; **b.** present.

1934. Scapus (corpus) pubis, relative length:

a. length no more than five times greater than breadth;

b. length at least six times greater than breadth.

Note.—See: Holtz (2000 [1998]: appendix I, character 312).

1935. Scapus (corpus) pubis, craniocaudal elaboration into neomorphic partes preacetabularis (**new term**; "prepubic process") et postacetabularis (**new term**; "postpubic process"), with interposed pars acetabularis pubici contributing to sectio ventralis of rima acetabularis, status:

a. absent; **b.** present.

Note.—See: D. A. Winkler et al. (1997: appendix 1, character 22); Novas et al. (2004: appendix, character 16).

1936. Scapus (corpus) pubis, pars cranialis (lateral perspective), dorsoventral curvature, status et forma (**unordered**):

a. present, dorsad, margo dorsalis convex;

b. absent, margo dorsalis essentially linear or straight;

c. present, ventrad, margo dorsalis concave.

Note.—See: Livezey (1986: appendix 1, character 115); Livezey (1989: table 1, character 115); Livezey (1996a: appendix 1, character 66); Livezey (1996b: appendix 1, character 35); J. D. Harris (1998: appendix 2, character 109); Makovicky and Sues (1998: appendix 1, character 79), in which state "c" in which element "anteriorly convex in lateral view"; Currie and Carpenter (2000: appendix 1, character 86); Holtz (2000 [1998]: appendix I, character 310); Norell et al. (2001: appendix 1, character 179); J. M. Clark et al. (2002a: appendix 2.2, character 181); Xu (2002: suite I, character 39; suite II, character 201); Xu et al. (2002a: supplement, character 146), in which cranial curvature ("anterior surface") of terminus and concavity of facies dorsocranialis were treated; Rauhut (2003: character 183); Hwang et al. (2004: supplement, character 178); Novas et al. (2004: appendix, character 16); Xu and Norell (2004: supplement, character 178).

1937. Scapus (corpus) pubis, distinct, semiorbiculate lobus at approximate midpoint (immediately caudal to processus caudoventralis ischii, status:

a. absent; **b.** present.

Note.—See: Livezey (1998b: appendix A, character 300).

1938. Scapus et apex pubis, pronounced (dorso) medial curvature and truncation distal to synchondrosis ischiopubica, status:
a. absent; **b.** present.
Note.—See: Cracraft (1988: series XIV, character 6). Illustrated by Shufeldt (1909: figs. 28, 48, 69).

1939. Scapus (corpus) pubis, sectio subterminalis, conformation of scapus and emergence of lamina symphysialis (where present) immediately proximal to symphysis pubica (**unordered**):
a. scapus lateromedially compressed, lamina extended from margo caudo-distalis;
b. scapus cylindrical, lamina extending mediad from middle;
c. scapus craniocaudally compressed, lamina extended from margo medialis;
x. noncomparable, symphysis pubica absent (Ornithurae).
Note.—See: J. D. Harris (1998: appendix 2, character 111); Azuma and Currie (2000: appendix 1, character 95); Norell et al. (2001: appendix 1, character 187); J. M. Clark et al. (2002a: appendix 2.2, character 180); Xu (2002: suite II, character 200); Xu et al. (2002a: supplement, character 145); Hwang et al. (2004: supplement, character 177); Xu and Norell (2004: supplement, character 177).

Apex pubis

Note.—The systematic literature includes various aspects of shape of the **"pubic boot"—**treated as one conformational state or complex of states of the "apex pubis" here, as opposed to "pars acetabularis" or "pubic pedicel or foot"—treated in various ways and encompassing diverse definitions of "size" and several components of "shape."

See: Ostrom (1976a); Gauthier (1986: text characters 48 and 79); Livezey (1986: appendix 1, character 117); Livezey (1989: table 1, character 117); Novas (1992: characters H and I); Sereno and Rao (1992); Chiappe and Calvo (1994: appendix I, character 54); Russell and Dong (1994a [1993a]: table 2, character 51); Russell and Dong (1994b [1993b]: troödontid character 18, part; list B, character 12); Holtz (1994a: appendix 1, characters 20–21, 30, and 98); Novas (1994 [1993]: appendix, character 44); Chiappe (1995a: legend for fig. 1); Chiappe (1995b: character 54); Elzanowski (1995: character C4); Chiappe (1996b: character 50); Hou et al. (1996: character 23, part); Livezey (1996a: appendix 1, character 67); Sereno et al. (1996: footnote 45, character 51); Sanz et al. (1995, 1997: character 52); Chiappe et al. (1996: appendix 1, character 49); Novas (1996: appendix, character M15); Novas (1996: appendix, character 66); Livezey (1997a: appendix 1, character 81; *corrigenda*, Livezey 1998a); Novas (1997: appendix, character 67); Novas and Puerta (1997), see identical characters in Novas (1997); Chiappe et al. (1998: character 74); Ji et al. (1998: supplement, character 74); Forster et al. (1998: supplement, character 77); J. D. Harris (1998: appendix 2, character 113); Makovicky and Sues (1998: appendix 1, character 82); Sereno et al. (1998: footnote 22, character 34); Chatterjee (1999: appendix II, character 69); Xu et al. (1999a: character 51); Xu et al. (1999b: character 58); Azuma and Currie (2000: appendix 1, character 96); Currie and Carpenter (2000: appendix 1, character 90); Holtz (2000 [1998]: appendix I, characters 315–317); Xu et al. (2000: supplement, character 43); Chiappe (2001a: appendix 1, character 134); Dyke (2001b: appendix 1, character 81); Chiappe (2002: appendix 20.2, character 134); Chiappe and Walker (2002: appendix 11.1, character 26). Nomenclature of Hutchinson (2001a: appendix 1, character 18) tentatively followed here. Most previous authors refer to feature as "pubic boot," reserving "pubic foot" for the proximal basis of the element.

1940. Apex pubis, forma dorsomediana:
a. dorsoventrally (craniocaudally) spatulate;
b. spatulation negligible, scapus pubis et apex pubis and essentially having parallel margines ventralis et dorsalis throughout lengths.
Note.—In paleontological literature, commonly referred to as the "pubic boot." See: Holdaway (1991: appendix 5.1, character 150); Norell and Clarke (2001: appendix I, character 167); Norell et al. (2001: appendix 1, character 177); J. M. Clark et al. (2002a: appendix 2.2, character 179); J. A. Clarke (2002: appendix I, character 168); J. A. Clarke and Norell (2002: appendix 2, character 168); Maryanska et al. (2002: appendix 1, character 167); Xu (2002: suite II, character 199); Zhou and Zhang (2002: appendix III, character 167); J. A. Clarke (2004: appendix 1, character 168); Hwang et al. (2004: supplement, character 176); Xu and Norell (2004: supplement, character 176); Ji et al. (2005: supplement, part I, character 167).

1941. Apex pubis, pronounced craniocaudal elongation, status et forma (**unordered**):
a. absent;
b. present, unidirectional, craniad (by ventral curvature → ventrad) only;
c. present, unidirectional, caudad (by ventral curvature → apex oriented in part dorsad) only;
d. present, unidirectional, caudad only, latter more than one-half of length of scapus pubis;
e. present, bidirectional, both craniad and caudad.
Note.—See: Gauthier (1986: 13), regarding absence of expanded *distal* "foot"; Holtz (1994a: appendix 1, character 30); Carroll (1997: 312); Holtz

(2000 [1998]: appendix I, character 315); Chiappe et al. (1999), regarding *Confuciusornis*; Sereno et al. (2002), regarding *Sinornis*; Xu et al. (2002a: supplement, character 144); Rauhut (2003: characters 184 and 187).

1942. Apex pubis, relative lengths of partes cranialis et caudalis (**ordered**):

a. pars caudalis of greater length than pars cranialis;

b. pars caudalis of approximately equal length to pars cranialis;

c. pars caudalis of shorter length than pars cranialis.

Note.—See: Holtz (1994a: appendix 1, character 20); Holtz (2000 [1998]: appendix I, character 316); Rauhut (2003: character 186).

1943. Apex pubis, significant lateromedial expansion (ventral perspective), status:

a. present, apex broadly triangular;

b. absent or marginal, apex narrow with subparallel margines.

Note.—See: Holtz (1994a: appendix 1, character 21); Rauhut (2003: character 185).

1944. Apex pubis or symphysis pubica (if present), length axis majoris relative to that of scapus pubis presymphysialis (**unordered**):

a. greater than 30% scapus, typically approximately one-half;

b. 0–30% scapus, typically less than one-third;

x. noncomparable by absence of differentiated apex (Neornithes).

Note.—See: Holtz (1994a: appendix 1, character 98); Holtz (2000 [1998]: appendix I, character 317); Norell et al. (2001: appendix 1, character 180); J. M. Clark et al. (2002a: appendix 2.2, character 182); Xu (2002: suite I, character 90; suite II, character 259); Hwang et al. (2004: character 179); Xu and Norell (2004: supplement, character 179).

1945. Apex pubis, axis majoris (lateral perspective), angulus dorsoventralis relative to axis majoris of subtending scapus pubis, forma (**unordered**):

a. craniodorsal;

b. straight, i.e., essentially a simple caudal extension;

c. cranioventral.

1946. Apex pubis, facies lateralis (dorsal perspective), lateromedial curvature relative to scapus pubis, forma lateromedialis (**ordered**):

a. negligible lateromedial departure from scapus;

b. slightly or moderately medial;

c. strongly medial, subtransverse.

1947. Apex pubis, facies lateralis (lateral perspective), dorsoventral components of axis majoris apicalis (**new term**) relative to axis craniocaudalis synsacralis, forma dorsoventralis (**ordered**):

a. caudal; **b.** caudoventral;

c. ventral; **d.** caudodorsal.

Note.—See: Shufeldt (1886a); Livezey (1986: appendix 1, character 116); Livezey (1989: table 1, character 116); Livezey (1997a: appendix 1, character 81; *corrigenda*, Livezey 1998a); Dyke (2001b: appendix 1, character 81).

Juncturae Ossis Coxae

1948. Synostosis cinguli membri pelvici definitivum, comprising synostoses ischiopubica, ilioischiadica, et iliopubica, status (**ordered**):

a. absent, none of included synostoses present;

b. partial, limited to synostosis ilioischiadica, synostoses involving os pubis lacking;

c. complete, all three synostoses present;

d. complete, but suturae variably persistent into adulthood, especially adjacent to vertebrae caudales stabiles.

Note.—See: Cracraft (1986: appendix, character 14); Gauthier (1986: 13, unindexed synapomorphy of Ornithurae); Cracraft (1988: series II, character 6); Rowe and Gauthier (1990); Sanz and Bonaparte (1992: character 15); Sereno and Rao (1992); Chiappe and Calvo (1994: appendix I, character 45); Holtz (1994a: appendix 1, character 118); Chiappe (1995b: character 45); Elzanowski (1995: character C6); Sanz et al. (1995, 1997: character 43); Chiappe (1996b: character 42); Chiappe et al. (1996: appendix 1, character 41); Novas (1996: appendix, character 72); Novas (1997: appendix, character 73); Novas and Puerta (1997), see identical characters in Novas (1997); Chiappe et al. (1998: character 62); Forster et al. (1998: supplement, character 85); J. D. Harris (1998: appendix 2, character 120); Ji et al. (1998: supplement, character 62); Holtz (2000 [1998]: appendix I, character 285); Chiappe (2001a: appendix 1, character 118); Norell and Clarke (2001: appendix I, character 153), treated similarly by J. A. Clarke (2002: appendix I, character 153), J. A. Clarke and Norell (2002: appendix 2, character 153), and J. A. Clarke (2004: appendix 1, character 153); Chiappe (2002: appendix 20.2, character 118); Sereno et al. (2002), regarding *Sinornis*; Zhou and Zhang (2002: appendix III, character 153); Ji et al. (2003a: 23); Ji et al. (2005: supplement, part I, character 153).

1949. Junctura (sutura) iliosynsacralis between margines cranialis et caudalis iliorum (dorsal perspective), forma definitiva (**unordered**):

a. "**leptolinear**," suturae parallel and separated by extremely to moderately narrow spatium;

b. "**vasiform**," narrow cranially—typically concealing fenestrae intertransversariae (dorsal perspective), widening to angular maximum between acetabulae, and gradually narrowing to various degrees caudad from maximum;

c. "**platylinear**," suturae (sub)parallel and well separated throughout.

1950. Junctura (synostosis) ischiosynsacralis, status:

a. absent;

b. present, primarily lateroventral.

Note.—Whereas most Neornithes immediately precede the symphysis postsynsacralis with one of several variants of junctura iliosynsacralis, the Rheidae possess a junctura ischiosynsacralis.

1951. Junctura (articulatio) interiliacus (**new term**) et/aut iliosynsacralis, status:

a. absent, margines dorsales iliorum separated and typically dorsal to synsacrum;

b. present, margines dorsales iliorum in contact (inclusive of synchondrosis) or ilii bilaterally contacting interposed spina dorsales synsacri et/aut processes transverses, evidently a result of pronounced mediodorsal inclination.

Note.—See: Holtz (1994a: appendix 1, character 70); Sues (1997: appendix 1, character 38); J. D. Harris (1998: appendix 2, character 105); Livezey (1998b: appendix A, characters 276–277); Makovicky and Sues (1998: appendix 1, character 74); Xu et al. (1999a: character 43); Azuma and Currie (2000: appendix 1, character 60); Rauhut (2003: character 171).

1952. Junctura ischiopubica (caudalis) distalis, status et typus (**unordered**):

a. absent;

b. variable (craniocaudally abbreviated) synchondrosis, often of limited robustness and permitting separation of elements during preparation, or (if distinguishable) articulatio;

c. substantial synchondrosis distalis, forming a dorsoventrally deep lamina;

d. variably extensive and oriented sutura distalis.

Note.—Distinct from synchondrosis ischiopubica bilateralis of ornithischian Dinosauria (treated elsewhere). See: Cracraft (1974: characters 15 and 17); Bledsoe (1988: appendix, character 42); K. Lee et al. (1997: appendix 1, character 26), often under term "pubo-ischial bar"; J. A. Wilson and Sereno (1998: appendix, character 95), concerning conditions among Sauropoda; Azuma and Currie (2000: appendix 1, character 88). Emendation "caudalis" to distinguish from that present in some taxa as margo caudalis of foramen obturatum.

1953. Synchondrosis (caudalis) ilioischiadica (et fenestra ilioischiadica definitivum), status:

a. absent, resulting in incisura ilioischiadica caudalis;

b. present.

Note.—Synchondrosis between caudal segmenta ossium ilii, ischii, et/aut pubici evidently derive from variable retention and ossification of a comparatively extensive cartilaginous lamina characteristic of embryonic Neornithes of diverse taxonomic relationships (W. K. Parker 1890: pls. 1–3, 5, 8). In a number of neognathous taxa an ontogenetic stage occurs in which a synchondrosis (caudalis) ilioischiadica is absent but later is formed (Pycraft 1900; D. Starck 1989), the former virtually mirrored by the definitive form of some palaeognathous taxa, e.g., *Aepyornis* (Andrews 1897: fig. 2). Apparently paedomorphic reversals to state "a" occur infrequently in some neognathous taxa, e.g., some anserines (Livezey 1996a: appendix I, character 62).

See: Cracraft (1974: 503, characters 15 and 17; 505, character 3); Cracraft 1985 (fig. 4b); Cracraft (1986: appendix, character 33); Cracraft (1988: series VI, character 1); Cracraft and Mindell (1989: table 1, character 20); Chatterjee (1995: character 14, part); Elzanowski (1995: character NG3); K. Lee et al. (1997: appendix 1, character 23, part); Livezey (1996a: appendix 1, character 62); Livezey (1997a: appendix 1, character 78; *corrigenda*, Livezey 1998a); Rotthowe and Starck (1998: appendix, character 4); Norell and Clarke (2001: appendix I, character 154), treated similarly by J. A. Clarke (2002: appendix I, character 154), J. A. Clarke and Norell (2002: appendix 2, character 154), and J. A. Clarke (2004: appendix 1, character 154); Ji et al. (2005: supplement, part I, character 154).

1954. Corpus ischii, margo dorsalis, tuberculum(ae) ischiadicum (tuberculum[ae] aut impressio[nes] membrana ilio-ischiadica et m. ischiotrochantericus), status:

a. absent, represented only by an impressio or area tuberculata;

b. present, expanded into tuberculum or processus ("proximal ischial process" or "process on caudal border of midshaft" or "ischium forked").

Note.—Reconciliation with characters by Hutchinson (2001a: appendix 1, characters 19–21)—"ischial tuberosity," "distal ischial tubercle," and "distal dorsal ischial process"—with those used by Ostrom (1976a) and others problematic. Apparently, first mentioned by Novas and Puerta (1997: 392, character *iv*); J. R. Hutchinson (pers. comm.) considered his "proximal dorsal ischial process (character 19, state 2) as equivalent to the "proximodorsal process of the ischium" of Novas and Puerta (1997) and Forster et al. (1998: supplement, character 84), and opined that Xu et al. (1999a–b, 2000) agree with his analysis; see also Xu et al. (2002a: supplement, character 139), regarding "semicircular scar [impressio] on posterior part of the proximal end." However, given reservations concerning homology expressed by Hutchinson (2001a: appendix 1, character 19), extreme caution is warranted. Recent authors delimit one of their ischial characters as "postacetabular process on proximal ischium behind iliac contact." The distal processes—Hutchinson (2001a: appendix 1, characters 20–21)—remain a problem and likely comprise three states of a single character (Hutchinson 2001a).

See: Forster et al. (1998: supplement, characters 83–84); Chatterjee (1999: appendix II, character 71), regarding "ischiadic peduncle"; Xu et al. (1999b: characters 63–64); Holtz (2000 [1998]: appendix I, character 325), in reference to "ischial proximodorsal process just distal to iliac process"; Xu et al. (2000: supplement, characters 47–48); Chiappe (2001a: appendix 1, character 128); Norell and Clarke (2001: appendix I, character 155), in reference to "dorsal process," treated similarly by J. A. Clarke (2002: appendix I, character 155), J. A. Clarke and Norell (2002: appendix 2, character 155), and J. A. Clarke (2004: appendix 1, character 155); Norell et al. (2001: appendix 1, characters 166 and 172), contrasting straight with presence of median posterior process; Chiappe (2002: appendix 20.2, character 128); J. M. Clark et al. (2002a: appendix 2.2, characters 168 and 177); Xu (2002: suite I, character 93; suite II, characters 189 and 257); Xu et al. (2002a: supplement, character 202), regarding "tubercle on anterior edge of ischium"; Hwang et al. (2004: characters 165 and 174); Xu and Norell (2004: supplement, characters 165 and 174); Ji et al. (2005: supplement, part I, character 155).

1955. Synchondrosis (articulatio) ilioischiadica, size relative to that of synchondrosis (articulatio) iliopubica, forma:

a. former larger than latter;

b. former smaller than latter;

x. noncomparable (palaeognathous Neornithes).

Note.—See: J. D. Harris (1998: appendix 2, character 107); Holtz (2000 [1998]: appendix I, character 304), citing Sereno et al. (1994); Dyke et al. (2003: appendix 1, character 70), employed again by Dyke (2003: table 1). Definition of "size" in this context presumably refers to areas of two facies articulares iliorum.

1956. Synchondrosis ischiopubica caudalis, status et forma (**ordered**):

a. absent, juncturae ischiopubica limited to synostosis within rima acetabularis;

b. present, incomplete, limited to or including synchondroses ischiopubicae medio-apicales (**new term**), i.e., those involving the apices pubici;

c. present, moderately and variably complete and robust synchondrosis between ischia (margo ventralis) et apex pubis;

d. present, complete, essentially joining ischia (margo ventralis) with os pubis (margo dorsalis) through majority of elements where in dorsoventral opposition, either cranially or caudally.

Note.—See: Cracraft 1985 (fig. 4b); Gauthier (1986: 14, unindexed synapomorphy of Aves); Chatterjee (1995: character 14, part); Xu et al. (2002a: supplement, character 137), pertaining to contact of processus obturatorius ischii et os pubis, associated with a foramen obturatum.

This character excludes apparent synchondroses deriving from synostoses caudales of foramen obturatum, as these represent ossification of the ligamentum ischiopubicum, i.e., ligamentum ischiopubicum ossificans, a character treated under foramen obturatum. Similarly, irregular ossifications of the interposed membrana ischiopubica are not included here.

1957. Sutura ischiopubica (caudalis) distalis (**new term**), if present, angulus sutura-synacralis:

a. distinctly less than 45º;

b. at least 45º.

1958. Symphysis pubica, status et typus (**ordered**):

a. present and expanded to form substantial carina or planum symphysialis pubica ("apron") that is transversely wide and proximodistally long, extending more than 50% of the os pubis;

b. present and moderately expanded to form limited carina or planum symphysialis pubica ("apron") that is limited to distal half of the os pubis;

c. present as simple symphysis pubica ("conjoined boots") or articulatio pubica, not expanded to form carina or planum symphysialis pubica (so-called "apron");

d. absent, articulatio or ossa pubica do not contact medially.

Note.—Embryological evidence suggests that symphysis pubica may be related ontogenetically to the same synchondrosis that effects caudal unions between ilia and ischia (W. K. Parker 1890). Crocodylia (e.g., *Caiman*) were considered without symphysis pubica, in that clearly defined ossa pubici were "united" only via large expanse of poorly ossified cartilaginous lamina also incorporating gastralia. A structural analog might be termed prosymphysis pubicus (**new term**).

See: Cracraft (1974: 503, character 16); Cracraft (1986: appendix, character 15); Bledsoe (1988: appendix, character 39); Cracraft (1988: series II, character 7); Gatesy (1990); Chiappe and Calvo (1994: appendix I, character 52); Chiappe (1995b: character 52); Sanz et al. (1995, 1997: character 50); Chiappe (1996b: character 48); Chiappe et al. (1996: appendix 1, character 47); Hou et al. (1996: character 23); Novas (1996: appendix, character 51), in reference to "apron"; Novas (1996: appendix, character 53), in reference to articulatio interpubica; Norell and Makovicky (1997); Novas (1997: appendix, characters 52 [symphysis] and 54 [articulatio]); Novas and Puerta (1997), see identical characters in Novas (1997); Chiappe et al. (1998: characters 72 [presence]) and 75 [size]); Forster et al. (1998: supplement, characters 89 [presence] and 88 [size]); J. D. Harris (1998: appendix 2, characters 110–112); Ji et al. (1998: characters 72 [presence] and 75 [size]); Makovicky and Sues (1998: appendix 1, character 78); J. A. Wilson and Sereno (1998: appendix, character 46), concerning caudomedial orientation of symphysis among Sauropoda; Chatterjee (1999: appendix II, character 70); Holtz (2000 [1998]: appendix I, characters 311 [contact] and 313 [symphysis, status et forma]); Azuma and Currie (2000: appendix 1, characters 93 and 95); Currie and Carpenter (2000: appendix 1, characters 87–89); Chiappe (2001a: appendix 1, character 132); Hutchinson (2001a: appendix 1, character 8, excluding basalmost state); Norell and Clarke (2001: appendix I, character 166), treated similarly by J. A. Clarke (2002: appendix I, character 167), J. A. Clarke and Norell (2002: appendix 2, character 167), and J. A. Clarke (2004: appendix 1, character 167); Sereno (2001: table 1, character 22), regarding Alvarezsauridae; Chiappe (2002: appendix 20.2, character 132); Gatesy (2002) for functional implications; Maryanska et al. (2002: appendix 1, character 168); Sanz et al. (2002: fig. 9.12); Xu et al. (2002a: supplement, character 204), pertaining to length of "apron" relative to that of corpus pubis, using one-third as break-point; Zhou and Zhang (2002: appendix III, character 166); Ji et al. (2003a: 23); Ji et al. (2005: supplement, part I, character 166). Examination of subadult *Struthio* indicates that the symphysis is composed of the union of a pair of late-developing, comparatively porous lobi.

1959. Symphysis pubica medio-apicalis (**new term**), caudomedial proximity, status et forma (**ordered**):

a. absent;

b. present, moderate caudomedial proximity, ankylosis absent;

c. present, caudomedial proximity pronounced, ankylosis absent;

d. present, extreme, ankylosis present, producing symphysis pubica medio-apicalis (**new term**).

Note.—Both morphological differences and taxonomic distributions served to support *a priori* treatment of this character as nonhomologous with the symphysis pubica of some nonavialian Theropoda and ratites.

1960. Symphysis pubica, planum or crista symphysialis, fenestra suturalis (**new term**), status et forma:

a. absent or restricted;

b. present and large;

x. noncomparable where symphysis pubica lacking (most Neornithes).

Note.—Fenestra suturalis may be closed by cartilago in life, and some consider the definitive condition to be found no further crownward than coelurosaurs (P. J. Currie, pers. comm.). See: Novas (1997: appendix, character 52); Novas and Puerta (1997), see identical characters in Novas (1997); J. D. Harris (1998: appendix 2, character 110); Currie and Carpenter (2000: appendix 1, character 87); Holtz (2000 [1998]: appendix I, character 314); Hutchinson (2001a: appendix 1, characters 11–12), in reference to "pelvic fenestra" in "ventral floor of the pelvic canal"; Rauhut (2003: character 182).

1961. Symphysis ischiadica, status et forma (**ordered**):

a. present, expanded to form a lamina (carina) symphysialis ischiadica (**new term**)—"apron" with ventral "keel"—of significant size;

b. present, sutura of variable length and discernability, carina symphysialis ischiadica (**new term**) essentially lacking;

c. absent, by medial components forming articulatio interischiadica (**new term**);

d. absent, neither symphysis nor articulatio interischiadica.

Note.—This ordered character including approach, expansion, and symphysis; the extreme state of absent articulation *and* widely separated alae postacetabulares iliorum not included here. See: Gadow (1885); Cracraft (1974: 503, character 17); Tarsitano and Hecht (1980); Chiappe and Calvo (1994: appendix I, character 51); Russell and Dong (1994b [1993b]: troödontid character 20); Chiappe (1995b: character 51); Sanz et al. (1995, 1997: character 49); Chiappe (1996: character 47); Chiappe et al. (1996b: appendix 1, character 46); Novas (1996: appendix, character 69), concerning "contact"; K. Lee et al. (1997: appendix 1, character 23, part); Novas (1997: appendix, character 70); Novas and Puerta (1997), see identical characters in Novas (1997); Chiappe et al. (1998: character 69); J. D. Harris (1998: appendix 2, character 118); Ji et al. (1998: supplement, character 69); Forster et al. (1998: supplement, character 80); Chatterjee (1999: appendix II, character 66); J. M. Clark et al. (1999: 8), including description and photograph of sutura foliata effecting akinetic symphysis in an oviraptosaurid; Currie and Carpenter (2000: appendix 1, character 95); Holtz (2000 [1998]: appendix I, character 328 [contact]); Chiappe (2001a: appendix 1, character 129); Hutchinson (2001a: appendix 1, character 9, excluding basalmost state); Norell et al. (2001: appendix 1, character 174); Chiappe (2002: appendix 20.2, character 129); Chiappe and Lacasa-Ruiz (2002), regarding *Noguerornis*; J. M. Clark et al. (2002a: appendix 2.2, character 175); Xu (2002: suite II, character 196); Xu et al. (2002a: supplement, character 141); Ji et al. (2003a: 23–24); Hwang et al. (2004: supplement, character 172); Xu and Norell (2004: supplement, character 172).

1962. Synchondrosis ischiopubica bilateralis, extending variably longitudinally between corpora ossium ischii et pubici (pars caudalis) separately bilaterad and not involving interposed membrana ossificans or symphysis coxis, status:

a. absent; **b.** present.

Note.—See: Benton (1990a: 26) for archetypical example in *Stegosaurus*, illustrating related bipartite form of os pubis comprising both pars preacetabularis and pars postacetabularis, the former of variable length and the latter synchondrotic to variable extent with os subparallel os ischium (e.g., *Kentrosaurus*) and superficially similar in position to that of crown Theropoda (e.g., Aves). The biprocessural form of os pubis among Ornithischia is the basis for the descriptor "tetraradiate" of the pelvis that is unique for the group, whereas the Saurischia are described instead as "triradiate."

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Note.—As with metric characters relating pectoral elements to each other and skeletal dimensions of other regions of the body, pelvic elements have been subjected to many related if not redundant ratios and proportions. These principally stemmed from analyses of fossil taxa where preservation of elements prompted alternative criteria (e.g., Murray and Vickers-Rich 2004: table 9, character 11). Initial assessments indicated that critical information of this kind could be captured by (*i*) a ranking of lengths of femora and tarsometatarsi, and (*ii*) grouping taxa having extremely truncated tarsometatarsi. Consequently, given comparison of modern taxa was the primary objective, many of the previously published criteria (listed below) were excluded from analysis: **femur to pubis**—Novas (1994 [1993]: appendix, character 6); **femur to tibiotarsus**—Sereno (1991a: appendix, ingroup character 27); Novas (1996: appendix, character 59); Novas (1997: appendix, character 60); Novas and Puerta (1997), repeated by Novas (1997); Sues (1997: appendix 1, character 45, part); Forster et al. (1998: supplement, character 111); Chatterjee (1999: appendix II, character 74, much modified); Xu et al. (1999a: characters 76 [part] and 77); Xu et al. (1999b: character 82); Azuma and Currie (2000: appendix 1, character 106); Xu et al. (2000: supplement, character 62); Maryanska et al. (2002: appendix 1, character 194); **femur to columna vertebralis**—Holtz (2000 [1998]: appendix I, character 178); Xu (2002: suite II, character 19); **tibiotarsus to tarsometatarsus—**Cracraft (1985: character 33); Livezey (1997a: appendix 1, character 88; *corrigenda*, Livezey 1998a); Xu et al. (1999a: character 78).

1963. Femur et tarsometatarsus, corpora, relative lengths (along axes majores ossium):

a. femur equal to or longer than tarsometatarsus or constituent ossa metatarsalia;

b. femur shorter than tarsometatarsus.

Note.—See: Rich (1979: table 43), for ratites and Dromornithidae; Gauthier (1986: 12); Weishampel et al. (1990); Holtz (1994a: appendix 1, character 54); Sues (1997: appendix 1, character 45); Chu (1998: appendix 1, character 109); Holtz (2000 [1998]: appendix I, character 369); Maryanska et al. (2002: appendix 1, character 195).

1964. Fibula et tibia, relative widths of corpora at midpoints:

a. former approximately one-fifth or more than that of latter;

b. former approximately one-fifth or less than that of latter.

Note.—See: Forster et al. (1998: supplement, character 99); Xu et al. (1999b: character 72); Xu et al. (2000: supplement, character 55).

Femur (Os Femoris)

Extremitas proximalis femoris

1965. Extremitas proximalis femoris, caput femoris, forma generalis (**unordered**):

a. massive or "bulky";

b. transversely elongate; **c.** subspheroidal.

Note.—See: Azuma and Currie (2000: appendix 1, character 47); Holtz (2000 [1998]: appendix I, character 331); G. Mayr (2004a: appendix 1, character 51), regarding length relative to width of corpus femoris.

1966. Extremitas proximalis femoris, caput femoris, lateromedial width relative to complement of extremitas proximalis femoris, forma:

a. diminutive, no more than one-half;

b. robust, at least one-half.

1967. Extremitas proximalis femoris (especially trochanter et collum femoris), pronounced craniocaudal compression, status et magnitudo (**ordered**):

a. absent or negligible, craniocaudal depth of trochanter approximately twice as great as that of caput femoris;

b. present, moderately pronounced, craniocaudal depth of trochanter less than 50% greater that of caput femoris;

c. present, prominent, craniocaudal depth of trochanter approximately equal to that of caput femoris.

Note.—See: Cracraft (1982: series 2, character 3); Cracraft (1988: series XI, character 5); G. Mayr and Clarke (2003: appendix A, character 96), in associated assessment of relative femoral shaft width.

1968. Extremitas proximalis femoris, caput femoris—with respect to axis majoris (proximodistalis) femoris—angulus distomedialis (**ordered**):

a. significantly less than 90°, i.e., distinctly acute;

b. approximately 90°, i.e., right or perpendicular;

c. significantly greater than 90°, i.e., distinctly obtuse.

Note.—See: J. D. Harris (1998: appendix 2, character 121); Currie and Carpenter (2000: appendix 1, character 97); Holtz (2000 [1998]: appendix I, character 330).

1969. Extremitas proximalis femoris, caput femoris—with respect to axis transversus condyli distales femoris—forma et angulus:

a. craniomedial, angulus craniomedialis, 20º–60º;

b. medial, angulus craniomedialis, 0º–20º.

Note.—Essentially reflects apparent torsion about axis majoris femoris. See: Parrish (1986); Livezey (1986: appendix 1, character 51); Livezey (1989: table 1, character 51); Holtz (1994a: appendix 1, character 12); Novas (1994 [1993]: appendix, character 19, part); Novas and Puerta (1997: 392, character *iii*); Livezey (1996a: appendix 1, character 69); J. D. Harris (1998); Azuma and Currie (2000: appendix 1, character 48); Hutchinson (2001b: appendix 1, character 1, excluding basalmost state); Rauhut (2003: character 195).

1970. Extremitas proximalis femoris, caput femoris, facies articularis acetabularis, incisura rimae acetabularis (**new term**) evidently serving as situs semistasis articulationis femoro-acetabularis, status (**ordered**):

a. absent;

b. present, single and craniodorsal, evidently accommodating the laterally splayed resting position of the femora;

c. present, double (dorsal et craniodorsal), evidently accommodating the laterally splayed resting and foraging positions of the femora.

Note.—See: Andors (1992: table 1, character 5).

1971. Extremitas proximalis femoris, caput femoris, fovea ligamentum capitis femoris, status:

a. absent; **b.** present.

Note.—See: Chiappe and Calvo (1994: appendix I, character 56); Novas (1994 [1993]: appendix, character 20), regarding "tuberosity that laterally bounds the ligament of the femoral head"; Chiappe (1995b: character 56); Sanz et al. (1995, 1997: character 54); Chiappe (1996b: character 51); Chiappe et al. (1996: appendix 1, character 50); Chiappe et al. (1998: character 77); Forster et al. (1998: supplement, character 94); Ji et al. (1998: supplement, character 77); Chatterjee (1999: appendix II, character 77); Hughes (2000: appendix 2, character 78), after Seibel (1988: character FE 3); Chiappe (2001a: appendix 1, character 136); Norell and Clarke (2001: appendix I, character 168), treated similarly by J. A. Clarke (2002: appendix I, character 169), J. A. Clarke and Norell (2002: appendix 2, character 169), and J. A. Clarke (2004: appendix 1, character 169); Norell et al. (2001: appendix 1, character 181); Chiappe (2002: appendix 20.2, character 136); J. M. Clark et al. (2002a: appendix 2.2, character 183); Xu (2002: suite II, character 202); Xu et al. (2002a: supplement, character 147); Zhou and Zhang (2002: appendix III, character 168); Rauhut (2003: character 197); Hwang et al. (2004: supplement, character 180); Xu and Norell (2004: supplement, character 180); Ji et al. (2005: supplement, part I, character 168).

1972. Extremitas proximalis femoris, collum femoris, facies medialis, impressio insertio m. iliofemoralis [m. pubo-ischio-femoralis] internus, forma:

a. indistinct;

b. distinct, typically orbiculate.

Note.—See: Hutchinson (2001b: appendix 1, character 11).

1973. Extremitas proximalis femoris, collum femoris, facies ventralis, pori et striae pneumaticae, numerus per area (**ordered**):

a. absent; **b.** sparse;

c. numerous.

Note.—Basal polarity to be determined with nonavian Theropoda.

1974. Extremitas proximalis femoris, collum femoris, facies articularis antitrochanterica, immediately distal to margo caudalis, situs centralis, foramen (rarely foramina) neurovascularia, status:

a. present; **b.** absent;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—Extremely conservative, apparent counterpart to distal foramina neurovascularia within fossa poplitea, subject to minor variation in subdivision (i.e., number of foramina), position, and/or size. See: G. Mayr et al. (2003: appendix 1, character 56); G. Mayr (2004d: appendix I, character 31); G. Mayr (2005a: appendix 1, character 32).

1975. Extremitas proximalis femoris, collum femoris, facies articularis antitrochanterica, margo caudalis, forma:

a. variably discernable, linear jugum, principally defined by concavitas marginis distalis;

b. prominent, often subrectangular cristula, extending beyond facies caudalis;

x. noncomparable (Dinornithiformes).

Note.—See: Hutchinson (2001b).

1976. Extremitas proximalis femoris, facies cranialis corporis, variably medial to crista trochantericus femoris, foramen pneumaticum et/aut pori pneumatici, status:

a. absent; **b.** present.

Note.—See: G. Mayr and Clarke (2003: appendix A, character 98); Dyke and van Tuinen (2004: appendix 1, character 70); G. Mayr (2004a: appendix 1, character 53); G. Mayr (2004d: appendix I, character 31); G. Mayr (2005a: appendix 1, character 32).

Trochantera femoris

Note.—Homologies of variously synonymous "trochanters"—variably prominent, typically cristulate or tumulate eminentia on facies lateralis of extremitas proximalis (rarely corpus) femoris have proven challenging to establish, and the nomenclature is confounded further by uncertainties concerning the musculi involved. The paleocommunity refers to the apparently single trochanter femoris recognized in the ornitho-anatomical literature as the "greater trochanter" in nonavian Theropoda. Uncertainties of merging and homologies, however, rendered a number of characters not amenable to coding for both basal Avialae and Neornithes. The most recent and inclusive of discussions available for these interrelated problems are those by Hutchinson (2001b) and Carrano and Hutchinson (2002), followed below:

- **"Greater trochanter."**—In wider taxonomic contexts (including present study), synonymous with trochanter femoris of Neornithes; distinguished as trochantericus major (**new term**). A reduced caudal jugum (cf. Romer 1956), which in Reptilia comprises a syncline culminating in the "greater trochanter" in Archosauria, apparently commonly interpreted as such by Ostrom (1973). The feature is diagnosable by proximal rima facies articularis femoris, and therefore is not itself a facies articularis. Caudally it is proximate to the "obturator ridge" of Aves (Padian 1986), continuous distally with the linea intermuscularis caudalis. "Greater trochanter" is evidently plesiomorphic for Archosauria, present in Crocodylia and basal Theropoda, but in more-derived taxa becomes less conspicuous with its margo cranialis confluent with the margo caudalis of "lesser trochanter" to form a single, unified "crista trochantericus."

  "Greater trochanter" evidently derives from the insertio m. pubo-ischio-femoralis (in reptilian contexts), synonymous with m. pubo-ischio-femoralis internus "2" among Crocodylia, and mainly m. obturatorius medialis among Aves. Hutchinson (2001b: 178) inferred that insertio m. pubo-ischio-femoralis became unassociated with the progressive loss of the "internal trochanter" and fossa intertrochantericus (**new term**). As the "greater trochanter" became progressively isolated through a graded rotation in coordination with the caput femoris in Aves, insertio m. pubo-ischio-femoralis would have shifted simultaneously from the caudal position present in Crocodylia to a lateral position typical of Aves.

  "Greater trochanter" performs as a pulley for insertion m. pubo-ischio-femoralis thereby enhancing lateral rotation of the moment arm of the muscle. Both mm. pubo-ischio-femoralis externus "1" and "3" underwent substantial reduction or loss in Aves, through which m. pubo-ischio-femoralis exernus "2" (avian m. obturatorius medialis) came to serve as primary insertio among Neornithes, and the tendo for this remaining muscle is often associated with a tuberculum or sulcus on the avian homologue of the "greater trochanter." Insertio m. ischiotrochantericus (synonymous with avian m. ischiofemoralis) is distal to the "greater trochanter" in extant Archosauria (Romer 1923a). Available evidence indicates that impressiones m. pubo-ischio-femoralis externus (avian m. obturatorius medialis), not features indicative of a facies articularis, account for the myological characters of the "greater trochanter" of most archosaurs. The specific area concerned was referred to as the "fossa trochanterica" and "facies articularis trochanterica" by Baumel and Witmer (1993).
- **"Trochanteric shelf."**—In Aves, at least in part, the "trochanteric shelf" is synonymous with impressiones insertiorum mm. iliofemoralis externus (laterally) et caudalis (craniolaterally). A generally conspicuous, curved complex of up to four "shelflike" features on facies lateralis of extremitas proximalis ossis femoris, that originated among Dinosauria and ultimately replaced evolutionarily by avialian "trochanters," gave rise to: (**a**) a proximal depression, (**b**) the "lesser trochanter" (cranial), (**c**) a "groove" (sulcus) passing from the "lesser" and "greater" trochanters to the "shelf," and (**d**) a "lateral intermuscular line." These features evidently compose a homologous character complex among (at least) Theropoda (Hutchinson 2001b). In Neornithes, the complex is represented by: (**a**) impressio insertii m. iliofemoralis externus (small lateral edge), and (**b**) impressio insertii m. iliotrochantericus caudalis (craniolateral rim of the trochanteric crest). Impressiones origiorum mm. femorotibiales externus et internus are immediately distal to the "shelf" in Aves.
- **"Posterior trochanter."**—In Aves, this "trochanter" represents tuberculum insertii m. ischiofemoralis. Prominent in basal Maniraptora but progressively reduced to tuberositates or impressiones among Neornithes, the avian homologue(s) of the "posterior trochanter" primarily manifest(s) margo distalis impressionis insertii m. ischiofemoralis (synonymous with m. ischiotrochantericus of other Maniraptora). This "trochanter" is caudolateral to the "lesser trochanter" and proximal to the "fourth trochanter" in *Dromaeosaurus* and *Troödon*.
- **"Lesser (anterior, minor) trochanter."**—In Aves this feature represents cristula (vestigialis) insertionis m. iliotrochantericus caudalis (**new term**). Intimately associated and structurally a subpart of the "trochanteric shelf" (Ostrom 1976a; Gauthier 1986; Sereno 1999; Holtz 2000 [1998]), this dis-

tinctly conformed feature is associated with impressio insertii m. iliotrochantericus caudalis (Hutchinson 2001b), which evidently shifted from its plesiomorphic, distal position to an apomorphic, proximal position characteristic of Neornithes (A. D. Walker 1977; Rowe 1986). The "lesser trochanter" is variably distal to the "greater trochanter."

- **"Accessory trochanter."**~~In~~ Aves, this trochanter represents impressiones (tuberculae) insertiorum mm. iliotrochantericus medius et cranialis (**new term**). Originating as a distal expansion of the "lesser trochanter" within Tetanurae (Makovicky and Sues 1998), the feature underwent progressive reduction through Eumaniraptora to a rudimentum (tuberositas or impressio) on facies craniolateralis of extremitas proximalis femoris, connected by a sulcus to margo cranialis cristae trochantericus femoris (Hutchinson 2001b). This feature represents the tuberculum(ae) or impressio(nes) insertionis m. pubo-ischio-femoralis internus "2" (reptilian nomenclature), or the apomorphic homologue associated with mm. iliotrochantericus medius et cranialis of Aves. "Accessory trochanter" amounts essentially to a distally located torus of the "lesser trochanter."
- **"Fourth trochanter."—**Absent in Aves, but impressio insertionis m. iliofemoralis internus on collum femoris is sometimes confused with this structure, this trochanter is cited frequently in the literature describing Mesozoic Theropoda. One of two ancestral "trochanters" of the Reptilia, "fourth trochanter," was used by Hutchinson (2001b) in reference to tuberculum insertionis m. caudofemoralis longus of some Archosauromorpha (W. K. Gregory and Camp 1918; Gauthier et al. 1988; Sereno 1991a: appendix, ingroup-clades, character 35), which (where present) is proximal to the "adductor ridge" (crista epicondyli medialis of Aves) and extends distad to margo proximalis condyli medialis femoris. Crista supracondylaris medialis marks margines mediales insertiorum mm. puboischiofemoralis lateralis and margines mediales origii mm. femorotibiales intermedius et medialis in Aves (Gauthier et al. 1988; Hutchinson 2001b).
- **"Internal trochanter."—**Also evidently absent in Aves, further compromised by uncertain homology among other Reptilia. One of two plesiomorphic "trochanters" of the Reptilia, this feature is homologous to the "trochanter major" of Chelonia, "internal trochanter" of Lepidosauria, absent in Archosauria (Romer 1956; Gauthier et al. 1988). One of three main components of the "ventral ridge system" (Romer 1956), this "trochanter" also includes the "posterior ridge" (nonavian homologue of "greater trochanter") and the "intertrochanteric fossa" (merely the comparatively depressed surface separating the proximal "trochanters").

1977. Extremitas proximalis femoris, trochanter (cranialis) femoris (cf. "greater trochanter"), status et forma:

a. essentially absent, confluent with caput femoris;

b. present, separated from caput femoris by a fissura or depressio.

Note.—See: Andors (1992: table 1, character 4), regarding distinctness of constriction; Novas (1992: character 11); Holtz (1994a: appendix 1, character 58); Novas (1994 [1993]: appendix, character 19, part); Forster et al. (1998: supplement, character 97); Xu et al. (1999b: character 27); Holtz (2000 [1998]: appendix I, character 332); Xu et al. (2000: supplement, character 53); Chiappe (2001a: appendix 1, character 137); Chiappe (2002: appendix 20.2, character 137); Rauhut (2003: character 194).

1978. Extremitas proximalis femoris, trochanter (cranialis) femoris, crista trochantericus, forma (**unordered**):

a. indistinct, crista obsolete, facies lateralis rounded, and craniocaudal depth subequal to that of caput;

b. distinct but comparatively modest, facies lateralis subrectangular in aspect but lacking notable crista and craniocaudal depth minimally greater than caput;

c. moderately developed, crista trochantericus moderately well developed craniad and/or proximad, moderately deeper craniocaudad than caput;

d. very prominent, crista trochantericus conspicuously elevated dorsad (proximad) and craniad, typically subtended by concavitates subcristulares (**new term**) or extensively concave facies articularis antitrochantericus (especially fossa trochanteris), and element substantially deeper craniocaudad than caput.

Note.—Considered comparable herein where "greater" and "lesser" trochanters merged to form unified crista trochantericus (Hutchinson 2001b). See: Livezey (1986: appendix 1, character 52); Siegel-Causey (1988: character 128); Livezey (1995a: appendix 1, character 9); Livezey (1995b: appendix 1, character 15); Livezey (1995c: appendix II, character 25); Livezey (1996a: appendix 1, character 68); Livezey (1998b: appendix A, characters 301–303, part); Chu (1998: appendix 1, character 110); Hutchinson (2001b); G. Mayr (2002a: legend fig. 9, node 1, character 2); G. Mayr and Clarke (2003: appendix A, character 97); Dyke and van Tuinen (2004: appendix 1, character 69); Murray and Vickers-Rich (2004: table 9, character 10; fig. 140A).

1979. Extremitas proximalis femoris, trochanter (cranialis) femoris (cf. "greater trochanter"), facies lateralis, margo cranialis, area tuberculata tendinorum insertii mm. iliotrochantericae, status:

a. absent; **b.** present;
x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—State in *Steatornis* unique in polyfacetate aspect of pars cranialis of the fossa trochanteris subtending the facet described above.

1980. Extremitas proximalis femoris, trochanter (cranialis) femoris (cf. "greater trochanter"), facies caudalis, margo lateralis, situs (tumulus aut impressio) insertii m. obturatorius lateralis (externus aut caudalis), forma generalis (**ordered**):
a. prominent tumulus;
b. moderately large boss;
c. variably discernable impressio;
x. noncomparable (Dinornithiformes).

Note.—See: Feduccia and Olson (1982: fig. 13); Hutchinson (2001b).

1981. Extremitas proximalis femoris, trochanter (cranialis) femoris (cf. "greater trochanter"), facies caudalis, margo lateralis, situs insertii (tumulus aut impressio) m. obturatorius lateralis (externus aut caudalis), impressio expansive and moderately deep and occupying much of facies caudalis extremitis proximalis femoris, status:
a. absent; **b.** present;
x. noncomparable (Aepyornithiformes, Dinornithiformes).

1982. Extremitas proximalis femoris, trochanter (cranialis) femoris (cf. "posterior trochanter" and "lateral ridge"), status et forma (**unordered**):
a. present, indistinct impressiones musculorum;
b. present, prominent jugum aut pluteum;
c. absent, not distinct from caput femoris.

Note.—See: Norell and Makovicky (1999); Norell and Clarke (2001: appendix I, character 169), treated similarly by J. A. Clarke (2002: appendix I, character 170), J. A. Clarke and Norell (2002: appendix 2, character 170), and J. A. Clarke (2004: appendix 1, character 170); Hutchinson (2001b); Sereno (2001: table 1, character 8), regarding Alvarezsauridae; Maryanska et al. (2002: appendix 1, characters 173–174), in reference to Oviraptorosauria; Zhou and Zhang (2002: appendix III, characters 169–170); Ji et al. (2005: supplement, part I, characters 169–170).

1983. Extremitas proximalis femoris, trochanter femoris *sensu lato* (cf. "lesser trochanter" or "anterior trochanter")—i.e., tuberculum insertii tendinis m. iliofemoralis of Crocodylia, or tuberculae tendinorum insertii mm. iliofemoralis externus et iliotrochantericus caudalis of Aves)—relative to caput femoris et/aut impressio insertii m. pubo-ischiofemoralis externus of Crocodylia or m. obturatorius medialis of Aves (cf. "greater trochanter"), status et forma (**unordered**):
a. absent; **b.** present, small tuberculum;
c. present, small spina; **d.** present, lamina;
e. present, appressed to "greater trochanter" et/aut caput;
f. present, united imperceptably with "greater trochanter" et/aut caput, forming crista trochantericus.

Note.—See: Ostrom (1976a); Tarsitano and Hecht (1980); Gauthier (1986: text characters 49 and 82); Currie and Russell (1988); Andors (1992: table 1, character 3); Novas (1992: characters 3 and 16); Russell and Dong (1994a [1993a]: table 2, character 54); Russell and Dong (1994b [1993b]: list B, character 15); Perle et al. (1993); Chiappe and Calvo (1994: appendix I, character 57); Holtz (1994a: appendix 1, characters 77, 92, and 117); Chiappe (1995b: character 57); Sanz et al. (1995, 1997: character 55); Chiappe (1996b: character 52); Chiappe et al. (1996: appendix 1, character 51); Sereno et al. (1996: footnote 45, character 13); Carroll (1997: 312); Novas (1997: appendix, character 58), identically by Novas and Puerta (1997); Sues (1997: appendix 1, character 43); Chiappe et al. (1998: character 78); Forster et al. (1998: supplement, character 91); J. D. Harris (1998: appendix 2, characters 123 and 125); Ji et al. (1998: supplement, character 78); Chatterjee (1999: appendix II, character 76); Xu et al. (1999a: characters 72–73, and 75); Xu et al. (1999b: character 67); Azuma and Currie (2000: appendix 1, character 43); Currie and Carpenter (2000: appendix 1, characters 99 and 101); Holtz (2000 [1998]: appendix I, characters 334–336); Norell et al. (2000: appendix 1, character 33); Xu et al. (2000: supplement, character 51); Chiappe (2001a: appendix 1, character 138); Hutchinson (2001b: appendix 1, characters 3 and 7); Norell and Clarke (2001: appendix I, character 176); Norell et al. (2001: appendix 1, character 183); Chiappe (2002: appendix 20.2, character 138); J. M. Clark et al. (2002a: appendix 2.2, character 185); Maryanska et al. (2002: appendix 1, character 175), in reference to "aliform" condition; Xu (2002: suite II, character 204); Xu et al. (2002a: supplement, characters 148 [distinctness] and 149 [shape]); Brochu (2003); Rauhut (2003: character 198); Hwang et al. (2004: supplement, character 182); Xu and Norell (2004: supplement, character 182).

1984. Extremitas proximalis femoris, trochanter femoris *sensu lato* (cf. "lesser trochanter" or "anterior trochanter")—tuberculum insertii tendinis m. iliofemoralis of Crocodylia or tuberculae tendinorum insertii mm. iliofemoralis externus et iliotrochantericus caudalis of Aves)—distinctness from "greater trochanter" (impressio insertii m. pubo-ischiofemoralis externus of Crocodylia or impressio m. obturatorius medialis of Aves), forma:
a. separate, by incisura;
b. coalesced, forming single crista trochantericus;
x. noncomparable (Crocodylia, *Euparkeria*).

Note.—This character is partly redundant with preceding, an explicit attempt to partition one aspect (distinctness between trochanters). See: Holtz (1994a: appendix 1, character 77); Norell and Clarke (2001: appendix I, character 171), similarly treated by J. A. Clarke (2002: appendix I, character 171), J. A. Clarke and Norell (2002: appendix 2, character 171), and J. A. Clarke (2004: appendix 1, character 171); Makovicky and Norell (2004: character 215) and Xu and Norell (2004: supplement, character 215), regarding "vertical ridge on lesser trochanter"; Ji et al. (2005: supplement, part I, character 171).

1985. Extremitas proximalis femoris, trochanter femoris *sensu lato* (cf. "lesser trochanter" or "anterior trochanter")—i.e., tuberculum insertii tendinis m. iliofemoralis in Crocodylia, or tuberculae tendinorum insertii mm. iliofemoralis externus et iliotrochantericus caudalis in Aves)—relative to caput femoris et "greater" trochanter, situs proximodistalis (**ordered**):

a. "lesser" trochanter equal to margo distalis of caput;

b. "lesser" trochanter proximal to caput but distal to "greater trochanter";

c. "lesser" trochanter equally or more proximal to "greater trochanter";

x. noncomparable by absence or indiscernability (Crocodylia, *Euparkeria*).

Note.—See: Gauthier (1986); Holtz (1994a: appendix 1, character 92); Sues (1997: appendix 1, character 42), with respect to "distinctness of greater (posterior) trochanter . . . from proximal head"; J. D. Harris (1998: appendix 2, character 124); Makovicky and Sues (1998: appendix 1, character 86), regarding proximodistal position relative to caput femoris; Currie and Carpenter (2000: appendix 1, character 100); Holtz (2000 [1998]: appendix I, character 336); Rauhut (2003: character 199).

1986. Extremitas proximalis femoris, trochanter femoris *sensu lato* (cf. "lesser trochanter" or "anterior trochanter")—i.e., tuberculum insertii tendinis m. iliofemoralis in Crocodylia, or tuberculae tendinorum insertii mm. iliofemoralis externus et iliotrochantericus caudalis in Aves)—relative to "posterior trochanter," situs proximodistalis:

a. well distal; **b.** approximately equal;

x. noncomparable by absence or indiscernability (Crocodylia, *Euparkeria*) or synostosis with crista trochantericus (Pygostylia).

Note.—*A posteriori*, closely related to proximity between "lesser" and "greater trochanters." See: Makovicky and Sues (1998: appendix 1, character 85); Norell et al. (2001: appendix 1, character 182); J. M. Clark et al. (2002a: appendix 2.2, character 184); Maryanska et al. (2002: appendix 1, character 177); Xu (2002: suite II, character 203); Hwang et al. (2004: supplement, character 181); Xu and Norell (2004: supplement, character 181).

1987. Extremitas proximalis femoris, trochanter femoris *sensu lato*, (cf. "trochanteric shelf"), status et forma (**unordered**):

a. absent or indistinct;

b. present, prominent crista;

c. present, small tuberculum;

d. present, jugum spinosa;

e. present, modest impressio.

Note.—See: Hutchinson (2001b: appendix 1, character 6); perhaps optimal to incorporate with previous character. See: Gauthier (1986: text character 49); Novas (1992: characters 2 and 17); Pérez-Moreno et al. (1993); Novas (1994 [1993]: appendix, character 33); Chiappe (1995b: character 57); Sanz et al. (1995, 1997: character 55); Chiappe (1996b: character 52); Novas (1996: appendix, characters M22 and 57); Azuma and Currie (2000: appendix 1, character 51); Holtz (2000 [1998]: appendix I, character 338).

1988. Extremitas proximalis femoris, trochanter femoris *sensu lato* (cf. "posterior trochanter"), tuberculum insertii tendinis m. ischiofemoralis (**new term**), status et forma (**unordered**):

a. absent or indistinct;

b. present, prominent pluteus or tumulus;

c. present, impressio vestigialium.

Note.—See: Ostrom (1969, 1976a); Gauthier (1986: text character 64); Chiappe and Calvo (1994: appendix I, character 61; appendix II, character 14); Russell and Dong (1994b [1993b]: list A, character 12); Chiappe (1995b: character 61); Sanz et al. (1995, 1997: character 59); Chiappe (1996b: character 56); Chiappe et al. (1996: appendix 1, character 55); Novas (1997: appendix, character 30); Novas and Puerta (1997), see identical characters in Novas (1997); Chiappe et al. (1998: character 79); Chiappe (2001a: appendix 1, character 139); Hutchinson (2001b: appendix 1, character 8), perhaps best to incorporate with following character emphasizing position; Norell and Clarke (2001: appendix I, character 150); Norell et al. (2001: appendix 1, character 184); Chiappe (2002: appendix 20.2, character 139); Chiappe and Walker (2002: appendix 11.1, character 27); J. M. Clark et al. (2002a: appendix 2.2, character 186); Xu (2002: suite II, character 205); Xu et al. (2002a: supplement, character 150), in which the erroneous reference of Gauthier (1986: text character 64) of this feature to the "greater trochanter" was replaced by the terminology advocated by Ostrom (1969, 1990), and which combined taxa having trochanter "absent" and those in which it is impressio; Hwang et al. (2004: supplement, character 183); Xu and Norell (2004: supplement, character 183). Taxa other than those treated by Hutchinson (2001b) with respect to femoral "trochanters" inadequately understood, especially those included by Holtz (2000 [1998]).

1989. Extremitas proximalis femoris, trochanter femoris *sensu lato* (cf. "posterior trochanter")—tuberculum insertii tendinis m. ischiofemoralis—relative to (in part) impressiones tendinorum insertii mm. iliofemoralis externus (laterally) et caudalis (craniolaterally) or "trochanteric crest or ridge," status et situs (**ordered**):

a. absent; **b.** present, cranial;
c. present, centered.

Note.—Provisional myological homology of osteological feature based on Romer (1923a), McGowan (1979), and Ostrom (1976a). See: Sanz et al. (1995, 1997: character 59); Novas (1996: appendix, character 28); Chiappe et al. (1998: character 79); Ji et al. (1998: supplement, character 79); Forster et al. (1998: supplement, character 93); Xu et al. (1999b: character 27); Holtz (2000 [1998]); Xu et al. (2000: supplement, character 52); Chiappe (2001a: appendix 1, character 139); Hutchinson (2001b); Chiappe (2002: appendix 20.2, character 139); Rauhut (2003: character 200).

1990. Extremitas proximalis femoris, trochanter femoris *sensu lato* (cf. "accessory trochanter")—impressiones (area tuberculata) tendinorum insertii mm. iliotrochantericus medius et cranialis *fide* Hutchinson (2001b)—status:

a. absent or vestigium; **b.** present.

Note.—See: Makovicky and Sues (1998); Hutchinson (2001b: appendix 1, character 10); Norell et al. (2001: appendix 1, character 186); J. M. Clark et al. (2002a: appendix 2.2, character 188); Xu (2002: suite II, character 207); Xu et al. (2002a: supplement, character 152); Hwang et al. (2004: supplement, character 185); Xu and Norell (2004: supplement, character 185).

1991. Extremitas proximalis femoris, trochanter femoris *sensu lato* (cf. "accessory trochanter")—i.e., impressiones (area tuberculata) tendinorum insertii mm. iliotrochantericus medius et cranialis or m. pubo-ischio-femoralis internus (part)—forma (**unordered**):

a. one or two impressio(nes) on facies lateralis;
b. "accessory trochanter";
c. fovea or sulcus on crista trochantericus.

Note.—See: Holtz (2000 [1998]); Hutchinson (2001b: appendix 1, character 9), regarding avian homologies of "accessory trochanter" of nonavian Archosauria.

1992. Extremitas proximalis femoris, trochanter femoris *sensu lato* (cf. "fourth trochanter")—i.e., tuberculum insertii tendinis m. caudofemoralis longus of Crocodylia or tuberculum insertii tendinis m. caudofemoralis partis caudalis of Aves—status:

a. present;
b. vestigial (cristula or linea) or absent.

Note.—See: Tarsitano and Hecht (1980); Gauthier (1986: text characters 63 and 83); Sereno (1991a: appendix); Russell and Dong (1994b [1993b]: list A, character 11; list B, character 16); Holtz (1994a: appendix 1, character 35); Chiappe (1996b); Novas (1996: appendix, character 3); Sereno et al. (1996: footnote 45, character 62); Carroll (1997: 312); Novas (1997: appendix, character 3); Novas and Puerta (1997), see identical characters in Novas (1997); Sues (1997: appendix 1, character 44); Forster et al. (1998: supplement, character 92); J. D. Harris (1998: appendix 2, character 126); Makovicky and Sues (1998: appendix 1, character 87); J. A. Wilson and Sereno (1998: appendix, character 11), pertaining to Sauropoda; Xu et al. (1999a: character 74); Xu et al. (1999b: character 68); Azuma and Currie (2000: appendix 1, character 45); Currie and Carpenter (2000: appendix 1, character 102); Holtz (2000 [1998]: appendix I, character 337); Hutchinson (2001b: appendix 1, character 4), regarding "fourth trochanter"; Norell et al. (2001: appendix 1, character 185); J. M. Clark et al. (2002a: appendix 2.2, character 187); Xu (2002: suite II, character 206); Xu et al. (2002a: supplement, character 151); Rauhut (2003: character 201); Hwang et al. (2004: supplement, character 184); Xu and Norell (2004: supplement, character 184).

J. R. Hutchinson (2001b, pers. comm.) broadly characterized the synclinal transformation of this feature as (*i*) a rounded crista or boss (e.g., Crocodylia, *Dilophosaurus*), to (*ii*) a small spina compressed to the corpus femoris (e.g., Ornithurae), to (*iii*) a mere impressio muscularis (e.g., Aves).

1993. Extremitas proximalis femoris, trochanter femoris *sensu lato* (cf. "fourth trochanter")—i.e., tuberculum insertii tendinis m. caudofemoralis longus of Crocodylia or tuberculum insertii tendinis m. caudofemoralis (pars caudalis) of Aves—forma:

a. poorly developed, an impressio;
b. well developed, a crista or elongate tuberculum.

Note.—See: Hutchinson (2001b: appendix 1, character 5, excluding third state); Maryanska et al. (2002: appendix 1, character 178).

1994. Extremitas proximalis femoris, trochanter femoris, crista trochanteris, facies caudalis, distal to facies articularis antitrochantericus and medial to impressiones obturatoriae, foramen et/aut recessus pneumaticum, status:

a. absent or only minute foramina neurovascularia;
b. present.

Note.—Assessment excludes mere pori pneumatici or foramina neurovascularia. See: Livezey (1998b: appendix A, character 302, part); Hughes (2000: appendix 2, character 77), after Seibel (1988:

character FE 2); Dyke and Gulas (2002: appendix 1, character 40); G. Mayr (2004a: appendix 1, character 52).

1995. Extremitas proximalis femoris, trochanter (cranialis) femoris (cf. "greater trochanter"), crista trochantericus, forma generalis (**ordered**):
a. area tuberculata tendinis;
b. eminentia or boss; **c.** crista verae.
Note.—See: Gauthier (1986); J. D. Harris (1998: appendix 2, character 122); Azuma and Currie (2000: appendix 1, character 46); Currie and Carpenter (2000: appendix 1, character 98); Holtz (2000 [1998]: appendix I, character 333), distinguishing only "rugosity" from "moundlike eminence"; Hughes (2000: appendix 2, characters 79–80), after Seibel (1988: character FE 4); Hutchinson (2001b: appendix I, character 3, third state only); Rauhut (2003: character 196).

1996. Extremitas proximalis femoris, trochanter (cranialis) femoris (cf. "greater trochanter"), crista trochantericus, pronounced lateromedial curvature or convexity (proximal perspective), status:
a. absent;
b. present, principally a reflection of craniomedial extension of crista.

1997. Extremitas proximalis femoris, trochanter femoris (cf. "greater trochanter"), fossa trochanteris et crista trochantericus, pars dorsalis (proximalis) cristae (**new term**), facies medialis, forma (**ordered**):
a. distinctly concave, forming typical fossa trochanteris;
b. slightly concave or essentially planar, merging indistinctly with facies articularis antitrochanterica;
c. convex, virtually continuous with facies articularis antitrochanterica or margo lateralis cristae rounded.
Note.—See: Bledsoe (1988: appendix, characters 43–44) and K. Lee et al. (1997: appendix 1, characters 42–43), assessing dorsal (proximal) extent of crista trochantericus relative to (implicitly concave) fossa trochanteris; Hope (2002: 367), in which "convexity" of "iliac fossa" was given as synapomorphy for Pelecaniformes.

Trochanter femoris, impressiones musculorum trochanteris

Note.—Among Neornithes, trochanter femoris, facies lateralis displays to variable degrees the following impressiones insertii (lateral perspective): mm. obturatorius medialis (regio dorsocaudalis trochanteris), iliotrochantericus caudalis (large, regio dorsomedialis trochanteris), iliotrochantericus cranialis (regio ventrocranialis trochanteris), ischiofemoralis (regio ventrocaudalis trochanteris), et iliofemoralis externus (regio ventromedialis trochanteris). These regiones trochanteris can be complicated further by impressiones ligamentosae.

1998. Extremitas proximalis femoris, trochanter femoris, situs insertii m. iliotrochantericus caudalis, forma (**unordered**):
a. deep, irregularly shaped fossa;
b. variably elevated, broadly crescentiform impressio;
c. broad, slightly elevated, irregular area.
Note.—See: Hutchinson (2001b).

1999. Extremitas proximalis femoris, trochanter femoris, situs insertii m. iliotrochantericus caudalis:
a. regio proximo*medianis* (comparatively cranial) of facies lateralis;
b. regio (apex) proximo*cranialis* of facies lateralis.
Note.—See: Hutchinson (2001b).

Corpus femoris

2000. Corpus femoris (lateral perspective), curvatura craniocaudalis:
a. strongly cranially convex (rarely bi-sigmoidal), including pars proximalis;
b. moderately to slightly cranially convex (rarely sublinear), curvature typically most pronounced in pars distalis.
Note.—See: Cracraft (1982: series 4, character 4); Gauthier (1986: text character 29), distinguishing *sigmoidal* from *monotonically curved*; Livezey (1986: appendix 1, character 55); Cracraft (1988: series XI, character 7), regarding "gaviomorphae"; Houde (1988: table 27, character 47); Benton (1990a: 21), considered cranial convexity of the femur synapomorphic of Theropoda; Sereno (1991a: appendix, ingroup-clades character 26), regarding basal Archosauria; Andors (1992: table 1, character 1, part); Livezey (1995a: appendix 1, character 10); Livezey (1995b: appendix 1, character 16); Livezey (1995c: appendix II, character 27); Livezey (1996b: appendix 1, character 36); Livezey (1996c: character 9); Livezey (1998b: appendix A, character 304); Holtz (2000 [1998]: appendix I, character 329), following Gauthier (1986); Hutchinson (2001b: appendix 1, character 20).

2001. Corpus femoris, "cortical" thickness of externum (**ordered**):
a. great, ratio of thickness divided by diameter corporis greater than 0.3;
b. moderate, ratio of thickness divided by diameter corporis 0.2–0.3;
c. small, ratio of thickness divided by diameter corporis less than 0.2.
Note.—See: Hutchinson (2001b: appendix 1, character 21).

2002. Corpus femoris, forma areae transversa (**unordered**):

a. subcircular;

b. oval, mediolaterally compressed;

c. distinctly oval, craniocaudally compressed.

Note.—See: J. A. Wilson and Sereno (1998: appendix, character 10) regarding Sauropoda.

2003. Corpus femoris, facies caudalis, lineae intermusculares, status, prominence, conformation, and inclusion of central eminentia (**ordered**):

a. lineae musculares prominent, bifurcatio lineae proximally positioned, eminentia (impressio muscularis linearis) positioned medially et proximally;

b. lineae musculares prominent, eminentia (impressio muscularis linearis) et bifurcatio lineae positioned centrally et proximally;

c. lineae musculares, bifurcatio lineae et eminentia (impressio muscularis linearis) indistinct.

Note.—See: Livezey (1986: appendix 1, characters 57–58, and 60); Livezey (1996b: appendix 1, character 37); Livezey (1995c: appendix II, characters 29–30); Ericson (1997: table 2, character 42).

2004. Corpus femoris, facies caudalis, lineae intermusculares, delimitation of subtriangular planum (depressio) suprapoplitea (**new term**) between lineae intermusculares distal to bifurcatio linea, status:

a. absent; **b.** present;

x. noncomparable (Dinornithiformes).

Note.—See: Holdaway (1991: appendix 5.1, character 161).

2005. Corpus femoris, facies cranialis, linea intermuscularis cranialis, pars mediodistalis (**new term**), status:

a. present, prominent, extending at least one-fourth of length of corpus;

b. absent or reduced.

Note.—See: Novas (1997: appendix, character 59), with respect to "adductor fossa and associated anterodistal crista of distal femur"; Novas and Puerta (1997), see identical characters in Novas (1997); Forster et al. (1998: supplement, character 95); Holtz (2000 [1998]: appendix I, character 343), with respect to "adductor fossa and associated caudodistal crest of distal femur"; Azuma and Currie (2000: appendix 1, character 49), in reference to "mediodistal crest." As interpreted by Hutchinson (2001b: 17), these misleadingly named features refer to distal and medial termina of the linea intermuscularis cranialis, and do not pertain to any adductor muscles, but instead probably mark origiones of the variously subdivided m. femorotibialis internus complex.

2006. Corpus femoris, facies cranialis, linea intermuscularis cranialis, status:

a. present, comparatively distinct;

b. absent or indistinct.

Note.—See: Holdaway (1991: appendix 5.1, character 161); Hutchinson (2001b: appendix 1, character 13), perhaps synapomorphic of the "Archosauriformes." Margo medialis of this linea proximally separates the origiones mm. femorotibiales medialis et lateralis; distally it is associated with the m. femorotibialis lateralis, notably a theropod novelty, caput distale of this muscle (McKitrick 1991a; Hutchinson 2001b).

Adjacent and variably involved with this character is the linea intermuscularis caudalis (Hutchinson 2001b: character 15)—bounding craniolaterally origiones mm. femorotibiales medialis et lateralis and caudomedially insertiones mm. puboischiofemorales medialis et lateralis—that evidently is synapomorphic for the Archosauriformes or a slightly less inclusive clade (in either case the character being of no utility in the present context).

2007. Corpus femoris, facies cranialis, linea intermuscularis cranialis, prominence and typically continuity distad to facies cranialis of condylus lateralis, forming cristula throughout length of element, status:

a. absent; **b.** present.

2008. Corpus femoris, facies cranialis, linea intermuscularis cranialis, distinct impressio or eminentia muscularis, status et forma (**unordered**):

a. absent; **b.** present, irregularly shaped;

c. present, elliptical.

Note.—See: Holtz (2000 [1998]: appendix I, character 339), citing Pérez-Moreno et al. (1993).

2009. Corpus femoris, facies lateralis, linea intermuscularis lateralis (**new term**), status:

a. absent; **b.** present;

x. noncomparable (Neornithes).

Note.—See: Norell et al. (2000: appendix 1, character 34); Hutchinson (2001b: appendix 1, character 14), who followed Norell and Makovicky (1999) in considering this feature a subdivision of origo m. femorotibialis externus (= m. femorotibialis lateralis avium) and other Maniraptoriformes.

Extremitas distalis femoris

Note.—Comparative examination of extremitas distalis femoris of *Mullerornis* revealed it to be substantially smaller than *Aepyornis* but qualitatively identical.

2010. Extremitas distalis femoris, condylus lateralis, trochlea fibularis, crista fibularis condylae (**new term**), proximodistal extent relative to crista tibiofibularis (distal perspective):

a. subequal; **b.** distinctly proximal.

Note.—See: Cracraft (1974: 498, character 2); Novas (1996: appendix, character 17); Bledsoe (1988:

appendix, character 46); K. Lee et al. (1997: appendix 1, character 44).

2011. Extremitas distalis femoris, condylus lateralis, trochlea fibularis, crista fibularis condylae (**new term**), marked reduction relative to crista tibiofibularis (caudal perspective), status et forma angularis:
a. absent;
b. present, crista fibularis subperpendicular to crista tibiofibularis.
Note.—See: Dyke and Gulas (2002: appendix 1, character 39).

2012. Extremitas distalis femoris, condylus lateralis, crista tibiofibularis, distal extent relative to condylus medialis (**ordered**):
a. subequal to condylus medialis;
b. moderately but consistently distal to condylus medialis;
c. distinctly and (typically) significantly distal to condylus medialis.
Note.—See: Cracraft (1974: 498, character 2); Livezey (1986: appendix 1, character 53); Novas (1996: appendix, character 17); Bledsoe (1988: appendix, character 46); K. Lee et al. (1997: appendix 1, character 44).

2013. Extremitas distalis femoris, condylus lateralis, forma marginis distalis:
a. rounded, not projecting distad;
b. conical, projecting distad.
Note.—See: Andors (1992: table 1, character 7); Chiappe and Calvo (1994: appendix II, character 15), listed as synapomorphy of Enantiornithes; Chiappe et al. (1998: character 80); Ji et al. (1998: supplement, character 80); Chiappe (2001a: appendix 1, character 140); Chiappe (2002: appendix 20.2, character 140).

2014. Extremitas distalis femoris, condylus lateralis, crista tibiofibularis, terminus proximalis on facies cranialis corporis, forma superficialis (**unordered**):
a. strongly convex, prominent well cranial to facies cranialis corporis;
b. moderately convex; **c.** sublinear;
d. concave, especially at proximal extreme;
e. poorly defined, tumulate.
Note.—See: Bledsoe (1988: appendix, character 47); Livezey (1998b: appendix A, character 306).

2015. Extremitas distalis femoris, condylus lateralis, impressio (fovea) tendinis origii m. tibialis cranialis (**new term**), status et forma (**unordered**):
a. absent;
b. present, variably distinct fovea;
c. present, deep fovea;
d. present, moderate or deep sulcus.
Note.—See: Chiappe et al. (1996: appendix 1, character 94), for "fossa for the femoral origin of M. tibialis cranialis"; K. Lee et al. (1997: appendix 1, character 50), in reference to "pit for the tibialis anticus"; Chiappe (2001a: appendix 1, character 144); Chiappe (2002: appendix 20.2, character 144).

2016. Extremitas distalis femoris, condylus lateralis, impressio ligamenti cruciati caudalis, status:
a. absent; **b.** present.
Note.—Feature often difficult to discern, being a variably expansive, sublinear to subcircular, shallow impressio on facies medialis of caudal terminus of crista tibiofibularis of condylus lateralis. See: J. D. Harris (1998: appendix 2, character 128), cited as evident in distal view; Azuma and Currie (2000: appendix 1, character 50), attributed to fossa poplitea; Currie and Carpenter (2000: appendix 1, character 104), describing the "ridge for cruciate ligaments" as being in "flexor groove."

2017. Extremitas distalis femoris, condylus lateralis, trochlea fibularis, "gaviomorph" specialization in which (*i*) cristae tibiofibularis et fibularis are of subequal caudal prominence, and (*ii*) entire trochlea of greater caudal prominence and lateromedial divergence from corpus than condylus medialis (distal and caudal perspectives), status:
a. absent; **b.** present.
Note.—See: Cracraft (1982: series 2, character 4); Cracraft (1985: character 51); Cracraft (1988: series XI, character 6); Rowe and Gauthier (1990); Holtz (2000 [1998]: appendix I, character 342), for "groove in lateral condyle of femur," citing Rowe and Gauthier (1990).

2018. Extremitas distalis femoris, condyli lateralis et medialis (and associated forma generalis distalis), forma:
a. condyli craniocaudally broad, facies lateralis condylae comparatively planar;
b. condyli rounded, extremitas distalis narrowed and well rounded.
Note.—See: Cracraft (1974: 498, character 2, part); Bledsoe (1988: appendix, character 48); K. Lee et al. (1997: appendix 1, character 45); Novas (1997: appendix, character 18); Novas and Puerta (1997), identically by Novas (1997); Holtz (2000 [1998]: appendix I, character 342), dichotomized "groove in lateral condyle of femur," citing Rowe and Gauthier (1990); Norell and Clarke (2001: appendix I, character 175), treated similarly by J. A. Clarke (2002: appendix I, character 175), J. A. Clarke and Norell (2002: appendix 2, character 175), and J. A. Clarke (2004: appendix 1, character 175); Rauhut (2003: character 203); Ji et al. (2005: supplement, part I, character 175).

2019. Extremitas distalis femoris, condylus lateralis, trochlea fibularis, terminus proximocaudalis trochlearis, fovea trochlearis (**new term**), forma (**ordered**):

a. trochlea terminates as sulcus that is comparatively uniform or monotonically divergent throughout;

b. trochlea terminates as sulcus distinguished by marked widening or divergence of delimiting cristae;

c. trochlea terminates in fovea trochlearis (**new term**), amplified by enclosed, terminal depressio in expanded area;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

2020. Extremitas distalis femoris, condylus lateralis, caudal prominence relative to axis proximodistalis femoris, status:

a. absent; **b.** present.

Note.—Of questionable utility. See: Cracraft (1974: 498, character 2, part); Sanz et al. (1995, 1997: character 78); K. Lee et al. (1997: appendix 1, character 47); Chiappe (2001a: appendix 1, character 145); Norell and Clarke (2001: appendix I, character 174), in reference to such with respect to margo lateralis condyli, treated similarly by J. A. Clarke (2002: appendix I, character 174), J. A. Clarke and Norell (2002: appendix 2, character 174), and J. A. Clarke (2004: appendix 1, character 174); Chiappe (2002: appendix 20.2, character 145); Chiappe and Walker (2002: appendix 11.1, character 28); Zhou and Zhang (2002: appendix III, character 174); Ji et al. (2005: supplement, part I, character 174).

2021. Extremitas distalis femoris, condylus lateralis, crista tibiofibularis, status:

a. absent; **b.** present.

Note.—See: Gauthier (1986: 13, synapomorphy of Ornithurae); Chiappe and Calvo (1994: appendix I, character 60); Chiappe (1995b: character 60); Sanz et al. (1995, 1997: character 58); Chiappe (1996b: character 55); Chiappe et al. (1996: appendix 1, character 54); Fuss (1996); Hou et al. (1996: character 24, in reference to "posterodorsal crest" of "outer distal condyle of femur"); Chiappe et al. (1998: character 82); Ji et al. (1998: supplement, character 82); Forster et al. (1998: supplement, character 96); Chiappe (2001a: appendix 1, character 143); Chiappe (2002: appendix 20.2, character 143).

2022. Extremitas distalis femoris, condylus lateralis, crista tibiofibularis, lateral prominence (distal perspective) with respect to planum of epicondylus lateralis, angulus:

a. minor, subdiagonal;

b. great, diagonal to subperpendicular;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

2023. Extremitas distalis femoris, facies caudalis, condylus lateralis, crista tibiofibularis, terminus proximocaudalis, forma:

a. not prominent, variably rounded;

b. elevated, with distinct apex;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

2024. Extremitas distalis femoris, condylus lateralis, crista fibularis, virtually linear form and caudally regressed position relative to crista tibiofibularis, exposing much of sulcus intercondylaris (lateral perspective), status:

a. absent, crista fibularis extending caudad somewhat in parallel with crista tibiofibularis;

b. present, crista fibularis *reduced* and *linear* in margo, largely exposing facies lateralis of trochlea fibularis.

2025. Extremitas distalis femoris, sulcus intercondylaris, status et forma proximodistalis (**ordered**):

a. absent or rudimentary;

b. present, shallow, limited to regio distalis;

c. present, variably deep, circum-delimiting extremitas distalis to regio dorsocaudalis.

Note.—Intractable variation in prominence of impressio ligamentum cruciati cranialis not included in assessments. See: J. D. Harris (1998: appendix 2, character 127); Chatterjee (1999: appendix II, character 78); Azuma and Currie (2000: appendix 1, character 44); Currie and Carpenter (2000: appendix 1, character 103); Chiappe (2001a: appendix 1, character 141); Hutchinson (2001b: appendix 1, character 19); Norell and Clarke (2001: appendix I, character 172), treated similarly by J. A. Clarke (2002: appendix I, character 172), J. A. Clarke and Norell (2002: appendix 2, character 172), and J. A. Clarke (2004: appendix 1, character 172); Chiappe (2002: appendix 20.2, character 141); Vickers-Rich et al. (2002), concerning *Avimimus*; Zhou and Zhang (2002: appendix III, character 172); Murray and Vickers-Rich (2004: table 9, character 13); Ji et al. (2005: supplement, part I, character 172).

2026. Extremitas distalis femoris, facies caudalis, incisura (sulcus) intercondylaris caudalis (**new term**), dorsoventral depth (relative to lateromedial width):

a. shallow and wide, margines gradually sloped;

b. deep and narrow, margines subperpendicular to facies caudalis corporis.

2027. Extremitas distalis femoris, facies caudalis (caudal perspective), condylus lateralis, width (lateromedial) relative to that of condylus medialis femoris, forma (**ordered**)

a. lateralis significantly wider;

b. condyli subequal;

c. lateralis significantly narrower, typically by lateral extension of latter.

Note.—Width of condylus lateralis includes both cristae tibiofibularis et fibularis. Combined widths related in part to width and conformation of sulcus intercondylaris caudalis (**new term**).

2028. Extremitas distalis femoris, facies caudalis, condylus lateralis, crista tibiofibularis, caudal extent relative to that of condylus medialis femoris (**ordered**):

a. distinctly greater; **b.** subequal;
c. distinctly less.

2029. Extremitas distalis femoris, condylus lateralis, crista supracondylaris lateralis, tuberculum m. gastrocnemialis lateralis, eminentia:

a. present, modest or prominent;
b. present, vaguely indicated.

Note.—Like the crista supracondylaris lateralis, the tuberculum aut impressio m. gastrocnemialis lateralis varies little among Neornithes. See: G. Mayr (2004d: appendix I, character 30); G. Mayr (2005a: appendix 1, character 31).

2030. Extremitas distalis femoris, condylus medialis (caudal perspective), forma generalis:

a. margo proximalis strongly sloping distally toward lateral terminus, width comparable to that of condylus lateralis;

b. margo proximalis approximately uniformly perpendicular to axis majoris corporis, width significantly greater than that of condylus lateralis in which condylus medialis extends laterad proximate to or in articulation with condylus lateralis.

Note.—See: Ligon (1967: fig. 3); Cracraft (1974: 498, character 3); Novas (1996: appendix, character 15); Bledsoe (1988: appendix, character 50); K. Lee et al. (1997: appendix 1, character 46); Livezey (1998b: appendix A, character 307); also, two aspects of the facies articularis of condylus medialis listed by Kurochkin (1995b: table 1, characters 22–23); Novas (1996: appendix, character 15), who contrasted "transversely narrow and distally convex" with "transversely wide and distally flat" in Alvarezsauridae; Novas (1996: appendix, character 56), with respect to dorsoventral depth; K. Lee et al. (1997: appendix 1, character 49); two aspects of the facies articularis of condylus medialis listed by Kurochkin (1995b: table 1, characters 22–23); Novas (1997: appendix, characters 16 and 57); Novas and Puerta (1997), see identical characters in Novas (1997); Murray and Vickers-Rich (2004: table 9, character 17).

2031. Extremitas distalis femoris (caudal perspective), condylus medialis, terminus lateralis marginis, contact with terminus medialis of condylus lateralis forming lamina at terminus proximocaudalis of sulcus articularis patellaris, status et forma:

a. absent, incisura intercondylaris conserved;
b. present, obstructing atrium distalis of incisura intercondylaris.

Note.—Synonymous and presumably homologous with "complete transverse ridge" between condyli distal to fossa poplitea, absence of which described as permitting continuation of fossa distad to sulcus intercondylaris. In this strict assessment, variants within Neornithes in which this lamina or jugum is distinctly invaginate (e.g., Anseriformes, Tytonidae) are treated as apomorphic, as some occlusion is evident.

See: Perle et al. (1993); Chiappe and Calvo (1994: appendix I, character 59); Chiappe (1995b: character 59); Sanz et al. (1995, 1997: character 57); Chiappe (1996: character 54); Chiappe et al. (1996b: appendix 1, character 53); Novas (1996: appendix, character M17), with respect to proximity of condylae femorales; Chiappe et al. (1998: character 81); Ji et al. (1998: supplement, character 81); Chatterjee (1999: appendix II, character 75); Currie and Carpenter (2000: appendix 1, character 105); Chiappe (2001a: appendix 1, character 142); Hutchinson (2001b: appendix 1, character 18); Norell and Clarke (2001: appendix I, character 176), treated similarly by J. A. Clarke (2002: appendix I, character 176), J. A. Clarke and Norell (2002: appendix 2, character 176), and J. A. Clarke (2004: appendix 1, character 176); Norell et al. (2001: appendix 1, character 188); Chiappe (2002: appendix 20.2, character 142); J. M. Clark et al. (2002a: appendix 2.2, character 190); Vickers-Rich et al. (2002), concerning *Avimimus*; Xu (2002: suite II, character 209); Xu et al. (2002a: supplement, character 154), in reference to fossa poplitea and extremitas distalis femoris being "open distally . . . or closed off distally by contact between distal condyles"; Zhou and Zhang (2002: appendix III, character 176), with respect to closure of fossa by "expansions of condylae"; Hwang et al. (2004: supplement, character 187); Murray and Vickers-Rich (2004: table 9, character 17); Xu and Norell (2004: supplement, character 187); Ji et al. (2005: supplement, part I, character 176).

2032. Extremitas distalis femoris (medial perspective), condylus medialis, facies cranialis corporis, terminus proximalis, forma:

a. comparatively gradual;
b. abrupt, subperpendicular or acuminate.

Note.—See: Livezey (1998b: appendix A, character 308); Murray and Vickers-Rich (2004: table 9, characters 16–17).

2033. Extremitas distalis femoris, condylae lateralis et medialis, caudal divergence from axis proximodistalis femoris, magnitudo:

a. slight to moderate; **b.** prominent.

Note.—See: Andors (1992: table 2, character 41).

2034. Extremitas distalis femoris, condylae lateralis et medialis, pronounced subangular orientation of extremitas distalis caudal to axis majoris, status:

a. absent; **b.** present;
x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—See: Murray and Vickers-Rich (2004: table 9, character 18).

2035. Extremitas distalis femoris, condylae lateralis et medialis, facies cranialis, extremitates proximales condylarum, condylus lateralis relative to that of condylus medialis, proximal extent (**ordered**):
a. lateral exceptionally proximal;
b. lateral moderately proximal;
c. lateral of subequal proximity;
d. lateral moderately distal.
Note.—Problematic in some taxa to discriminate between crista sulci patellaris from respective, more-distal condylus.

2036. Extremitas distalis femoris, condylae lateralis et medialis, facies cranialis, comparative lateromedial thickness and cranial prominence, forma:
a. subequal;
b. medial more thick and prominent than latter.

2037. Extremitas distalis femoris, crista supracondylaris medialis, status:
a. absent or obsolete;
b. present, discernable for at least one-quarter of length of corpus femoris.
Note.—See: Kurochkin (1995b: table 1, character 24); Novas (1996: appendix, character 58), in reference to "adductor fossa and . . . craniodistal crista of distal femur"; Livezey (1998b: appendix A, character 310); Holtz (2000 [1998]: appendix I, character 340); Norell et al. (2001: appendix 1, character 186); J. M. Clark et al. (2002a: appendix 2.2, character 189); Xu (2002: suite II, character 208); Xu et al. (2002a: supplement, character 153), in reference to "longitudinal crest" on "anterior surface of femur proximal to medial distal condyle"; Hwang et al. (2004: supplement, character 186); Xu and Norell (2004: supplement, character 186).

2038. Extremitas distalis femoris, sulcus patellaris, status et forma craniomedialis (**ordered**):
a. absent;
b. present, broad, shallow, and shallowly demarcated;
c. present, narrow, deep, and distinctly demarcated.
Note.—This sulcus accommodates intrappendicular kinesis within articulatio femoropatellaris. See: Ligon (1967: fig. 4); Cracraft (1974: 498, character 1); Gauthier (1986: 13); Livezey (1986: appendix 1, character 54); Siegel-Causey (1988: character 125); Andors (1992: table 1, character 8); Chiappe and Calvo (1994: appendix I, character 58); Chiappe (1995a: legend for fig. 1); Chiappe (1995b: character 58); Sanz et al. (1995, 1997: character 56); Chiappe (1996b: character 53); Chiappe et al. (1996: appendix 1, character 52); Livezey (1995c: appendix II, character 26); K. Lee et al. (1997: appendix 1, character 48), concerning "rotular groove"; Holtz (2000 [1998]: appendix I, character 341), in reference of possible relevance to "extensor groove in craniodistal region of femur" and credited to J. D. Harris (1998); Maryanska et al. (2002: appendix 1, character 179); Vickers-Rich et al. (2002), concerning *Avimimus*; Rauhut (2003: character 202), regarding "broad groove on cranial surface of distal femur," but listed as absent in "Aves"; Murray and Vickers-Rich (2004: table 9, character 14).

2039. Extremitas distalis femoris, sulcus patellaris, regio proximalis, ovate subfossa accessoria (**new term**), status:
a. absent; **b.** present.

2040. Extremitas distalis femoris, sulcus patellaris, facies articularis patellaris, exceptional depth, width, and linearity of delimiting cristae supracondylares medialis et lateralis relative to width of element, status:
a. absent; **b.** present.
Note.—This character coincident with several other femoral synapomorphies of most or all Cuculidae, including abrupt termini cranioproximales condylarum, caudal angulation of extremitas caudalis femoris, and a prominent, uniquely conformed epicondylus medialis.

2041. Extremitas distalis femoris, sulcus patellaris, crista medialis sulci patellaris, status:
a. present, variably elongate and delimited;
b. absent, terminus cranioproximalis condyli abrupt.
Note.—Crista is comparatively fine proximal augmentation of typically rounded condylus medialis, facies cranialis. Distribution of distinct crista lateralis sulci patellaris follows this pattern reasonably closely.

2042. Extremitas distalis femoris, facies caudalis, condylus medialis, crista supracondylaris medialis, forma relative to condylus medialis et facies caudalis corporis (medial perspective):

a. absent or rudimentary, condylus not extended by crista, caused by one distinct (often abrupt) angulus or incisura supracondylaris (**new term**), rarely also a second (comparatively proximal), interrupting an otherwise gradual curving crista;

b. present and prominent, condylus continued by crista without interruption by angulus or incisura supracondylaris;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

Note.—In that character is reflection of interaction of several features—condylus medialis, crista supracondylaris medialis, facies insertii m. gastrocnemialis medialis—some assignments proved problematic.

2043. Extremitas distalis femoris, condylus medialis, crista supracondylaris medialis, facies medialis, depressio infracristalis (**new term**) extending from terminus cristae proximally and enlarging to terminus distalis proximal to epicondylus medialis, status:

a. absent; **b.** present;

x. noncomparable (Aepyornithiformes, Dinornithiformes).

2044. Extremitas distalis femoris, epicondylus medialis, tuberculum m. gastrocnemialis medialis, forma *sensu* separation from condylus medalis:

a. distinct, separated from latter by deep incisura;

b. united within single complex comprising condylus medialis et crista supracondylaris medialis.

Note.—Provisionally accounts for references to "ectocondylar tuber of distal femur," but may be homologous with the generally elevated region treated by Hutchinson (2001b: appendix 1, character 16) as the "craniomedial distal scar and crest" or to the epicondylus medialis *sensu lato*, the latter not obvious in most Theropoda. Novas (1996: appendix, character P7); Novas (1996: appendix, character 16); Novas (1997: appendix, character 17); Novas and Puerta (1997), Novas (1997); Holtz (2000 [1998]: appendix I, character 344); Norell and Clarke (2001: appendix I, character 173), treated similarly by J. A. Clarke (2002: appendix I, character 173), J. A. Clarke and Norell (2002: appendix 2, character 173), and J. A. Clarke (2004: appendix 1, character 173); Zhou and Zhang (2002: appendix III, character 173); Ji et al. (2005: supplement, part I, character 173).

2045. Extremitas distalis femoris, facies caudalis, condylus medialis, crista supracondylaris medialis, tuberculum m. gastrocnemialis medialis, prominence relative to margo medialis of corpus femoris et margo proximalis of condylus medialis, situs et forma:

a. a comparatively distal, variably prominent jugum or tuberculum, often incorporated within crista supracondylaris medialis;

b. comparatively proximal, variably raised, elongate, linear aut crescentiform, often rugose impressio or sharply emarginate, subcircular concavitas.

Note.—See: Livezey (1986: appendix 1, character 59); Livezey (1995c: appendix II, character 31), in reference to "raised ridge," perhaps synonymous with the "ligamental attachment" of Howard (1929); Livezey (1998b: appendix A, characters 309 and 311).

2046. Extremitas distalis femoris, epicondylus medialis, forma as distinctly raised, medially smooth, irregularly subovate eminentia, status:

a. absent;

b. present, evidently a cranioventral enclosure for impressio ligamentum collateralis medialis.

Note.—Coincident with at least one additional character of extremitas distalis femoris of Cuculidae, concerning sulcus patellaris and abrupt caudal orientation of condyli distales.

2047. Extremitas distalis femoris, fossa poplitea, forma (**ordered**):

a. very shallow, weakly delimited;

b. distinct, enclosing moderate number of foveae et/aut pori;

c. distinct, enclosing numerous foveae et/aut pori.

Note.—See: Bledsoe (1988: appendix, character 49); Holdaway (1991: appendix 5.1, characters 164–165); Andors (1992: table 1, characters 9–10); K. Lee et al. (1997: appendix 1, character 51); Murray and Vickers-Rich (2004: table 9, character 15).

2048. Extremitas distalis femoris, fossa poplitea, enclosure of pori et/aut foveae pneumatici, status et forma (**ordered**):

a. absent, lacking foveae et/aut pori, imperforate exclusive of proximomedial cluster of foramina and single distal foramen profundus, apparently neurovascular and universally distributed among Aves;

b. present, enclosing moderate number of foveae et/aut pori;

c. present, enclosing numerous foveae et/aut pori.

Note.—See: Livezey (1986: appendix 1, character 56); Livezey (1995b: appendix 1, character 17); Livezey (1995c: appendix II, character 28); Livezey (1996b: appendix 1, character 38); Livezey (1996c: character 10); Livezey (1998b: appendix A, character 305); Dyke et al. (2003: appendix 1, character 77).

2049. Extremitas distalis femoris, facies caudalis, fossa poplitea, margo distalis immediately proximal to sulcus patellaris, arcus ligamentum cruciati caudalis (**new term**), status:

a. absent; **b.** present.

2050. Extremitas distalis femoris, impressiones ansae m. iliofibularis, status:

a. absent; **b.** present, variably prominent.

Note.—Typically the ansae ligamentosus m. iliofibularis comprise three components (two femoral and one fibular): (*i–ii*) pars femoralis, comprising two capita, one immediately proximal to crista medialis of sulcus patellaris, and one proximal to crista lateralis of sulcus patellaris; and (*iii*) pars fibularis, immediately distal to the collum fibularis (**new term**).

See: Holdaway (1991: appendix 5.1, character 192); Andors (1992: table 1, character 11); Hutchinson (2001b: appendix 1, character 17); Livezey (1998b: appendix A, character 312).

Patella et Menisci Genus

Note.—Herein the definition of the patella is restricted to the sesamoideum developed in the tendo insertii common to mm. femorotibialis et m. iliotibialis lateralis on crista patellaris tibiotarsi. Although typically a nodulus or discus located somewhat proximal to terminus distalis tendinis and occupying the sulcus patellaris femoris, the patella is modified, especially in some water birds, by development of a syndesmosis with the tibiotarsus and a protrusion that effectively extends the proximal limit of the tibiotarsus. Through these modifications the patella plays a new role as situs origii of various mm. flexores et extensores that typically originate only on the tibiotarsus; consequently the patella may develop cristae and fossae almost continuous with those of the tibiotarsus.

This phenomenon, along with an inaccurate generalization concerning an inverse relationship between the lengths of patellae and crista cnemiales craniales (cf. Cracraft 1982: fig. 7), led K. Pearson and Davin (1921: 387–388) to conclude that such patellae arose probably by fracturing of the crista cnemialis cranialis in certain taxa. Conversely, a perceived similarity between the patella of *Hesperornis* and the long crista cnemialis cranialis of loons (Gaviidae) led D. W. Thompson (1890: 12) to equate the two structures and to conclude that the patella of the loon is " . . . fused with the upper extremity of the tibia." Comparison of presumptive homologues of loons and grebes (Podicipedidae)—the former having a long crista cnemialis cranialis and minute patella, the latter having a long patella paralleling a long crista cnemialis cranialis—prompted Shufeldt (1904: 46) to state that " . . . probably the true patella [of *Gavia*] has co-ossified in the adult with the elongated cnemial process of the tibio-tarsus." Lacking a skeleton of a juvenile loon, dissections of hatchling chicks of *Gavia immer* and *Podilymbus podiceps* by necessity served for direct examinations herein. The essential crista cnemialis cranialis and patella of both species were preformed as cartilagines almost exactly as it appears in adults—that is, showing a well-developed patella in the podicipedid and no patella or subdivision of the cnemial crest in *the* gaviid.

Another hypothesis relevant to this subject is that traction epiphyses, found in some mammals, occur also in birds. A traction epiphysis (epiphysis tritus; **new term**) is a projection, usually from a terminus corporis ossis, onto which an insertio tendinis is located and in which a separate center of ossification occurs. Many such projections in mammals represent pre-existing intra-tendinous sesamoidea that secondarily unite by synostosis with the os primus (Barnett and Lewis 1958). These authors use a species of diving petrel (Procellariiformes: *Pelecanoides*) and a grebe (Podicipediformes: *Tachybaptus ruficollis*) as examples (included figs. 2d–e, pl. 1, fig. 5). However, an epiphysis tibialis apparently was misinterpreted as a traction epiphysis in this work. Birds, often thought to lack epiphyses in development of the long bones, show histological differentiation consistent with epiphyses (Fell 1925), although (with one exception) a separate center of ossification was not evident.

The exception occurs at extremitas proximalis tibiotarsi where a separate ossification of the epiphysis is visible in some skeletons of juvenile individuals. The tibial epiphysis avium has been described (Shufeldt 1881a, 1886a; F. G. Parsons 1905; H. Fuchs 1908; Haines 1942) and is distributed widely if not universally among modern birds (e.g., exemplified by 15 orders in USNM skeletons). The epiphysis includes cristae cnemiales et patellaris, one of which—crista cnemialis cranialis—manifests profound apomorphy in some water birds (Baumel and Witmer 1993: 109). Facies articulares tibiotarsi are also part of the tibial epiphysis, although this epiphysis may be the last portion of the element to ossify. We interpret the figures of Barnett and Lewis (1958) to show the: (*i*) large patella of *Phalacrocorax* (their "c"), (*ii*) extended tibial epiphysis of *Pelecanoides* ("d"; also see pl. 1, fig. 5 for "epiphysial line"), and (*iii*) large tibial epiphysis and adherent patella of *Tachybaptus* ("e"). In our specimen of a juvenile *Tachybaptus ruficollis* (USNM 560771), the limitus epiphysialis is distad from that shown in their illustration and the entire facies articularis tibiotarsi is included in the epiphysis; the adherent patella also is present.

Comparison of the crista cnemialis cranialis tibiotarsi with the olecranon ulnae—within the conceptual framework of pectoral-pelvic symmetry prevalent at the time—led K. Pearson and Davin (1921: 387) to consider it " . . . not unreasonable to suppose that if the olecranon can give rise to sesamoids, a similar change can take place in the cnemial crest." This inference lacks direct supporting evidence in birds (Gadow and Selenka 1891: 83).

In summary, with respect to birds, we find no support for claims that patellae fused with cnemial crests or extremitas proximalis tibiotarsi, or that the patellae have originated by fracturing of the cristae cnemiales. Instead, we found that the form of the tibial epiphysis foreshadows the highly modified crista cnemialis cranialis found in adults of some birds, and that the patella exhibits intermediate stages of specialization between those typical of birds and those of *Hesperornis* and grebes. In those taxa possessing separate patellae, the junctura patello-tibiotarsi involves syndesmosis with crista patellaris tibiotarsi, ligamentum patellae (homologous with tendo mm. femorotibiales), and interposed corpus adiposum retropatellare (situated within the fossa retropatellaris tibiotarsi), effecting articulatio femoropatellaris within sulcus patellaris femoris.

See: Pycraft (1899b: fig. 1); Barnett and Lewis (1958).

2051. Patella ossea, status:
a. absent; **b.** present.

Note.—State for Aepyornithidae inferred from rugositas ancorae on crista cnemialis. See: Shufeldt (1902b); Sibley and Ahlquist (1972: table 1); Livezey (1998b: appendix A, character 313); G. Mayr (2004b: appendix 1, character 43).

2052. Patella (sesamoidea patellares), numerus modalis et forma (**unordered**):
a. one, variably substantial sesamoideum;
b. two or three, irregular cuneate calculae;
c. several, irregularly shaped ossiculae, flattened in planum tendinis;
d. two, distinct ossiculae;
x. noncomparable by absence of patella (Tinamidae, *Puffinus*, *Pelecanoides*, Heliornithidae, *Rostratula*).

Note.—Henceforth, unless indicated otherwise, "patella" refers either to a single element or a conglomerate of provisionally homologous sesamoidea.

2053. Patella, association with ligamentum patellae or tendo patellae ossificans, status et forma (**unordered**):
a. absent, essentially independent or only weakly constrained;
b. present, associated with robust ligamentum patellae;
c. present, co-ossified with robust tendo patellae ossificans;
d. present, associated with abbreviate ligamentum patellae;
x. noncomparable by absence of patella (Tinamidae, *Puffinus*, *Pelecanoides*, Heliornithidae, *Rostratula*).

Note.—We use the term ligamentum patellae although it is homologous to a portion of tendo mm. femorotibiales (Baumel and Raikow 1993: 170). The patella serves as situs insertii m. femorotibialis intermedius. In turn, a collagenous ligamentum anchors the patellae with crista patellaris tibiotarsi. Ligamentum patellae may be ossified regardless of the state of ossification of the adjacent segment of tendo mm. femorotibiales. Where present, tendo insertii m. ambiens typically crosses facies cranialis ligamenti patellae immediately distal to the patella.

2054. Patella, facies (distalis) cranialis, forma generalis (**unordered**):
a. nondescript or weakly demarcated;
b. bilobate—distinct tumulus or jugum;
c. cristate—marked dorsoventrally oriented crista partitioning approximately equal depressiones lateralis et medialis;
d. cuneate—prominent, elongate, broadly based eminentia aligned with axis majoris tibiotarsi;
e. angular—extremely prominent, elongate, acute eminentia aligned with axis majoris tibiotarsi;
x. noncomparable by absence of patella (Tinamidae, *Puffinus*, *Pelecanoides*, Heliornithidae, *Rostratula*).

Note.—See: Marsh (1880); Shufeldt (1884c, 1913b); Livezey (1992a).

2055. Patella, sulcus (canalis) tendinis m. ambientis, forma modalis definitivum:
a. nondescript or sulcus transversus aut obliquus tendinis m. ambientis;
b. canalis tendinis m. ambientis;
x. noncomparable by absence of patella.

Note.—See: Marsh (1880); Shufeldt (1884c, 1913b); Hudson (1937); L. D. Martin and Tate (1976); S. L. Olson and Hasegawa (1979, 1985, 1996); Stephan (1979: fig. 43); S. L. Olson (1980: fig. 3H); Cracraft (1982: series 3, character 4); Livezey (1992a); Livezey (1998b: appendix A, character 313); G. Mayr (2004b: appendix 1, character 43).

2056. Patella, distinct protrusion proximal to crista cnemialis cranialis tibiotarsi, status et forma (**ordered**):
a. absent, in close proximity to extremitas proximalis tibiotarsi;
b. present, cuneate, contiguous with and extending slightly proximad to crista cnemialis cranialis tibiotarsi;
c. present, pyramidal, contiguous with and extending well proximad to crista cnemialis cranialis tibiotarsi;
x. noncomparable by absence of patella (Tinamidae, *Puffinus*, *Pelecanoides*, Heliornithidae, *Rostratula*).

Note.—See: Sibley and Ahlquist (1972: table 1), contrasted Gaviidae as lacking patella with Podicipedidae as having "large and pyramidal" patellae.

Tibiotarsus

Note.—Comparative examination of tibiotarsi of *Mullerornis* revealed it to be substantially smaller than *Aepyornis* (former approximating 45 cm in length, including cristae cnemiales) but virtually identical qualitatively. Among Dromornithidae (or Dromornithiformes), an exceptional variation in size is evident—*Dromornis* > *Bullockornis* > *Genyornis* > *Ilbindornis* > *Barawertornis*—although most qualitative features were uniform.

Extremitas proximalis tibiotarsi

2057. Tibiotarsus (i.e., tibiotarsus exclusive of fibula), extremitas proximalis tibiotarsi, craniocaudal width relative to lateromedial width:
a. former significantly longer than latter, often twice, distinctly oblong;
b. former subequal to latter, subcircular.

Note.—See: Forster et al. (1998: supplement, character 98); Xu et al. (1999b: character 71); Xu et al. (2000: supplement, character 54); Chiappe (2001a: appendix 1, character 148); Chiappe (2002: appendix 20.2, character 148); Murray and Vickers-Rich (2004: table 9, character 26).

2058. Extremitas proximalis tibiotarsi, incisura intercondylaris, area (incisura) intercondylaris (effecting caudal separation of facies articularis fibularis et margo medialis of caput tibiotarsi), status:
a. absent; **b.** present.
Note.—See: Rauhut (2003: character 205).

2059. Extremitas proximalis tibiotarsi, caput tibiotarsi, area intercondylaris, forma (**ordered**):
a. obsolete; **b.** weakly defined;
c. comparatively distinct.
Note.—See: Livezey (1998b: appendix A, character 317).

2060. Extremitas proximalis tibiotarsi, caput tibiotarsi, facies articularis lateralis, forma generalis (**unordered**):
a. enlarged, often irregularly shaped, subtuberculum, substantially more prominent proximally than facies articularis medialis, especially adjacent to area intercondylaris;
b. globular or subspheroidal, moderately more prominent proximally than facies articularis medialis;
c. dorsally reduced, subequal in proximal prominence to facies articularis medialis.
Note.—Some problematic assignments encountered.

2061. Extremitas proximalis tibiotarsi, caput tibiotarsi, facies articularis medialis, forma generalis:
a. subovate or broadly crescentiform;
b. narrowly crescentiform, medially constricted.

2062. Extremitas proximalis tibiotarsi, caput tibiotarsi, facies articularis medialis, forma superficialis:
a. subplanar or shallowly concave or convex;
b. deeply concave, emphasized further by prominently elevated area interarticularis.

2063. Extremitas proximalis tibiotarsi, caput tibiotarsi, facies articularis lateralis, forma in which facies dorsalis is subplanar, combined with caudal elevation leading to proximal displacement and enhanced delimitation of facies adjacent to area intercondylaris, status:
a. absent; **b.** present.

2064. Extremitas proximalis tibiotarsi, caput tibiotarsi, facies articulares laterales et mediales, margines immediately caudal to area intercondylaris (subtending margo caudalis capitis), forma (**unordered**):
a. well developed as prominent labia and subtended by concavitates et (typically) foramina pneumatica;
b. neither prominently produced nor subtended by deep concavitates;
c. prominently produced, apneumatic concavitates.
Note.—See: Ericson (1997: table 1, character 67). Based on Ballmann (1969a: fig. 3), these depressiones mark the ancorae origii m. flexor digitorum longus (laterally) et m. plantaris (medially).

2065. Extremitas proximalis tibiotarsi, caput tibiotarsi, facies articularis lateralis, forma superficialis:
a. variably tumid or convex;
b. distinctly concave.
Note.—*Rhea* marginally apomorphic. See: Bledsoe (1988: appendix, character 56).

2066. Extremitas proximalis tibiotarsi, caput tibiotarsi, facies articularis lateralis, margo lateralis (typically immediately caudal to incisura tibialis), facies articularis fibularis proximalis (**new term**)—i.e., facies for caput fibulae—status:
a. absent or weakly evident—e.g., small, sessile, emarginate;
b. present, prominent, proximodistally elongate.

2067. Extremitas proximalis tibiotarsi, caput tibiae, facies articularis medialis, forma marginalis (dorsal perspective):
a. variable, typically crescentiform or reniform;
b. suborbiculate.
Note.—See: Sanz et al. (1995, 1997: character 82).

2068. Extremitas proximalis tibiotarsi, caput tibiae, facies articulares medialis et lateralis, distinctness of mutual delimitation by area interarticularis et fossae retrocristales, forma:
a. obsolete, facies medialis essentially merges with facies lateralis;
b. marked.
Note.—See: Murray and Vickers-Rich (2004: table 9, character 27), which emphasized facies articularis (“proximalis”) medialis or “proximal ectocondyle” in Dromornithidae.

2069. Extremitas proximalis tibiotarsi, caput tibiotarsi, cristae cnemiales, substantial reduction or virtual absence of *both* cristae (typically in both proximal and craniolateral dimensions), status (**unordered**):
a. absent, at least one crista distinct;
b. present, cristae lacking but for proximolaterally compressed vestigia;
c. present, lacking both cristae entirely.
Note.—See: G. Mayr (2003c: appendix, character 24).

2070. Extremitas proximalis tibiotarsi, caput tibiae, crista cnemialis cranialis, status:

a. absent; **b.** present.

Note.—Crista cnemialis lateralis generally is assumed to be homologous to the single crista present in nonavian Theropoda. Crista cnemialis cranialis is considered to be a neomorph derived from an amalgam of a sesamoideum with the corpus tibiotarsi proprius (Fell 1925), perhaps together with its lateral counterpart, an example of a "traction epiphysis" (Haines 1942, 1969; Barnett and Lewis 1958), and not related ontogenetically to the patella. Definitive features of the tibiotarsus derived from or at least rudimentary in these "traction epiphyses" include both cristae cnemiales, facies gastrocnemialis, and area interarticularis (juvenile *Spheniscus humboldti*: UCLB 4868).

See: Ligon (1967: table 6); Cracraft (1974: 502, character 8); Cracraft (1986: appendix, character 37); Gauthier (1986: 13–14, unindexed synapomorphy of Ornithurae), who included in diagnosis of Ornithurae the statement " . . . tibia with cnemial epiphysis . . . "; Bledsoe (1988: appendix, characters 51–54); K. Lee et al. (1997: appendix 1, character 33); Novas (1992: character 4); Chiappe and Calvo (1994: appendix I, character 63); Chiappe and Calvo (1994: appendix II, character 16), listed as synapomorphy of Enantiornithes the presence of "a single and smooth cnemial crest on craniomedial margin"; Novas (1994 [1993]: appendix, character 4); Chatterjee (1995: character 15); Chiappe (1995b: character 63); Sanz et al. (1995, 1997: character 61); Chiappe (1996b: character 58); Chiappe et al. (1996: appendix 1, character 57); Novas (1996: appendix, character M18), in reference to "accessory (medial) cnemial crest on tibia"; Chatterjee (1999: appendix II, character 79); Sereno (2000: table 4, character 7), citing a purported synapormorphy of Enantiornithes as being "tibial cnemial crest located anteromedially"; Chiappe (2001a: appendix 1, character 147); Norell and Clarke (2001: appendix I, character 178), phrased in terms of number of cristae, treated similarly by J. A. Clarke (2002: appendix I, character 178), J. A. Clarke and Norell (2002: appendix 2, character 178), and J. A. Clarke (2004: appendix 1, character 178); Norell et al. (2001: appendix 1, character 193); Chiappe (2002: appendix 20.2, character 147); J. M. Clark et al. (2002a: appendix 2.2, character 195); Maryanska et al. (2002: appendix 1, character 181), in reference to count of crests; Vickers-Rich et al. (2002), concerning *Avimimus*; Xu (2002: suite II, character 214); Xu et al. (2002a: supplement, character 159), with respect to "medial cnemial crest"; Zhou and Zhang (2002: appendix III, character 178), regarding number of cnemial crests; Hwang et al. (2004: supplement, character 192); Xu and Norell (2004: supplement, character 192); Ji et al. (2005: supplement, part I, character 178).

2071. Extremitas proximalis tibiotarsi, caput tibiotarsi, cristae cnemiales, crista cnemialis cranialis ("internal" cnemial crest), proximal extent, forma (**ordered**):

a. obsolete, barely extending proximad to facies articulares tibiotarsales;

b. moderately prominent, distinct from surrounding facies articulares and extending a distinct but limited distance proximad, cranial extent typically greater than proximal;

c. exceptionally prominent, crista extending proximad to facies articularis at least one-third of length of corpus tibiotarsi.

Note.—Eichstätt *Archaeopteryx* showed neither crista definitively. Ultimately combine with preceding presence-absence character.

See: Ligon (1967: table 6); Cracraft (1982: series 2, character 5); Livezey (1986: appendix 1, character 63); Bledsoe (1988: appendix, character 53); Cracraft (1988: series XI, character 8); Livezey (1989: table 1, character 63); Livezey (1996a: appendix 1, character 70); Ericson (1997: table 1, character 66; table 2, character 43); K. Lee et al. (1997: appendix 1, character 34); Livezey (1997a: appendix 1, character 85; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, character 316); G. Mayr (2003a: appendix I, character 36); G. Mayr and Clarke (2003: appendix A, character 99); G. Mayr (2004b: appendix 1, character 44); G. Mayr (2004d: appendix I, character 32); Murray and Vickers-Rich (2004: table 9, character 28); G. Mayr (2005a: appendix 1, character 33).

2072. Extremitas proximalis tibiotarsi, caput tibiotarsi, crista cnemialis cranialis, facies lateralis, distinct and approximately uniform concavity of surface, status:

a. absent; **b.** present.

2073. Extremitas proximalis tibiotarsi, caput tibiotarsi, cristae cnemiales cranialis et lateralis, margines proximodorsales, vertex cristae (**new term**), distinct lateral hamulation of (primarily) crista cnemialis cranialis, status et forma (**ordered**):

a. absent;

b. present, intermediate prominence, largely limited to cranial (subterminal) portion of crista;

c. present, exceptional prominence, involving crista from extremitas cranialis to terminus proximodorsalis.

Note.—See: Ligon (1967: table 6), regarding Cathartidae and Ciconiidae.

2074. Extremitas proximalis tibiotarsi, caput tibiotarsi, cristae cnemiales cranialis et lateralis, margines proximodorsales, margo cristae transversa cnemialis (**new term**), extension significantly mediad to crista cnemialis cranialis, status:

a. absent; **b.** present.

Note.—Crista transversa cnemialis is the lateromedially oriented margo cranialis of facies articularis tibiotarsi, caudal to crista cnemialis cranialis propria.

2075. Extremitas proximalis tibiotarsi, caput tibiotarsi, cristae cnemiales cranialis et lateralis, margines proximodorsales, vertex cristae (**new term**), forma in which cristae intersect perpendicularly (emphasized by planar, cranial orientation of crista cnemialis cranialis) and margines proximodorsales are of equal height and in proximity of angulus of intersection, status:

a. absent, angulae or marginal inequalities characteristic;

b. present.

2076. Extremitas proximalis tibiotarsi, caput tibiotarsi, cristae cnemiales cranialis et lateralis, exceptional, proximodistally extensive cranial prominence and lateral concavity of crista cnemialis cranialis, status:

a. absent; **b.** present.

2077. Extremitas proximalis tibiotarsi, caput tibiotarsi, cristae cnemiales cranialis et lateralis, margines cranialis et lateralis, respectively, reinforcement with thickened jugae, status:

a. absent; **b.** present.

Note.—See: G. Mayr (2004a: appendix 1, character 54).

2078. Extremitas proximalis tibiotarsi, caput tibiotarsi, cristae cnemiales cranialis et lateralis, crista cnemialis lateralis, margo dorsalis cristae, laterad to intersectio with crista cnemialis cranialis, forma marginalis (**unordered**):

a. concave essentially throughout;

b. sigmoidal, convex laterally and concave medially;

c. linear and variably sloping throughout;

d. convex essentially throughout.

Note.—See: Murray and Vickers-Rich (2004: table 9, character 20; fig. 140B).

2079. Extremitas proximalis tibiotarsi, caput tibiotarsi, sulcus (intercnemialis) intercristalis cnemialis, pori superficiae (**new term**) cristae (internal or external to sulcus), status et forma (**unordered**):

a. absent, facies internae sulci essentially smooth, imperforate;

b. present, facies sulci with pori pneumatici, nutrientes, et/aut neurovasculariae;

c. present, facies sulci with typically suborbiculate foramina pneumatica;

d. present, facies sulci conspicuously sculpted with multilayered, overlapping, irregularly shaped, spiculae tubiformes et marginally rounded fenestrae.

Note.—See: Murray and Vickers-Rich (2004: table 9, character 22).

2080. Extremitas proximalis tibiotarsi, caput tibiotarsi, cristae cnemiales cranialis et lateralis, intersection of margines on facies cranialis tibiotarsi forming sulcus intercristalis, pars profundus, forma (**unordered**):

a. crista lateralis uniting with corpus distinctly lateral to (perpendicular) line of union for crista medialis, delimiting a comparatively broad sulcus intercristalis;

b. crista lateralis uniting with corpus virtually coincidentally with (perpendicular) line of union for crista medialis, forming a subperpendicular intersection of plana cristae, and delimiting a comparatively narrow sulcus intercristalis;

c. crista lateralis joining crista cranialis well cranial to basis cristae for latter, thereby sharing common basis cristae cnemiales (**new term**), and crista lateralis appearing as large tuberculum.

Note.—See: Cracraft (1971a: fig. 12). Ballmann (1969a: figs. 2–3) reported that sulcus intercristalis largely accommodates insertio m. extensor digitorum longus (Vanden Berge and Zweers 1993: annotation 115); G. Mayr et al. (2003: appendix 1, character 57, part); G. Mayr (2004d: appendix I, character 32); G. Mayr (2005a: appendix 1, character 33).

2081. Extremitas proximalis tibiotarsi, caput tibiotarsi, cristae cnemiales cranialis et lateralis, apex cristae, margo proximalis immediately lateral to crista cnemialis cranialis, foramen neurovascularia, status:

a. absent; **b.** present.

Note.—Incisura margines at same situs in other Falconiformes may accommodate homologous vena(e) or nervus, therefore representing related, alternative state of this character.

2082. Extremitas proximalis tibiotarsi, caput tibiotarsi, crista cnemialis cranialis, pronounced lateral curvature (especially proximally), status:

a. absent; **b.** present.

Note.—Curvature in this context refers to lateral curvature of basis cristae, i.e., would remain in evidence if crista were lateromedially flattened.

2083. Extremitas proximalis tibiotarsi, caput tibiotarsi, crista cnemialis cranialis, craniodistal continuation of margo cranialis ligamenti by fascia aut tendo ossificans as lamina, linea extensoria, aut arcus distalis cristae (**new term**), status et forma (**ordered**):

a. absent;

b. present, limited to variably extensive osseous remnants;

c. present, consolidated to form lamina aut arcus.

Note.—State "c" refers to a lamina or slender arcus that encloses a fenestra within the distal portion of the crista cnemialis cranialis.

2084. Extremitas proximalis tibiotarsi, caput tibiotarsi, crista cnemialis lateralis, jugum cristae (**new

term) delimiting sublinear extension of crista on facies lateralis of corpus tibiotarsi, status:

a. absent, no jugum or distal extension of crista, emerges abruptly laterad;

b. present, terminus distalis of crista et jugum of variable extent relative to crista fibularis, seldom extending to crista fibularis.

Note.—See: Holtz (1994a: appendix 1, character 97); Holtz (2000 [1998]: appendix I, character 346), in which it was implied that crista cnemialis lateralis (characteristic of basal Theropoda) tends to be oriented caudad in nonavian Theropoda.

2085. Extremitas proximalis tibiotarsi, caput tibiotarsi, crista cnemialis cranialis, jugum cristae (**new term**) on facies cranialis of corpus tibiotarsi relative to crista fibularis, forma (**ordered**):

a. present, terminus entirely proximal to crista fibularis;

b. present, terminus between terminus proximalis and midpoint of crista;

c. present, terminus distal to midpoint of crista fibularis.

Note.—Jugum refers to ridge on corpus tibiotarsi, facies cranialis. See: Cracraft (1985: character 52); Livezey (1986: appendix 1, character 65); Mader and Bradley (1989); Holdaway (1991: appendix 5.1, character 204); Livezey (1995a: appendix 1, character 12); Livezey (1995b: appendix 1, character 19); Livezey (1995c: appendix II, character 33); Livezey (1996c: character 12); Livezey (1998b: appendix A, character 315); Sereno (2000: table 4, character 7); G. Mayr et al. (2003: appendix 1, character 57, part); G. Mayr (2004d: appendix I, character 32); G. Mayr (2005a: appendix 1, character 33).

2086. Extremitas proximalis tibiotarsi, caput tibiotarsi, crista cnemialis lateralis including jugum cristae (**new term**), situs corporis tibiotarsi (**ordered**):

a. distinctly aligned along axis oblique and intermediate to axis majoris corporis and margo lateralis corporis, jugum cristae slanting mediad to margo medialis of crista fibularis;

b. slightly oblique with respect to axis majoris, subparallel;

c. principally aligned with margo lateralis of corpus tibiotarsi et crista fibularis and comparatively linear in orientation.

2087. Extremitas proximalis tibiotarsi, caput tibiotarsi, crista cnemialis cranialis, facies lateralis—sculpting by variably overlapping fenestrae and subdivided by spiculae orbiculares resulting in vermiform aspect, status:

a. absent; **b.** present.

2088. Extremitas proximalis tibiotarsi, caput tibiotarsi, crista cnemialis cranialis, rudimentation such that crista (although basis cristae evident) reduced to rounded, truncated jugum, status:

a. absent, crista of variable but significant prominence;

b. present, rudimentation profound.

Note.—Rudimentary state of crista cnemialis cranialis, where present, often paralleled by condition of crista cnemialis lateralis.

2089. Extremitas proximalis tibiotarsi, caput tibiotarsi, crista cnemialis cranialis, facies lateralis cristae, forma (**ordered**):

a. essentially planar;

b. only slightly concave, as lateroproximal jugum, or obsolete, strictly proximodistally oriented jugum;

c. moderately, typically heterogeneously concave, pronounced proximally;

d. deep, elongate, distally diminished sulcus.

Note.—Eichstätt *Archaeopteryx* showed neither crista definitively. Unique crista in Strigiformes (state "c" here) is treated separately elsewhere. See: Murray and Vickers-Rich (2004: table 9, character 20; fig. 140B), termed "ectocnemial crest."

2090. Extremitas proximalis tibiotarsi, caput tibiotarsi, crista cnemialis cranialis, margo cranialis cristae (lateromedial perspective), forma (**unordered**):

a. parallel sublinear—cranioproximal prominence lacking;

b. sloping sublinear—sublinear slope from proximocranial angulus to facies cranialis corporis;

c. shallow subangular—suborbiculate dorsad, distinct intermediate angulus, sublinear junctura with corpus distad;

d. deep subangular or suborbiculate.

Note.—Eichstätt *Archaeopteryx* showed neither crista definitively. See: Cracraft (1971a: fig. 12), regarding Coraciiformes.

2091. Extremitas proximalis tibiotarsi, caput tibiotarsi, crista cnemialis cranialis, facies medialis et basis cristae medialis, extraordinarily deep fossa m. gastrocnemius internus (**new term**), status:

a. absent;

b. present, facies transformed to fossa.

2092. Extremitas proximalis tibiotarsi, facies medialis corporis approximately parallel to terminus distalis of crista cnemialis cranialis on facies cranialis corporis or terminus proximalis of crista fibularis, distinct medial eminentia (craniocaudal view) providing foundation for area insertii m. femorotibialis internus, pars distalis, status:

a. absent or indiscernable;

b. present and discernable in profile.

Note.—See: Ballmann (1969a: fig. 3); Vanden Berge and Zweers (1993: annotation 107).

2093. Extremitas proximalis tibiotarsi, caput tibiotarsi, crista cnemialis lateralis, position relative to facies articularis fibularis and interposition by incisura tibialis (proximal perspective), forma:

a. confluent with crista cnemialis lateralis;

b. offset and separated by incisura tibialis from crista cnemialis lateralis.

Note.—See: Rauhut (2003: character 204); also related but not equivalent, Murray and Vickers-Rich (2004: table 9, characters 23–24; fig. 140B), termed “cavum ectocnemialis,” in reference to variation among Dromornithidae.

2094. Extremitas proximalis tibiotarsi, caput tibiotarsi, crista cnemialis lateralis, lateral prominence relative to articulated os fibula, forma:

a. not lateral to caput fibulae;

b. extending lateral to caput fibulae.

2095. Extremitas proximalis tibiotarsi, caput tibiotarsi, crista cnemialis lateralis, subequal craniad to crista cnemialis cranialis, status:

a. absent; **b.** present.

2096. Extremitas proximalis tibiotarsi, caput tibiotarsi, crista cnemialis lateralis, terminus cristae broad, subovate, laterodistally oriented and thickened, status:

a. absent; **b.** present.

Note.—See: Murray and Vickers-Rich (2004: table 9, character 21), termed “basis processus cnemialis.”

2097. Extremitas proximalis tibiotarsi, caput tibiotarsi, crista cnemialis lateralis, terminus cristae, distinct cranial orientation in parallel with crista cnemialis cranialis, status:

a. absent; **b.** present.

Note.—See: Murray and Vickers-Rich (2004: table 9, character 21), termed “basis processus cnemialis.”

2098. Extremitas proximalis tibiotarsi, caput tibiotarsi, crista cnemialis lateralis, rudimentation such that crista patellaris of exceptionally limited lateral prominence, proximal extent, or distal continuation as linea, status:

a. rudimentation absent, crista cnemialis lateralis well developed;

b. rudimentation present.

2099. Extremitas proximalis tibiotarsi, caput tibiotarsi, cristae cnemiales cranialis et lateralis, *comparative* distal extents on corpus tibiotarsi, forma (**ordered**):

a. crista cranialis terminating distinctly distad to crista lateralis;

b. cristae subequal in distal extent (typically truncate), both lacking jugae;

c. crista lateralis terminating distinctly distad to crista cranialis;

x. noncomparable (*Phaethon*, *Pterocles*, Caprimulgiformes, Apodiformes).

Note.—Jugum is a palpable “ridge” *sensu stricto*, therefore a mere linea continuing beyond crista is not included in assessments of distal extent.

2100. Extremitas proximalis tibiotarsi, caput tibiotarsi, cristae cnemiales cranialis et lateralis, apparent “torsion” of cristae relative to facies cranialis of corpus tibiotarsi as reflected by relative positions of cristae et sulcus intercristalis (**unordered**):

a. crista lateralis lateral in position, cranialis craniomedial, sulcus obliquely slanting distolaterad;

b. crista lateralis craniolateral in position, cranialis (cranio)medial, sulcus approaching cranial exposure;

c. crista lateralis laterocranial in position, cranialis medial (medial cristula frequent distally), sulcus cranial in exposure, medially positioned, and subtriangular in form delimited by intersection of cristae cnemiales.

2101. Extremitas proximalis tibiotarsi, caput tibiotarsi, cristae cnemiales cranialis et lateralis, angulus proximalis cristae (**new term**), enclosure of ovate depressio enclosing translucentium aut foramen, status:

a. absent; **b.** present.

2102. Extremitas proximalis tibiotarsi, caput tibiotarsi, crista cnemialis caudalis (**new term**), prominent crista extending caudad from apex cristae cnemiales to divide fossa retropatellaris, status:

a. absent; **b.** present.

2103. Extremitas proximalis tibiotarsi, caput tibiotarsi, cristae cnemiales cranialis et lateralis, moderately great distal extent by respective jugae, termina distales of which converge on facies cranialis tibiotarsi to delimit triangular sulcus intercristalis, status:

a. absent; **b.** present.

2104. Extremitas proximalis tibiotarsi, caput tibiotarsi, cristae cnemiales et facies lateralis corporis (pars proximalis), fossa insertii m. gastrocnemius pars internus (**new term**), expansion by caudal reflection of caput fibulae, broadened incisura tibialis et crista fibularis, status:

a. absent; **b.** present.

2105. Extremitas proximalis tibiotarsi, caput tibiotarsi, crista cnemialis lateralis, crista patellaris, forma (**unordered**):

a. variable with respect to thickness and angularity, margo ventralis cristae approximately diagonal with respect to margo lateralis tibiotarsi;

b. subtubercular;

c. thick, blunt, hamulate, or strongly angular;

d. thin, acuminate, very prominent laterally, and hamulate;

e. prominent and crescentiform, imbedded within vertex lateroproximalis of cristae cnemiales, subperpendicular to margo lateralis tibiotarsi;

f. truncate and crescentiform, imbedded within vertex lateroproximalis of unified cristae cnemiales, at obtuse angulus with corpus tibiotarsi.

Note.—See: Ligon (1967: fig. 5); Cracraft (1982: series 2, character 5, part); Cracraft (1988: series II, character 15; series XI, character 9); Siegel-Causey (1988: character 133); Kurochkin (1995b: table 1, character 25); Dyke and Gulas (2002: appendix 1, character 44); Dyke et al. (2003: appendix 1, character 81), also Dyke (2003: table 1); Murray and Vickers-Rich (2004: table 9, character 25), termed "tuberculum epicnemialis."

2106. Extremitas proximalis tibiotarsi, caput tibiotarsi, crista cnemialis lateralis, crista patellaris, proximal extent relative to caput tibiotarsi, facies articulares, forma (**ordered**):

a. former exceptionally proximad to latter;

b. former well proximad to latter, defining distinct fossa(e) retropatellaris(es) caudally;

c. former subequal to latter.

2107. Extremitas proximalis tibiotarsi, caput tibiotarsi, crista cnemialis lateralis, crista patellaris, situs origii m. fibularis (peroneus) longus, forma:

a. variably distinct broadening of margo proximalis cristae patellaris;

b. variably prominent, distinctly elliptical, terminally ahamulate facet on unusually rounded, truncated crista patellaris.

Note.—See: Ballmann (1969a).

2108. Extremitas proximalis tibiotarsi, caput tibiotarsi, facies articularis fibularis, status et forma (**ordered**):

a. absent or virtually indistinguishable from margo capitis;

b. present, shallow incisura;

c. present, short jugum extending distad from margo capitis et/aut distinct lateral extension of rima capitis.

Note.—See: Livezey (1998b: appendix A, character 314). Articulatio between capita fibulae et tibiotarsi lacking in Podicipedidae and Gaviidae.

2109. Extremitas proximalis tibiotarsi, caput tibiotarsi, fossa flexoria (craniocaudal perspective), altitudo lateromedialis (**ordered**):

a. absent or obsolete;

b. comparatively shallow;

c. comparatively deep.

Note.—Conformation of this "fossa" (curva marginis) in articulated crura can confound fossa flexoria propria (i.e., feature of facies lateralis tibiotarsi) and the form of margo medialis of the laterally bounding os fibula (latter coded separately). Present character assessed by lateromedial depth of fossa relative to margo lateralis of caput tibiotarsi proximally and terminus proximalis cristae fibularis distally, typically reflected most obviously by excavatio immediately distal to caput (exclusive of crista patellaris) in caudal perspective.

2110. Extremitas proximalis tibiotarsi, caput tibiotarsi, facies (gastrocnemialis) medialis (medial perspective), forma superficialis (**unordered**):

a. concave, frequently an oblique sulcus;

b. concave distally, convex proximally;

c. (sub)planar.

2111. Extremitas proximalis tibiotarsi, caput tibiotarsi, facies (gastrocnemialis) medialis, crista (interna) medialis, forma:

a. essentially smooth or with indistinct margo capitis;

b. markedly textured by impressiones, jugae, et concavitas subcristalis.

2112. Extremitas proximalis tibiotarsi, caput tibiotarsi, fossae retropatellares, status et forma (**ordered**):

a. absent; **b.** present, shallow;

c. present, deep.

Note.—See: Bledsoe (1988: appendix, character 55), regarding "channeling" adjacent to "intercondylar eminence"; Livezey (1998b: appendix A, character 318). Synonymous with fossa retrocristalis (Butendieck 1980; Butendieck and Wissdorf 1981; Butendieck et al. 1981), fossa retropatellaris typically is partitioned (if present) by variably distinct jugum into lateral and medial subparts, and is occupied *in vivo* by corpus adiposus retropatellaris (Baumel and Witmer 1993: annotation 268).

2113. Extremitas proximalis tibiotarsi, caput tibiotarsi, fossa retropatellaris, ostia pneumatica—recessus et/aut foramina (pori) pneumatici—status et forma:

a. absent, neither recessus nor separate foramina/pori evident;

b. present, limited to foramina et/aut pori;

c. present, recessus enclosing foramina et/aut pori.

Note.—Assessments intended to exclude pori neurovascularia.

2114. Extremitas proximalis tibiotarsi, caput tibiotarsi, impressio ligamenti collateralis medialis, status et forma (**ordered**):

a. present, prominent tuberculum, conspicuously convex caudomedially;

b. present, moderate eminentia, jugum, or distinct impressio evident (craniocaudal perspective) as medial convexity;

c. present, distinct impressio, a superficial feature not producing medial convexity.

Note.—See: Ballmann (1969a: fig 2), "labeled tuberositas interna"; Andors (1992: table 1, character 14), in reference to "internal ligamental prominence." Where discernable, typically located distomedial to tuberositas poplitea, opposite terminus proximalis of crista fibularis; in some cases, two former features can shift toward one another, complicating differentiation of the two.

2115. Extremitas proximalis tibiotarsi, facies caudalis, fossa flexoria, foramina pneumatica, status:
a. absent; **b.** present.
Note.—Many taxa lack foramina pneumatica while manifesting a few, scattered pori neurovascularia (assigned state "a"). Where present, pori et/aut foramina pneumatica frequently dispersed proximad to concavitas inframarginis (**new term**) adjacent to caput tibiotarsi, facies articularis medialis et lateralis.

2116. Extremitas proximalis tibiotarsi, caput tibiotarsi, incisura tibialis, medial extent relative to facies articularis medialis:
a. less than one-half;
b. more than two-thirds.
Note.—See: J. D. Harris (1998: appendix 2, character 130); Siegel-Causey (1988: character 130); Azuma and Currie (2000: appendix 1, character 105); Currie and Carpenter (2000: appendix 1, character 106), under name "fibular fossa"; Holtz (2000 [1998]: appendix I, character 347), citing J. D. Harris (1998).

Corpus tibiotarsi

2117. Corpus tibiotarsi, generalized, pronounced, craniocaudal compression (especially distally), status:
a. absent; **b.** present.
Note.—See: Cracraft (1982: series 4, character 5); Cracraft (1988: series XI, character 10).

2118. Corpus tibiotarsi, craniocaudal curvature in which facies cranialis corporis (concurvilinear with axis majoris) is convex, status:
a. absent; **b.** present.

2119. Corpus tibiotarsi, lateromedial curvature in which facies lateralis corporis is generally convex, status:
a. absent; **b.** present.

2120. Corpus tibiotarsi, pars distalis, facies cranialis, forma superficialis and in planum transversus:
a. convex, cylindrical;
b. distinctly laminate or flat, typically extending proximad for distal one-third to one-half of corpus, and including segment proximal to sulcus extensorius.
Note.—See: Andors (1992: table 1, character 12); Novas (1994 [1993]: appendix, character 21); Livezey (1998b: appendix A, character 324).

2121. Corpus tibiotarsi, crista fibularis, lateral prominence, status (**unordered**):
a. absent;
b. present, rudimentary or obsolete;
c. present, moderately prominent;
d. present, very prominent, lateromedial width of crista exceeding maximal width of spina fibulae.
Note.—Benton (1990a: 21) considered "fibula closely appressed to tibia and attached to a tibial crest" to be synapomorphic of Theropoda. See: Pérez-Moreno et al. (1993); Livezey (1998b: appendix A, character 319); Holtz (2000 [1998]: appendix I, character 350); Norell and Clarke (2001: character 175); Maryanska et al. (2002: appendix 1, character 180); Zhou and Zhang (2002: appendix III, character 175).

2122. Corpus tibiotarsi, crista fibularis, margo lateralis cristae (craniocaudal perspective), forma marginalis (**unordered**):
a. essentially linear, i.e., crista of approximately uniform breadth;
b. distally deepening, i.e., crista distinctly broadest distally, least broad proximally;
c. concave, i.e., sectio intermedius cristae of minimal lateral breadth;
d. convex, i.e., sectio intermedius cristae of maximal lateral breadth;
e. distally diminishing, i.e., crista distinctly broadest proximally, least broad distally;
x. noncomparable (Aepyornithiformes, Dinornithiformes, *Phaethon*, *Turnix*).
Note.—Where more than one pattern applies, principal trend coded as representative. In all cases, margo medialis of os fibulae tends to assume complementary form.

2123. Corpus tibiotarsi, crista fibularis, continuity proximad to margo lateralis capitis (i.e., crista traverses fossa flexoria), status (**ordered**):
a. absent;
b. present, extending proximad to margo lateralis capitis;
c. present, crista separated by hiatus from margo lateralis capitis.
Note.—See: Rauhut (2003: character 206). Although hiatus characterizes Neornithes, proximodistal length of same varies considerably among taxa.

2124. Corpus tibiotarsi, crista fibularis, situs proximodistalis (**unordered**):
a. proximal, crista fibularis entirely limited to proximal one-fourth of corpus tibiotarsi;
b. subproximal, crista fibularis entirely or largely limited to proximal one-third of corpus tibiotarsi;
c. subdistal, crista fibularis extending over majority of proximal one-half of corpus tibiotarsi;
d. distal, crista fibularis entirely or largely limited to intermediate one-third of corpus tibiotarsi.
Note.—See: Holtz (2000 [1998]: appendix I, character 351); Maryanska et al. (2002: appendix 1, character 180). Alternative interpretation of this character is to relate the relative proximodistal lengths of

the spatium tibiofibularis proximalis et spatium tibiofibularis distalis (**new terms**) delimited by ossa tibiotarsus et fibula and the interconnecting crista or syndesmosis (Livezey 1998b: appendix A, character 320).

2125. Corpus tibiotarsi, crista fibularis, situs caudolateralis:
a. caudal; **b.** lateral.
Note.—See: Welles and Long (1974); Russell and Dong (1994a [1993a]: table 2, character 55); Holtz (1994a: appendix 1, character 100); J. D. Harris (1998: appendix 2, character 131), cast in terms of presence or absence; Holtz (2000 [1998]: appendix I, character 348), in reference to "sharp ridge on tibia anterolaterally for clasping fibula."

2126. Corpus tibiotarsi, facies lateralis, crista fibularis (lateral perspective), angulus with respect to axis majoris tibiotarsi:
a. essentially parallel;
b. terminus proximalis cristae angled caudad, caput fibulae comparatively caudad.
Note.—Caudal orientation of caput fibulae relative to extremitas proximalis tibiotarsi is augmented by curvature of the spina fibulae, notably in Columbiformes.

2127. Corpus tibiotarsi, facies medialis (craniocaudal perspective), margo medialis (sectio proximalis), apparent medial torsion of crista cnemialis cranialis and distal prominence of linea extensoria, status:
a. absent;
b. present, opposite crista fibularis.
Note.—Linea extensoria (Butendieck 1980: 116–117; Butendieck and Wissdorf 1981); Butendieck et al. 1981) evidently represents a cristula between origiones m. extensor digitorum longus et m. fibularis longus. See: Dyke and van Tuinen (2004: appendix 1, character 71).

2128. Corpus tibiotarsi, margo lateralis (fibularis), foramen interosseum proximale, forma:
a. approximately ovate, relatively spacious;
b. sublinear and incisurate, relatively narrow.
Note.—Assessments complicated by diversity in absolute sizes of elements and warping of ossa fibulae.

2129. Corpus tibiotarsi, margo lateralis (fibularis), foramen interosseum distale, status et forma *sensu* length relative to that of foramen interosseum proximale (**unordered**):
a. absent, spina fibulae terminating or effectively free-standing at crista fibularis, thereby failing to define foramen interosseum distale;
b. present, essentially occluded by proximity to tibiotarsus et septum interosseum, distinctly shorter than foramen interosseum distale;
c. present, moderately elongate, subequal to foramen interosseum proximale;
d. present, elongate, significantly longer than foramen interosseum proximale.
Note.—See: Livezey (1998b: appendix A, character 320).

2130. Corpus tibiotarsi, margo lateralis (fibularis), proximodistal broadening of crista and laterally convex curvature of elongate os fibula, resulting in foramen interosseum distale being two to three times as long as foramen interosseum proximale, status:
a. absent; **b.** present.

2131. Corpus tibiotarsi, tuberositas poplitea, forma:
a. distinct crista or jugum, infrequently in combination with conspicuous impressio;
b. poorly defined impressio aut jugum truncatus, or absent entirely.
Note.—Where present, typically assumes form of cristate support for margo caudalis of facies articularis tibiotarsi, most commonly aligned with area et/aut incisura interarticularis tibiotarsi.

2132. Corpus tibiotarsi, linea extensoria, status:
a. absent; **b.** present.
Note.—See: Chiappe and Calvo (1994: appendix I, character 64); Chiappe et al. (1996: appendix 1, character 58); Forster et al. (1998: supplement, character 112); Vickers-Rich et al. (2002), concerning *Avimimus*.

2133. Corpus tibiotarsi, linea extensoria, tuberositas proximalis retinaculi mm. extensorum, status et forma (**unordered**):
a. present, modestly elevated jugum, eminentia, aut tuberculum;
b. present, sessile impressio;
c. absent;
d. present, prominent cristulate processus.
Note.—Feature represents situs ancorae of proximomedial terminus of retinaculum under which tendines mm. extensorum pass proximal (in those taxa possessing feature), the deep members of which continuing to the osseous restraint effected by the pons supratendineus (treated separately). Tuberositas tends to be comparatively proximal in position in those taxa lacking pons supratendineus.

2134. Corpus tibiotarsi, facies cranialis, sulcus extensorius, status:
a. absent or obsolete;
b. present, presenting continuum of proximal extents, widths, and delimitation.
Note.—See: Welles and Long (1974); Gauthier (1986: 14, unindexed synapomorphy of Ornithurae); Chiappe (1995b: character 64); Sanz et al. (1995, 1997: character 62); Chiappe (1996b: character 59); Livezey (1998b: appendix A, character 322); Mak-

ovicky and Sues (1998: appendix 1, character 90); Chatterjee (1999: appendix II, character 81), with respect to "extensor canal"; Azuma and Currie (2000: appendix 1, character 3); Chiappe (2001a: appendix 1, characters 150 and 152); Chiappe (2002: appendix 20.2, characters 150 and 152); Chiappe and Walker (2002: appendix 11.1, character 29).

2135. Corpus tibiotarsi, facies cranialis, sulcus extensorius, pars distalis, situs relative to axis majoris corporis (**ordered**):

a. distinctly medial;

b. approximately co-aligned;

c. distinctly lateral.

Note.—This character is distinct from terminal curvature of pars distalis of sulcus extensorius in the extremitas distalis tibiotarsi, e.g., that emphasized by the pons supratendineus (where present), but instead distinguished broad classes of orientation of the sulcus proprius with respect to the margines lateralis and medialis of corpus tibiotarsi.

2136. Corpus tibiotarsi, linea extensoria, tuberositas distalis retinaculi mm. extensorum, status:

a. absent or mere impressio;

b. present, tuberculum or cristula.

Note.—See: Chiappe et al. (1999: fig. 43), regarding "tibiotarsal distal tubercle" in *Confuciusornis*; Norell and Clarke (2001: appendix I, character 181), treated similarly by J. A. Clarke (2002: appendix I, character 181), J. A. Clarke and Norell (2002: appendix 2, character 181), and J. A. Clarke (2004: appendix 1, character 181), in which feature identified as tuberositas retinaculi extensoris and credited to Baumel and Witmer (1993) was described as "short medial ridge or tubercle proximal to the condyles close to the midline and a more proximal second ridge on the medial edge"; Ji et al. (2005: supplement, part I, character 181).

2137. Corpus tibiotarsi, tuberculum ligamenti tibiometatarsale intercondylare (**new term**), status:

a. absent or indiscernable;

b. present and prominent;

x. noncomparable (Dinornithiformes).

Note.—Feature, mislabelled as "tubersositas distalis retinaculi mm. extensorum" by Butendieck (1980), Butendieck and Wissdorf (1981), Butendieck et al. (1981), is laterodistal to pons supratendineus and proximomedial to condylus lateralis tibiotarsi (Baumel and Raikow 1993: annotation 171). See: Cracraft (1988: series XII, character 3), pertaining to "large tubercle whose concave distal surface is continuous with anterior intercondylar fossa" (p. 352); Livezey (1998b: appendix A, character 321), in which feature confused with more-proximal tuberositas distalis retinaculi mm. extensorium; G. Mayr and Clarke (2003: appendix A, character 101); G. Mayr and Ericson (2004: character 72).

2138. Corpus tibiotarsi et/aut extremitas distalis tibiotarsi, lineae m. fibularis (peronei), tuberculum retinaculi m. fibularis (peronei), status et forma (**unordered**):

a. absent, at most indicated by linea aut jugum;

b. present, a moderately prominent tuberculum aut eminentia;

c. present, a prominent cristula.

Note.—See: Livezey (1998b: appendix A, character 327); G. Mayr (2004d: appendix I, character 33), referred to as "proximal end with ridge opposite crista fibularis"; G. Mayr (2005a: appendix 1, character 34). Linea m. fibularis *per se*, arising proximally at terminus distalis cristae fibularis, proximate and terminating distomedial to tuberositas distalis retinaculi mm. extensorium (latter situs of tuberculum, if present), varies from completely absent to weakly evident and defied partitioning into discrete states accordingly. Tuberculae or other eminentiae at the terminus distalis of this linea vary in position on extremitas distalis tibiotarsi, ranging from immediately proximal to condylus lateralis on facies cranialis tibiotarsi to facies lateral tibiotarsi.

Extremitas distalis (tibiotarsi) tibialis

2139. Extremitas distalis tibialis, facies articularis distalis (distal perspective), forma (**unordered**):

a. subrectangular, only slightly broader lateromedially than deep craniocaudally;

b. subrectangular, with small processus lateralis;

c. narrow and triangular, strongly lateromedially broadened;

d. rectangular, lateromedial breadth at least three times greater than craniocaudal depth.

Note.—See: Rauhut (2003: character 208).

2140. Extremitas distalis tibiotarsi et ossa tarsi proximales, distalmost (composite) lateromedial width relative to that at midpoint of corpus tibiotarsi:

a. former greater than latter, extremitas distalis only weakly triangular in profile;

b. former approximately equal to latter, extremitas distalis virtually undistinguished in width from corpus.

Note.—See: Hou et al. (1995); Norell and Clarke (2001: appendix I, character 186), treated similarly by J. A. Clarke (2002: appendix I, character 186), J. A. Clarke and Norell (2002: appendix 2, character 186), and J. A. Clarke (2004: appendix 1, character 186), and using term "sulcus cartilaginis tibialis"; Zhou and Zhang (2002: appendix III, character 186); Ji et al. (2005: supplement, part I, character 186).

2141. Extremitas distalis tibiotarsi, condylus lateralis, situs marginalis condyli relative to margo lateralis corpus tibiotarsi (**ordered**):

a. distinctly lateral; **b.** coplanar;

c. distinctly medial.

Note.—Alignment assessed by relative positions of planum lateralis condyli (exclusive of irregularities of angling or terminal displacement) et planum lateralis corpus tibiotarsi. See: Cracraft (1974: 501, character 6; figs. 5–6); Bledsoe (1988: appendix, characters 60–62, part); Novas (1996: appendix, character M19), in reference to craniocaudal breadth relative to the "calcaneum"; K. Lee et al. (1997: appendix 1, characters 36 and 41, part); Livezey (1998b: appendix A, character 325); Azuma and Currie (2000: appendix 1, character 107).

2142. Extremitas distalis tibiotarsi, condylus lateralis, breadth relative to condylus medialis (**ordered**):

a. narrow, former distinctly less wide than latter;

b. of approximately equal width;

c. broad, former distinctly wider than latter.

Note.—See: Cracraft (1974: 501, character 6); Bledsoe (1988: appendix, characters 60–61); Novas (1996: appendix, character M19), in reference to craniocaudal breadth relative to the "calcaneum"; K. Lee et al. (1997: appendix 1, character 36); Azuma and Currie (2000: appendix 1, character 107); Norell and Clarke (2001: appendix I, character 182), treated similarly by J. A. Clarke (2002: appendix I, character 182), J. A. Clarke and Norell (2002: appendix 2, character 182), and Chiappe and Walker (2002: fig. 11.13); Ji et al. (2005: supplement, part I, character 182).

2143. Extremitas distalis tibiotarsi, condylus lateralis, lateral prominence relative to corpus tibiotarsi (proximal perspective), facies lateralis, forma generalis (**ordered**):

a. great, bulging from surface of tibiotarsus;

b. moderate, considerable concavity of corpus tibiotarsus, margo lateralis, proximal to condylus;

c. minimal, lateral prominence of condylus slight.

Note.—See: Azuma and Currie (2000: appendix 1, character 108, polarity reversed); Holtz (2000 [1998]: appendix I, character 349).

2144. Extremitas distalis tibiotarsi, condylae medialis et lateralis (latter sine tuberositas distales retinaculae), forma *sensu* cranial prominence:

a. condylus medialis distinctly more cranially prominent than condylus lateralis;

b. condylus medialis approximately equal in cranial prominence as condylus lateralis.

Note.—See: Cracraft (1974: 501, character 7; figs. 5–6); Livezey (1986: appendix 1, character 64); Bledsoe (1988: appendix, characters 60, 64–65); Cracraft (1988: series VIII, character 9; series XIII, character 4); Andors (1992: table 1, characters 13 and 15; table 2, character 42); Elzanowski (1995: character E3); Livezey (1995a: appendix 1, character 11); Livezey (1995b: appendix 1, character 18); Livezey (1995c: appendix II, character 32); Sanz et al. (1995, 1997: character 79); Livezey (1996c: character 11); K. Lee et al. (1997: appendix 1, character 38); Livezey (1997a: appendix 1, character 86; *corrigenda*, Livezey 1998a); Chiappe et al. (1998: character 84) and Ji et al. (1998: supplement, character 84), with respect to cranial prominences of margines medialis et lateralis of corpus; Livezey (1998b: appendix A, character 329); Chiappe (2001a: appendix 1, character 151); Norell and Clarke (2001: appendix I, character 179), treated similarly by J. A. Clarke (2002: appendix I, character 179), J. A. Clarke and Norell (2002: appendix 2, character 179), and J. A. Clarke (2004: appendix 1, character 179); Chiappe (2002: appendix 20.2, character 151); Dyke and Gulas (2002: appendix 1, character 42); Zhou and Zhang (2002: appendix III, character 182); Zhou and Zhang (2002: appendix III, character 179, part); G. Mayr (2004a: appendix 1, character 55), regarding "prominent tubercle latero-distal to pons supratendineus"; Ji et al. (2005: supplement, part I, character 179).

2145. Extremitas distalis tibiotarsi, condylus medialis relative to condylus lateralis tibiotarsi, forma *sensu* distal extent (**ordered**):

a. distinctly distal; **b.** subequal;

c. distinctly proximal.

Note.—See: Cracraft (1985: character 32); G. Mayr (2003a: appendix I, character 37); G. Mayr (2004b: appendix 1, character 45).

2146. Extremitas distalis tibiotarsi, condylus lateralis (cranial perspective), rima condylaris, proximodistal length relative to that of condylus lateralis, rima condylus (**ordered**):

a. distinctly greater;

b. approximately equal; **c.** distinctly less.

Note.—See: Chiappe (2002: appendix 20.2, character 149), worded as "medial border of tibiotarsus at nearly the level of lateral border or strongly projected proximally." In at least some cases, angulus or incisura condyli marks a situs ancorae of terminus laterodistalis of retinaculum mm. extensorium.

2147. Extremitas distalis tibiotarsi, condylus lateralis, rima condylaris, margo cranialis, intersectio corporis (basis cranialis condyli), angulus aut incisura, status:

a. absent, condylus essentially of monotonic curvature and terminating on facies cranialis tibiotarsi comparatively gradually or attaining unmodified apex separated from corpus by shallow depressio;

b. present, condylus marked by distinct angulus aut incisura cranial to basis.

Note.—In at least some cases, angulus or incisura condyli marks intrusion of situs ancorae of terminus laterodistalis of retinaculum mm. extensorium, a feature manifested at least in part as tuberculum in many taxa. See: Murray and Vickers-Rich (2004:

table 9, character 32; fig. 140C), for a related assessment of lateral profile of condylus lateralis among Dromornithidae.

2148. Extremitas distalis tibiotarsi, medial inflection of condylus medialis from axis majoris condyli relative to axis proximodistalis tibiotarsi, status:
a. absent; **b.** present, comparatively subtle.
Note.—See: Andors (1992: table 2, character 43); Livezey (1997a: appendix 1, character 87; *corrigenda*, Livezey 1998a), regarding slope of condylus and associated medial expansion of area intercondylaris.

2149. Extremitas distalis tibiotarsi, facies cranialis, condyli medialis et lateralis, distinct departure in parallel from axis majoris tibiotarsi, status et forma (**unordered**):
a. absent; **b.** present, laterad;
c. present, mediad.
Note.—See: Murray and Vickers-Rich (2004: table 9, character 33), regarding alignment of condylae (caudal perspective) in Dromornithidae.

2150. Extremitas distalis tibiotarsi, facies cranialis, condylus medialis, medial displacement resulting in craniomedial departure from perpendicularity associated with axis majoris tibiotarsi (distal perspective) and bulbous aspect (cranial perspective), status:
a. absent; **b.** present.

2151. Extremitas distalis tibiotarsi, facies lateralis, condyli medialis (especially) et lateralis, rima condylaris, forma marginalis:
a. suborbiculate;
b. distinctly subrectangular and craniocaudally elongate distally, with rounded craniodistal and caudodistal vertices.
Note.—Assessments intended to exclude effects of depressio epicondylares on margines.

2152. Extremitas distalis tibiotarsi, facies lateralis, condylus medialis, incisura supracondylaris (**new term**), forma angularis (medial perspective):
a. absent or indistinct;
b. present and distinct.

2153. Extremitas distalis tibiotarsi, facies cranialis, condylus medialis et margo (crista) medialis of trochlea cartilaginis tibialis (caudal perspective), distinct lateral angulus cristae with facies caudomedialis corporis forming broad, shallow, and smooth sulcus caudad to epicondylus medialis, status:
a. absent; **b.** present.
Note.—See: G. Mayr (2004a: appendix 1, character 56).

2154. Extremitas distalis tibiotarsi, condylus medialis, depressiones epicondylares medialis et lateralis, status (**unordered**):
a. absent;
b. present, depressio medialis only;
c. present, depressio lateralis only;
d. present, both depressiones medialis et lateralis, typically demarcating condylae propriae from crista cartilagines.
Note.—See: Cracraft (1974: 501, character 7); Bledsoe (1988: appendix, character 63); K. Lee et al. (1997: appendix 1, characters 37 and 39); Cracraft (1988: series XV, character 7), in reference to rima “flattened anterolaterally” and “thickened posteriorly,” the latter forming a “medial wall” for sulcus intercondylaris caudalis tibiotarsi. Described by Baumel and Witmer (1993: annotation 281).

2155. Extremitas distalis tibiotarsi, condylae medialis et lateralis, incisura intercondylaris (distal perspective), foveae (sulcus) transcondylares medialis et lateralis (**new terms**), status:
a. absent; **b.** present.
Note.—Evidently related to enlarged tuberculum ligamenti tibiometatarsale intercondylare. Potentially special case of state “d” for foveae ligamentosae. See: G. Mayr and Clarke (2003: appendix A, character 102).

2156. Extremitas distalis tibiotarsi, depressiones condylorum medialis et lateralis, foveae ligamentosae (**new term**), status et forma (**unordered**):
a. absent or indiscernable;
b. present, limited to fovea (incisura) medialis, typically dividing condylus proprius from crista sulci;
c. present, limited to fovea medialis, but uniquely conformed as sulcus obliquus condyli (**new term**) oriented proximolaterad to distomediad;
d. present, comprising both foveae medialis et lateralis.
Note.—See: Cracraft (1985: character 32, part); Livezey (1986: appendix 1, character 66); Livezey (1995c: appendix II, character 34); Livezey (1998b: appendix A, character 32).

2157. Extremitas distalis tibiotarsi, epicondylus lateralis, depressio epicondylaris lateralis, fovea ligamenti collateralis lateralis (**new term**), status:
a. absent or indistinct, at most vaguely distinguished from cranial terminus of depressio epicondylaris lateralis proper;
b. present, well delimited and suborbiculate.

2158. Extremitas distalis tibiotarsi, condylus medialis et epicondylus medialis, depressio epicondylaris medialis, marked, stepped, medial displacement of pars proximocranialis (distal perspective), status:
a. absent; **b.** present.

2159. Extremitas distalis tibiotarsi, epicondylus medialis, depressio epicondylaris medialis, fovea ligamenti collateralis medialis (**new term**), status:
a. absent or indistinct, at most vaguely distinguished from cranial terminus of depressio epicondylaris medialis proprius;
b. present, well delimited and suborbiculate.

Note.—See: Murray and Vickers-Rich (2004: table 9, character 29; fig. 140D), regarding form of "impressio ligamentum collateralis medialis" in Dromornithidae.

2160. Extremitas distalis tibiotarsi, condylae lateralis et medialis, et incisura intercondylaris, distinct structures from ontogenetic primordia of tibiotarsus et ossa proximalia tarsi, forma:

a. poorly developed; **b.** well developed.

Note.—See: Xu et al. (2002a: supplement, character 158), with respect to production of condylae distales tibiotarsales (and interposed sulcus) by ossa proximalia tarsi.

2161. Extremitas distalis tibiotarsi, incisura intercondylaris, breadth relative to that of facies cranialis tibiotarsi (**ordered**):

a. broad, approximately one-third of width of facies cranialis tibiotarsi;

b. narrow, less than one-third of width of facies cranialis tibiotarsi;

c. obsolete, condylae essentially unseparated cranially.

Note.—See: Cracraft (1974: 498, character 4); Andors (1992: table 1, character 18; table 2, character 44); Chiappe and Calvo (1994: appendix II, character 18), listed as synapomorphy of Enantiornithes a "narrow intercondylar notch"; Novas (1996: appendix, character M20), with respect to "astragalocalcaneal intercondylar groove"; K. Lee et al. (1997: appendix 1, character 40); Hughes (2000: appendix 2, character 57); Norell and Clarke (2001: appendix I, character 184), treated similarly by J. A. Clarke (2002: appendix I, character 184), and J. A. Clarke (2004: appendix 1, character 184); Norell et al. (2001: appendix 1, character 192); J. A. Clarke and Norell (2002: appendix 2, character 184); J. M. Clark et al. (2002a: appendix 2.2, character 194); Zhou and Zhang (2002: appendix III, character 184); G. Mayr et al. (2003: appendix 1, character 59); Hwang et al. (2004: supplement, character 191); Murray and Vickers-Rich (2004: table 9, characters 30–31), termed "facies rotularis posterior," "intercondylar groove," or "incisura intercondylaris" in Dromornithidae; Xu and Norell (2004: supplement, character 191); Ji et al. (2005: supplement, part I, character 184).

2162. Extremitas distalis tibiotarsi, incisura intercondylaris, bilateral pair of shallow sulci internal to condylae lateralis et medialis, in combination with subrectangular forma of incisura (planum transversus), status:

a. absent; **b.** present.

2163. Extremitas distalis tibiotarsi, facies cranialis, incisura intercondylaris (distal perspective), proximodistal depth relative to lateromedial width (at cranial extremities of condylae), forma (**ordered**):

a. short—former distinctly less than one-half of latter, typically sulci caudalis et cranialis of comparable depths;

b. intermediate—former between one-half and equality of latter;

c. long—former at least as great as latter.

2164. Extremitas distalis tibiotarsi, condylae lateralis et medialis, et incisura intercondylaris, comparative medial tapering, status:

a. present, gradual; **b.** absent.

Note.—See: Norell and Clarke (2001: appendix I, character 183), in reference to "gradual sloping medial constriction of [both] condyles," treated similarly by J. A. Clarke (2002: appendix I, character 183), J. A. Clarke and Norell (2002: appendix 2, character 183), and J. A. Clarke (2004: appendix 1, character 183); Zhou and Zhang (2002: appendix III, character 183); Ji et al. (2005: supplement, part I, character 183).

2165. Extremitas distalis tibiotarsi, facies cranialis, incisura intercondylaris, area intercondylaris, forma lateromedialis (**ordered**):

a. fossa of variable depth, in most taxa not prominent in regio lateral to condylus medialis;

b. sulcus extending between condylae but narrowed and more shallow laterally through infilling by basis lateralis retinaculum;

c. obsolete or narrow sulcus extending and of uniform width between condylae.

2166. Extremitas distalis tibiotarsi, facies cranialis, incisura intercondylaris, area intercondylaris, status et forma circumcondylaris (**ordered**):

a. distally delimiting pila transversa intercondylaris (**new term**) comparatively prominent distally, virtually occluding (craniocaudal perspective) incisura intercondylaris distally;

b. distally delimiting pila transversa intercondylaris (**new term**) comparatively recessed distally, but accommodating approximately one-half of distal depth (craniocaudal perspective) of incisura intercondylaris;

c. absent, incisura uninterrupted, continuous around extremitas distalis tibiotarsi.

2167. Extremitas distalis tibiotarsi, facies cranialis, incisura intercondylaris, area intercondylaris, comparative (craniocaudal) depth (**ordered**):

a. absent or obsolete;

b. present, moderately deep;

c. present, exceptionally deep, distinctly deeper than more-distal pila transversa intercondylaris.

Note.—This character assesses depth of area intercondylaris relative to that of pila transversa intercondylaris (**new term**) and other adjacent features, whereas preceding character treats distal exclusion of incisura intercondylaris by pila transversa intercondylaris.

2168. Extremitas distalis tibiotarsi, incisura intercondylaris, area intercondylaris, impressio ligamenti intercondylaris, forma et situs (**unordered**):

a. comparatively central, essentially encompassed within area intercondylaris;

b. comparatively medial, delimiting bifurcate, medial invaginationes on facies lateralis of condylus medialis;

c. profoundly medial, manifesting a distinct excavatio in facies lateralis of condylus medialis.

Note.—See: Livezey (1998b: appendix A, character 330); Hughes (2000: appendix 2, character 57).

2169. Extremitas distalis tibiotarsi, impressio et sulcus capitis tibiale m. fibularis (peronei) brevis, forma profunda et proximodistalis (**unordered**):

a. depressio et sulcus shallow, indistinctly delimited;

b. depressio moderately deep, distinctly delimited, sulcus shallow, poorly defined;

c. depressio deep, distinctly delimited, sulcus raised, well distinguished, infrequently refined to margines of retinaculum or osseous canalis.

Note.—Impressio extends from terminus distalis cristae fibularis to sulcus proximolateral to condylus lateralis tibiotarsi. See: Bledsoe (1988: appendix, character 59) regarding "ridge extending laterally from extensor canal" in some ratites; Chu (1998: appendix 1, character 112).

2170. Extremitas distalis tibiotarsi, trochlea cartilaginis tibialis, sulcus cartilaginis tibialis margines lateralis et medialis trochleares, forma proximocaudalis (**ordered**):

a. margines et sulcus weakly developed;

b. margines et sulcus moderately developed;

c. margines et sulcus substantially developed, with deep sulcus cartilaginis tibialis.

Note.—See: Livezey (1998b: appendix A, character 328); Hughes (2000: appendix 2, character 57); Norell and Clarke (2001: appendix I, character 185), similarly by J. A. Clarke (2002: appendix I, character 185), J. A. Clarke and Norell (2002: appendix 2, character 185), and J. A. Clarke (2004: appendix 1, character 185); Zhou and Zhang (2002: appendix III, character 185). Trochlea cartilagines tibialis ontogenetically derives from os tibiale, hence vernacular synonym of "astragular condyles"; Ji et al. (2005: supplement, part I, character 185).

2171. Extremitas distalis tibiotarsi, trochlea cartilaginis tibialis, status et forma *sensu* lateromedial (transverse) width relative to condyli tibiotarsalia (**unordered**):

a. absent, essentially undefined;

b. present, trochlea distinctly narrower than condyli;

c. present, trochlea subequal in width to condyli.

Note.—See: Cracraft (1988: series XIV, character 8), pertaining to last state; Cracraft (1988: series XII, character 4), pertaining to (p. 352) "anterior intercondylar fossa deeper than anterodistal edge of posterior intercondylar sulcus, i.e., fossa undercuts sulcus);" Zhou and Zhang (2002: appendix III, character 180, part).

2172. Extremitas distalis tibiotarsi, trochlea cartilaginis tibialis, cristae trochleares, bilateral symmetry of margines medialis et lateralis, status et forma (**unordered**):

a. symmetrical, margines trochleares essentially proximodistally oriented;

b. symmetrical, margines trochleares approximately equally convergent by "proximal tapering" or opposing slope toward axis majoris corporis;

c. asymmetrical, margo trochlearis medialis displaced distolateralis.

Note.—Butendieck (1980), Butendieck and Wissdorf (1981), and Butendieck et al. (1981) termed this feature "cristae sulci." See: Dyke and Gulas (2002: appendix 1, character 41); Dyke et al. (2003: appendix 1, character 78).

2173. Extremitas distalis tibiotarsi, trochlea cartilaginis tibialis, cristae trochleares, exceptionally prominent caudal extension and aliform status:

a. absent; **b.** present.

2174. Extremitas distalis tibiotarsi, trochlea cartilaginis tibialis, cristae trochleares, significantly greater caudal extent of crista lateralis relative to crista medialis, status:

a. absent; **b.** present.

2175. Extremitas distalis tibiotarsi, trochlea cartilaginis tibialis, margo proximalis trochlearis, vertices proximomedialis et proximolateralis (**new terms**), forma *sensu* relative proximal extents (**unordered**):

a. medial distinctly less than lateral;

b. approximately equal;

c. medial extremity distinctly proximad to lateral, often with either or both termina subtubercular.

Note.—See: Bledsoe (1988: appendix, character 58) regarding some ratites; G. Mayr (2002a: legend for fig. 9, node 1, character 3).

2176. Extremitas distalis tibiotarsi, facies cranialis, pons supratendineus definitivum, status:

a. absent, constraint of tendines (at least among included Neornithes) typically imposed by retinaculum ligamentosus;

b. present.

Note.—Minimal intraspecific variation (e.g., *Haematopus*) attributable to late developmental ossification of ligamentum pontis, resulting in partial or absent pons ossificans in prepared skeletons of some young. See: Marsh (1880: pl. XIV); Cracraft (1974: 501, character 5, part); Thulborn (1984: 126–127, character 20); Cracraft (1986: appendix, character 5); Gauthier (1986: 14, unindexed synapomorphy of Aves); Bledsoe (1988: appendix, character 57); Cracraft (1988: series IV, character 7); Houde (1988: table 27, character 48); Cracraft and Mindell (1989: table 1, character 7); Elzanowski (1995: character N'7); Kurochkin (1995b: table 1, character 27); Hou et al. (1996: legend for fig. 3); Ericson (1997: table 1, character 68); K. Lee et al. (1997: appendix 1, character 35); J. A. Clarke and Chiappe (2001: character 64); Cracraft and Clarke (2001: appendix 2, character 29); Norell and Clarke (2001: appendix I, character 180), treated similarly by J. A. Clarke (2002: appendix I, character 180), J. A. Clarke and Norell (2002: appendix 2, character 180), and J. A. Clarke (2004: appendix 1, character 180); Zhou and Zhang (2002: appendix III, character 180, part); G. Mayr and Clarke (2003: appendix A, character 100); G. Mayr et al. (2003: appendix 1, character 58); Dyke and van Tuinen (2004: appendix 1, character 72); Ji et al. (2005: supplement, part I, character 180).

2177. Extremitas distalis tibiotarsi, facies cranialis (sulcus extensorius), pons supratendineus, comparative caudal depth (cranial perspective) within corpus tibiotarsi, forma:

a. comparatively shallow, pons typically convex and prominently arched craniad to facies cranialis tibiotarsi;

b. comparatively deep and restricted, pons typically compressed caudad and canalis occult;

x. noncomparable by absence of sulcus et/aut pons (ratites, Psittaciformes, Strigiformes, some Caprimulgiformes).

Note.—Apomorphic state suggestive of means by which pons lost and sulcus reduced.

2178. Extremitas distalis tibiotarsi, facies cranialis (sulcus extensorius), pons supratendineus, canalis extensorius, situs lateromedialis (**ordered**):

a. medial; **b.** mesial; **c.** lateral;

x. noncomparable by absence of vestigia of pons et/aut canalis (ratites).

Note.—Distinct from foregoing characterization of lateromedial position of sulcus extensorius on corpus tibiotarsi. Assessment based on alignment of centroid on pons central with respect to canalis. Also, to be distinguished from position of pons *per se*, in that whereas pons can extend across entire facies cranialis of extremitas distalis tibiotarsi, the canalis extensorius can be distinctly lateral or medial with respect to the overlying pons. See: Andors (1992: table 1, character 17).

2179. Extremitas distalis tibiotarsi, facies cranialis (sulcus extensorius), pons supratendineus, conspicuous depression caudad and significant narrowing and reduced depth of canalis extensorius, status:

a. absent; **b.** present;

x. noncomparable (ratites).

2180. Extremitas distalis tibiotarsi, facies cranialis (sulcus extensorius), pons supratendineus, canalis extensorius, ostium distomedialis mm. extensorius et fenestra distolateralis pontifica (**new terms**), status:

a. only ostium distomedialis present;

b. both ostium distomedialis et fenestra distolateralis pontificus present;

x. noncomparable by absence of pons (ratites, Psittaciformes, Strigiformes, some Caprimulgiformes).

Note.—See: Jollie (1977a: fig. 180). In a minority of taxa (e.g., Phalacrocoracidae, *Tigrisoma*, *Balaeniceps*, *Raphus*), a fovea or canaliculus occurs having a similar lateral ostium essentially identical to the fenestra distolateralis pontificus related to the bifucation of canali caudal to the pons supratendineus of some Falconiformes. Evidently, both derive ontogenetically from variation in form and synostosis between processus ascendens of os tibiale—although the former appears separate from the latter in juveniles of some taxa (e.g., Spheniscidae)—and os tibia (Jollie 1977a). Fenestra lateralis in not known to admit tendines, nervi, et/aut venae.

2181. Extremitas distalis tibiotarsi, facies cranialis (sulcus extensorius), pons supratendineus, canalis extensorius, orientation:

a. canalis principally aligned with axis majoris tibiotarsi, with minor, obliquely distomedial component;

b. canalis obliquely distolaterad in orientation, with pronounced, obliquely lateromedial component;

x. noncomparable by absence of pons (ratites, Psittaciformes, Strigiformes, some Caprimulgiformes).

Note.—See: Ligon (1967: fig. 5); Cracraft (1974: 501, character 5, part); Jollie (1977a: fig. 180); Cracraft (1988: series XV, character 8); Worthy (1988); Siegel-Causey (1988: character 132), regarding related but less tractable feature of relative curvilinearity of margines pontifica; Ericson (1997: table 1, character 69; table 2, character 44); Livezey (1998b: appendix A, character 323).

2182. Extremitas distalis tibiotarsi, facies cranialis, pons supratendineus, canalis extensorius, ostium distomedialis, orientation relative to condylus medialis et incisura intercondylaris (**unordered**):

a. directly toward incisura intercondylaris, typically ostium extending across lateromedial expanse of incisura;

b. laterad to facies lateralis of condylus medialis or obliquely through incisura intercondylaris;

c. essentially toward condylus medialis proprius;

x. noncomparable by absence of pons (ratites, Psittaciformes, Strigiformes, some Caprimulgiformes).

Note.—Although related in part to orientation of canalis extensorius *per se*, also a function in part of distance between ostium and condylus medialis. Feature also serves to subdivide taxa largely included under majority state of character pertaining to canalis extensorius.

2183. Extremitas distalis tibiotarsi, facies cranialis (pons supratendineus), canalis extensorius et area intercondylaris, foramina pneumatica extensive and perforating facies caudalis tibiotarsi, sulcus cartilaginis tibialis, status:
a. absent;
b. present in canalis deep to pons or ansa, as well as in area intercondylaris (especially impressiones ligamenti intercondylaris) and adjacent to sulcus cartilaginis tibialis.
Note.—Perforation of sulcus cartilaginis tibialis Bucerotidae approached by translucentia in same region in other taxa (e.g., Pandionidae).

Fibula

Note.—See: Baur (1885b); Shufeldt (1885a, 1894b); Streicher and Müller (1992).

2184. Caput fibulae, facies articularis femoralis, forma:
a. essentially horizontal (lateral perspective), facies articularis elongate-ellipsoidal;
b. distinctly angled (lateral perspective), maximally proximal caudad, facies articularis subelliptical.
Note.—Pertains to aspectus fibulae involved in articulatio femorofibularis (by way of condylus lateralis femoris, trochlea fibularis), a lateral adjunct to articulatio femorotibialis, together comprising the juncturae genus.

2185. Caput fibulae, facies articularis tibialis, jugum medialis fibulae (**new term**), status:
a. absent; **b.** present.
Note.—This facies articularis, listed following caput fibulae, pertains to the most proximal of juncturae tibiofibulares. See: Rowe and Gauthier (1990); Rauhut (2003: character 209), regarding "ridge on medial side of proximal end of fibula, that runs anterodistally from the posterproximal [*sic*] end."

2186. Caput fibulae, facies articularis tibialis, margo (terminalis) proximalis (lateral perspective), forma (**ordered**):
a. convex; **b.** sharply linear;
c. distinctly concave.

2187. Caput fibulae, facies articularis tibialis, forma (**ordered**):
a. distinctly, variably deeply concave;
b. essentially planar; **c.** distinctly convex.
Note.—See: Holtz (2000 [1998]: appendix I, character 356), in reference to "sulcus in proximomedial region of fibula" and attributed to Sereno et al. (1994); Xu et al. (2002a: supplement, character 156). Conceivably confusable with adjacent fovea (fossa) m. poplitea.

2188. Caput fibulae, lateromedial width relative to that of extremitas proximalis (caput) tibiotarsi:
a. former more than 75% of latter;
b. former less than 75% of latter.
Note.—See: Holtz (2000 [1998]: appendix I, character 354), citing Sereno et al. (1996); Dyke and Gulas (2002: appendix 1, character 43), who used a criterion of distinction of two-thirds; Dyke et al. (2003: appendix 1, character 80), employed again by Dyke (2003: table 1).

2189. Caput fibulae, fovea (sulcus) m. poplitea, status et forma (**ordered**):
a. absent or obsolete, surface flat;
b. present, sulcus shallow, covering less than two-thirds the width of corpus fibulae;
c. present, sulcus variably deep, covering more than two-thirds the width of corpus fibulae.
Note.—See: Chiappe et al. (1996: appendix 1, character 74); Novas (1996: appendix, character 73); Novas (1997: appendix, character 74), regarding "medial fossa" on proximal end; Sereno et al. (1996: footnote 45, character 63), with respect to medial "fibular fossa"; Novas and Puerta (1997), identically treated by Novas (1997); Chiappe et al. (1998: character 85); Forster et al. (1998: supplement, character 101); Ji et al. (1998: supplement, character 85); Makovicky and Sues (1998: appendix 1, character 88), with respect to proximomedial "fibular fossa"; Xu et al. (1999a: character 80); Xu et al. (1999b: character 74); Holtz (2000 [1998]: appendix I, character 355), in reference to "proximal region of fibular medial face," citing Pérez-Moreno et al. (1993); Chiappe (2001a: appendix 1, character 153); Norell et al. (2001: appendix 1, character 190); Chiappe (2002: appendix 20.2, character 153); J. M. Clark et al. (2002a: appendix 2.2, character 192); Maryanska et al. (2002: appendix 1, character 182); Xu (2002: suite II, character 211); Xu et al. (2002a: supplement, character 157); Rauhut (2003: character 210), referring only to "deep groove on medial side of proximal end of fibula"; Hwang et al. (2004: supplement, character 189); Xu and Norell (2004: supplement, character 189).

2190. Caput fibulae, tuberositas ligamentum collateralis lateralis, status:
a. absent or indistinct, represented at most by impressio or eminentia;
b. distinct or prominent, represented by variably prominent tuberculum.

Note.—See: Holtz (1994a: appendix 1, character 57); J. A. Wilson and Sereno (1998: appendix, character 49), regarding "lateral trochanter" of fibula among Sauropoda; Holtz (2000 [1998]: appendix I, character 357), in reference to "cranial protuberance on fibula below expansion"; Norell et al. (2001: appendix 1, character 191); J. M. Clark et al. (2002a: appendix 2.2, character 193); Xu (2002: suite II, character 212), as with preceding two, described as "deep oval fossa on medial surface of fibula"; Hwang et al. (2004: supplement, character 190); Xu and Norell (2004: supplement, character 190).

2191. Corpus fibulae, terminus spinae, situs proximodistalis (**ordered**):

a. margines distales of ossa proximalia tarsi to articulate (independently) with ossa distalia tarsi within articulatio intertarsales;

b. margines proximales of ossa proximalia tarsi, typically terminus of os fibulare resting within fossa of os fibulare;

c. facies lateralis of (typically synostotic) ossa proximalia tarsi (typically within sulcus or lateral fovea between ossa tarsi proximales et os tibia propria aut condylus cartilaginis tibialis) but proximal to margines proximales of ossa proximalia tarsi;

d. less than entirety of tibiotarsus but at least three-fourths of tibiotarsus;

e. less than three-fourths but typically at least one-half of tibiotarsus;

f. less than one-half of tibiotarsus but at least one-fourth of tibiotarsus.

Note.—An evolutionary trend of distal truncation results in many Neornithes with fibulae terminating proximad to articulatio (intertarsalis, tibiotarsotarsometatarsalis); diminished robustness of os fibulare and union of latter with ossa tarsi proximales et tibia are treated separately. Notoriety conferred upon examples of "complete" ossa fibulae in neognathus Neornithes fundamentally misplaced.

See: Shufeldt (1894b); Ostrom (1969: fig. 67), regarding *Deinonychus*; Ostrom (1976a), regarding *Archaeopteryx*; Ostrom (1978), regarding *Compsognathus*; Welles (1984), regarding *Dilophosaurus*; Cracraft (1986: appendix, character 21); Gauthier (1986: 12, unindexed synapomorphy of Avialae); Cracraft (1988: series XIV, character 7); Benton (1990a: 18); Rowe and Gauthier (1990); Sereno (1991a); Currie and Zhao (1994b [1993b]), regarding *Sinraptor*; Holtz (1994a: appendix 1, character 2); Chiappe and Calvo (1994: appendix I, character 66); Russell and Dong (1994b [1993b]: troödontid character 21); Chiappe (1995b: character 66); Elzanowski (1995: character O8); Sanz et al. (1995, 1997: character 64); Chiappe (1996b: character 61); Chiappe et al. (1996: appendix 1, character 60); Novas (1996: appendix, character M23, part); Novas (1996: appendix, character 60); Sereno et al. (1996: footnote 45, character 15); Novas (1997: appendix, character 61); Novas and Puerta (1997), identically by Novas (1997); Azuma and Currie (2000: appendix 1, character 8); De Klerk et al. (2000); Holtz (2000 [1998]: appendix I, character 359); Currie and Chen (2001); Norell and Clarke (2001: appendix I, character 187), treated similarly by J. A. Clarke (2002: appendix I, character 187), J. A. Clarke and Norell (2002: appendix 2, character 187), and J. A. Clarke (2004: appendix 1, character 187); Norell et al. (2001: appendix 1, character 189); Chiappe (2002: appendix 20.2, character 155); J. M. Clark et al. (2002a: appendix 2.2, character 191); Maryanska et al. (2002: appendix 1, character 183); Suzuki et al. (2002), regarding *Shuvuuia*; Xu (2002: suite II, character 210); Xu et al. (2002a: character 155); Zhou and Zhang (2002: appendix III, character 187); G. Mayr et al. (2003: appendix 1, character 60); Hwang et al. (2004: supplement, character 188); Xu and Norell (2004: supplement, character 188); Ji et al. (2005: supplement, part I, character 187).

2192. Corpus fibulae, forma *sensu* proximodistal taper relative to midpoint of corpus and tuberculum insertii m. iliofibularis:

a. essentially gradual and uniform from caput distal to midpoint;

b. abruptly attenuated distal to insertio m. iliofibularis.

Note.—See: Rauhut (2003: character 212). Confining assessment to segment distal to midpoint et/aut tuberculum insertii m. iliofibularis is equivalent to limiting characterization to spina fibulae.

2193. Corpus fibulae, crista articularis tibialis, status et forma:

a. absent, junctura(e) tibiofibularis limited to those at either or both extremitates proximalis et/aut distalis;

b. present, as jugum or impressio rugosum along margo medialis fibulae and aligned approximately with axis majoris tibiotarsi.

2194. Corpus fibulae et junctura (syndesmosis) tibiofibularis, situs craniocaudalis relative to crista articularis tibialis, forma principalis:

a. lateral throughout, essentially confined to margo lateralis cristae;

b. distocaudal, much of junctura along margo lateralis, but pars distalis cristae extends craniad to spina fibulae as amplexus or jugum.

2195. Corpus fibulae, pars proximalis, axis (majoris) proximodistalis fibulae, caudal departure from parallelism with axis (majoris) proximodistalis tibiotarsi, status et forma (**ordered**):

a. absent, os fibula virtually parallel to axis majoris tibiotarsi throughout length, including extremitas proximalis;

b. present, moderate;

c. present, pronounced, typically delimiting (lateral perspective) a fissuriform foramen between elements proximally.

Note.—See: Chiappe (1995b: character 65); Sanz et al. (1995, 1997: character 63); Chiappe (1996b: character 60).

Curvature of os fibula proximal to crista fibularis tibiotarsi can co-occur with caudal angulation of crista fibularis (coded separately), increasing the caudal displacement of caput fibulae. Parrots, owls, and goatsuckers are marginally apomorphic, assessments for which confounded by sloping cristae, caudal concavities proximal to tuberculum m. iliofibularis (e.g., galliforms), and/or short ossa fibulae.

2196. Corpus fibulae, lateromedial concavity of margo lateralis corporis (craniocaudal perspective) proximal to terminus proximalis of crista fibularis tibiotarsi, status:

a. absent, essentially linear; **b.** present.

Note.—Emphasis in apomorphic state is curvature *sensu stricto* as opposed to mere lateral emargination.

2197. Corpus fibulae, facies lateralis, sharp, curving linea passing from terminus proximalis cristae fibularis tibiotarsi laterodistad to tuberculum m. iliofibularis, i.e., linea m. poplitea lateralis (**new term**), status:

a. absent or indistinguishable;

b. present and distinct.

Note.—Feature suggests a moderately constrained passage or boundary for a laterocranial expansion of musculus or tendo.

2198. Corpus fibulae, tuberculum insertii m. iliofibularis, status (**ordered**):

a. absent;

b. present, distinct eminentia, prominent tuberculum, or rugose processus;

c. obsolete or indistinguishable.

Note.—See: Mader and Bradley (1989); Holtz (1994a: appendix 1, character 57); Rauhut (2003: character 211).

2199. Corpus fibulae, tuberculum insertii m. iliofibularis, orientation of facies ancorae (**ordered**):

a. craniolateral; **b.** lateral;

c. caudolateral or caudal;

x. noncomparable by obsolescence of tuberculum (Caprimulgiformes).

Note.—See: Chiappe and Calvo (1994: appendix I, character 65); Forster et al. (1996); Chiappe et al. (1996: appendix 1, character 59); Novas (1996: appendix, character 70); Novas (1997: appendix, character 71); Novas and Puerta (1997), identically by Novas (1997); Chiappe et al. (1998: character 86); Forster et al. (1998: supplement, character 100); Ji et al. (1998: supplement, character 86); Xu et al. (1999b: character 73); Holtz (2000 [1998]: appendix I, character 358); Xu et al. (2000: supplement, character 56); Chiappe (2001a: appendix 1, character 154); Chiappe (2002: appendix 20.2, character 154).

2200. Corpus fibulae, tuberculum insertii m. iliofibularis, situs proximodistalis relative to crista fibularis tibiotarsi (**ordered**):

a. opposite (lateral) to terminus proximalis cristae;

b. opposite (lateral) to pars intermedia cristae, typically approximately centered;

c. opposite (lateral) to terminus distalis cristae;

x. noncomparable by obsolescence of tuberculum (Caprimulgiformes).

Note.—See: Shufeldt (1894b).

2201. Corpus fibulae, spina fibulae, forma generalis:

a. essentially cylindrical throughout;

b. laminate, craniocaudally or lateromedially compressed.

Note.—See: Livezey (1998b: appendix A, character 331).

2202. Corpus fibulae, spina fibulae, midpoint of corpus fibulae relative to distal craniocaudal width, forma:

a. former greater than twice that of latter;

b. former less than twice that of latter.

Note.—See: Holtz (1994a: appendix 1, character 101); J. D. Harris (1998: appendix 2, character 134); Currie and Carpenter (2000: appendix 1, character 108); Holtz (2000 [1998]: appendix I, character 360).

Sesamoidea et Menisci Tibialis et Intertarsale

Note.—Cartilago tibialis, virtually never showing significant if any ossification, accordingly proved not amenable to reliable recovery and comparison for exemplar taxa. Articulatio cartilago-tibiotarsalis—junctura involving cartilago tibialis with extremitas distalis tibiotarsi—articulates with the trochlea cartilaginis tibialis on facies caudalis of extremitas distalis tibiotarsi; tendines mm. gastrocnemius et flexores superficiales pass across the wide surface of the cartilago, and those of deep mm. flexores digitorum pedis pass through canali within it. The present structure forms the caudal wall of articulatio intertarsalis (Shufeldt 1890; F. G. Parsons 1904, 1905, 1908; Hudson 1937; Fujioka 1962; Komárek 1979).

Os sesamoideum intertarsale, poorly known with respect to taxonomic distribution, represents the ossified angulus mediodistalis of cartilago tibialis (Hudson 1937; Hudson et al. 1959; Cracraft 1971a; Baumel and Raikow 1993: annotation 166). This ossicula represents an osseous extremitas mediodistalis of cartilago tibialis, the latter occupying the spatium immediately caudal to the trochlea cartilaginis tibialis. The part that ossifies in some taxa serves as articulatio with facies plantaris of extremitas proximalis tarsometatarsi. Like the preceding element, its status remains insufficiently understood for inclusion here.

2203. Menisci medialis et lateralis, status:
a. absent or poorly developed;
b. present, well developed.

Note.—See: Stolpe (1935a); Haines (1942); Barnett (1954); Baumel and Raikow (1993: annotation 168). Where present, meniscus medialis participates with meniscus lateralis (latter strongly attached to ligamentum collaterale) in articulatio intertarsalis of extremitas proximalis tarsometatarsi.

Ossa Tarsi et Metatarsi

Note.—Ontogenetic interrelationships among the ossa tarsi proximales, tibia, et fibula have been studied in some detail (Romanoff 1960; Hinchliffe 1977; L. D. Martin and Stewart 1985; McGowan 1985; G. B. Müller and Alberch 1990), and have benefited from the recent recognition of the theropod ancestry of Aves and ontogenetic studies of nonavian theropods (Welles and Long 1974; Welles 1984) and Archosauria generally (Sereno 1991a). A recent survey including both phylogenetic and functional implications of arrangements and synostoses among ossa metatarsales illustrated a diversity of forms among Theropoda, which gave rise to the class of morphologies termed "arctometatarsalian" (Holtz 1994b: fig. 1, table 2); the latter condition apparently shows significant homoplasy among nonavian Theropoda, and tends to predominate among "long-footed" taxa (e.g., *Sinosauropteryx*, *Oviraptor*, *Chirostenotes*), and is less typical of "short-footed" taxa (e.g., *Dromaeosaurus*), a relationship that probably contributes to homoplasy (P. J. Currie, pers. comm.).

A controversial dichotomy persists between "crocodile-normal" morphology of the ankle in **Crocodylotarsi**. Sereno (1991a: appendix, character 19) differentiated these types as—(*i*) "crocodile-normal" (CN), in which articulatio (gomphosis) intertarsalia proximalia comprises a condylus pilaformis ("peg") ossis fibularis (calcaneum) et cotyla ("socket") ossis tibialis (astragalus); and (*ii*) "crocodile-reversed" (CR), in which the reverse pertains regarding components of ossa tarsi proximales in gomphosis (Benton and Clark 1988). This distinction primarily serves to separate a virtual arthrological "isomer" in the "crocodile-opposite" **Ornithodira** from the archosaurian lineage inclusive of Aves (Parrish 1986), a differentiation moot for phylogenetic inferences pertaining to Aves. Functional and topological aspects suggest that this "dichotomy" may be related to two other characters of these elements showing changes in this phylogenetic context: (*i*) os fibulare (calcaneum), separate *vs*. continguous facies tibialis (astragalus) et articulares fibularis (Sereno 1991a: appendix, character 3); (*ii*) os fibulare (calcaneum), status of tuberculum caudalis (Gauthier 1986; Benton and Clark 1988; Sereno 1991a: appendix, character 29).

Current consensus holds that among modern birds, **ossa tarsi proximalia** comprise two major elements that correspond *largely* with those of other theropods. Among birds, the larger of the two ossa proximalia tarsi (those tarsal elements that ultimately are incorporated into the extremitas distalis tibiotarsi among birds) is the **os tibiale**, a medial element deriving solely from the ossification and synostosis of **cartilago tibiale**; i.e., the os tibiale is homologous to the "astragalus" of other amniotes *exclusive of* contributions by additional elements (e.g., the "intermedium" and "centralia") in some groups that are lost among crown theropods, and perhaps are absent among all Archosauria (P. J. Currie, pers. comm.). A distinct source of conformational variation within this element is the prominence of the **processus ascendens tibialis** ("ascending process"), confused with the "intermedium" (e.g., Morse 1880).

The second of the two ossa proximalia tarsi in birds (i.e., incorporated into the extremitas distalis tibiotarsi) is the **os fibulare** (homologous to "calcaneum" of related taxa), which derives from the **cartilago fibulare**; this lesser, lateral element evidently does not ossify in most or all palaeognathous birds, although in Struthionidae and some Rheidae this element (and the definitive condylus lateralis tibiotarsi that derives therefrom) may ossify (Baumel and Witmer 1993: annotation 283).

A minor controversy attends the apparent incorporation of an additional element—**os pretibiale**—in birds, although authors differ with respect to the os proximalis tarsi with which it primarily associates. McGowan (1985) averred that it is related mostly with the os tibiale, whereas L. D. Martin and Stewart (1985) concluded that it was an associate with both major primordia but most with the os fibulare. In either case, the comparatively early ossification of this minor primordium effectively precludes its homology with the "intermedium" of other amniotes. Preliminary examination of palaeognathous birds (especially moas) and juvenile neognathous birds suggests that a separate ossification gives rise to the pons supratendineus of the extremitas distalis tibiotarsi, associated with both ossa fibulare et tibiale, that may represent the os pretibiale in Neornithes.

Despite early inferences (e.g., Romanoff 1960), a single "distal tarsal" occurs in birds (**os tarsi distale**). Rightly considered jointly with the compound "tarsometatarsus" in avian contexts, this element unites by synostosis with the proximal ends of the ossa metatarsalia (notably II–IV), and constitutes a primary contributor to the definitive hypotarsus and extremitas proximalis tarsometatarsi (e.g., the cotylae lateralis et medialis, area intercotylaris). Possible intertaxonomic differences in the ossification of the os tarsi distale, together with a modest diversity in orientation among ossa metatarsalia II–IV, may effect variation in the definitive hypotarsus (e.g., the apparent absence of ossified hypotarsus in some ratites); these sources of phylogenetic information are considered elsewhere in this work.

See: Morse (1872), for a treatise on the ossa proximalia tarsi (including argument for an "intermedium" in Aves), the latter augmented by Jollie (1977a), who evidently concluded that an "intermedium" was incorporated into the condylus medialis tibiotarsi; Hudson (1937), regarding presence of cartilago tibialis in avian taxa; Fujioka (1962); Komárek (1979); Shufeldt (1890); Romanoff (1960); Hinchliffe (1977); Hogg (1980), regarding articulatio; G. B. Müller and Alberch (1990), for os tarsi distale; Turvey and Holdaway (2005), regarding ontogeny of Dinornithiformes.

Ossa Tarsi Proximalia

Note.—Diagnosable in Aves only in early developmental stages.

2204. Os tibiale (astragalus), processus ascendens (**new term**), complementation by processus caudodorsalis tibialae (**new term**), status (**ordered**):

a. absent; **b.** present.

2205. Os tibiale (astragalus), processus ascendens, par(te)s distales of os tibiale from which processus arises and relative (height) or proximal extent (**ordered**):

a. arises from pars lateralis ("ceratosauroid" condition), definitive element broad and proximodistally truncate—i.e., "height" of processus less than that of corpus of os tibiale;

b. arises from pars lateralis ("allosauroid" condition), definitive element narrow and moderately elongate proximodistally—i.e., "height" of processus one to two times that of corpus of os tibiale;

c. arises from entire basis distalis ("ornithomimoid-albertosauroid" conditions, in part), definitive element wide and markedly elongate proximodistally—i.e., "height" of processus at least twice that of corpus of os tibiale;

x. indiscernable because tibiale synostotic with tibia (most Neornithes).

Note.—"Height" of processus ascendens related to "epipodium." Homology of processus ascendens among Archosauria has engendered some dispute (L. D. Martin et al. 1980; McGowan 1984, 1985; L. D. Martin and Stewart 1985) because of variation in form and variable synostosis with os fibulare (calcaneum).

See: Welles and Long (1974); Thulborn (1984: 126–127, character 21); Gauthier (1986: text characters 50 and 65); Sereno and Arcucci (1994 [1993]); Holtz (1994a: appendix 1, characters 81 and 99); Russell and Dong (1994b [1993b]: list A, character 13); Elzanowski (1995: character NG4); Novas (1996: appendix, character M21, part); Sereno et al. (1996: footnote 45, character 16); J. D. Harris (1998: appendix 2, character 135); Makovicky and Sues (1998: appendix 1, character 89); J. A. Wilson and Sereno (1998: appendix, character 84), concerning relative lengths among Sauropoda; Azuma and Currie (2000: appendix 1, character 5); Currie and Carpenter (2000: appendix 1, character 109); Holtz (2000 [1998]: appendix I, character 362); Norell et al. (2001: appendix 1, character 194); J. M. Clark et al. (2002a: appendix 2.2, character 196); Maryanska et al. (2002: appendix 1, characters 184–186); Xu (2002: suite II, character 215); Xu et al. (2002a: supplement, character 160, part), which included information on "medial notch"; Rauhut (2003: characters 214 [basis] and 215 [relative height]), in which states "a" and "b" of former were merged; Hwang et al. (2004: supplement, character 193); Xu and Norell (2004: supplement, character 193).

2206. Os tibiale (astragalus), processus ascendens (**new term**), depressio supracondylaris tibialis (**new term**) delineating processus ascendens from pars condylaris (**new term**), status:

a. absent, processus confluent with corpus;

b. present, processus offset from corpus.

Note.—Depressio supracondylaris tibialis—which is typically conformed as a *subcircular* depression *immediately proximal* to the condyles—is distinct from the basal, transverse sulcus of astragalus (i.e., sulcus basilaris tibialis), typically a transverse, elongate groove on the condylar surface. Status in Neornithes confirmed only through study of early juveniles.

See: Welles and Long (1974); Mader and Bradley (1989); Sereno et al. (1993: legend for fig. 3a); Holtz (1994a: appendix 1, character 123); Azuma and Currie (2000: appendix 1, characters 4 and 7); Holtz (2000 [1998]: appendix I, character 363); Rauhut (2003: character 216), characterized in terms of "groove" and associated confluence between processus ascendens and corpus of os tibiale, and related to "albertosoid" and "ornithomimoid" conditions of Welles and Long (1974).

2207. Os tibiale (astragalus), facies cranialis, processus ascendens, pila obliqua (**new term**), status:

a. present;

b. absent, facies cranialis tibialis essentially planar.

Note.—Status in Neornithes confirmed only through study of early juveniles. See: Rauhut (2003: character 207), regarding either of two bracing structures, (*i*) "distinct 'step' running obliquely from mediodistal to lateroproximal" parts, or (*ii*) "bluntly rounded vertical ridge on medial side" of processus ascendens; latter limited to *Chilantaisaurus* and Baryonychidae, and excluded from analysis.

2208. Os tibiale (astragalus), facies lateralis, facies articularis fibulae, status et forma:

a. present, prominent, and partially oriented proximad;

b. reduced and oriented laterad, or absent.

Note.—Status in Neornithes confirmed only through study of early juveniles. See: Holtz (1994a), modified; Rauhut (2003: character 213).

2209. Os tibiale (astragalus), medial extent and contribution to tibiotarsus relative to extremitas distalis tibiotarsi, condylae lateralis et medialis:

a. great, composing entirety of extremitas distalis tibiotarsi, facies articulares tarsometatarsi;

b. restricted, forming only part of tibiotarsus, extremitas distalis tibiotarsi, typically only condylus lateralis.

Note.—Status in Neornithes confirmed only through study of early juveniles. Plesiomorphic conditions of Ornithurae are found in *Antrodemus*, *Stegosaurus*, and *Monoclonius* (Romer 1956: fig. 177). See: Paul (1988); J. M. Clark et al. (1994); Novas (1992: character 12); Novas (1994 [1993]: appendix, character 22); Sereno et al. (1996: footnote 45, character 17); Xu et al. (1999a: character 82, modified).

2210. Os tibiale (astragalus), partes condylarum, position and size relative to pars condylae ossis tibia:

a. partes condylarum of os tibiale largely distal and oriented distad relative to those of os tibia;

b. partes condylarum of os tibiale significantly expanded and oriented proximad on facies cranialis tibiotarsi.

Note.—Status in Neornithes confirmed only through study of early juveniles. See: Sereno et al. (1996); Rauhut (2003: character 217).

2211. Os tibiale (astragalus), derived condylae, facies cranialis, distinct horizontal sulcus basilaris tibialaris (**new term**), status:

a. absent; **b.** present.

Note.—Status in Neornithes confirmed only through study of early juveniles. See: Welles and Long (1974); Sereno (1991a: appendix, ingroup-clades character 28), regarding basal Archosauria; Holtz (1994a: appendix 1, character 23); Sereno et al. (1996: footnote 45, character 19); J. D. Harris (1998: appendix 2, character 137); Azuma and Currie (2000: appendix 1, character 6); De Klerk et al. (2000: 330, character 3); Holtz (2000 [1998]: appendix I, character 365); Norell et al. (2001: appendix 1, character 195); J. M. Clark et al. (2002a: appendix 2.2, character 197); Xu (2002: suite II, character 216); Xu et al. (2002a: supplement, character 161); Rauhut (2003: character 218); Hwang et al. (2004: supplement, character 194); Xu and Norell (2004: supplement, character 194).

2212. Os tibiale (astragalus), processus ascendens (**new term**), margo medialis, orientation relative to axis majoris corporis tibiae (**unordered**):

a. ventral; **b.** cranioventral;

c. variably proximad on facies cranialis of extremitas distalis tibiotarsi.

Note.—Status in Neornithes confirmed only through study of early juveniles. See: Cracraft (1986: appendix, character 38); Novas (1994 [1993]: appendix, character 7); Russell and Dong (1994a [1993a]: table 2, character 56); Novas (1996: appendix, character M21, part); Sereno et al. (1996: footnote 45, character 18); J. D. Harris (1998: appendix 2, character 136); Xu et al. (1999a: character 81); Azuma and Currie (2000: appendix 1, character 8); Currie and Carpenter (2000: appendix 1, character 110); Holtz (2000 [1998]: appendix I, character 364).

2213. Os tibiale (astragalus), processus ascendens (**new term**), deep incisura medialis processi (**new term**) limiting processus to margo lateralis of facies cranialis of extremitas distalis tibiotarsi, status:

a. absent or weakly developed;

b. present.

Note.—Status in Neornithes confirmed only through study of early juveniles. See: Lambe (1917); Osmólska et al. (1972); Barsbold (1974); Madsen (1976); McGowan (1985); Sanz and Bonaparte (1992); Perle et al. (1994); Sereno et al. (1994: footnote 12); Makovicky and Sues (1998: appendix 1, character 91); Xu et al. (2002a: supplement, character 160, part), in this context that state ("c") pertaining to presence of "medial notch."

2214. Os fibulare (calcaneum), facies articularis tibiale, status:

a. absent, os fibulare articulates only with os tibiale;

b. present, os fibulare articulates with both ossa tibiale et tibia.

Note.—Status in Neornithes confirmed only through study of early juveniles. See: Sereno et al. (1996: footnote 45, character 14); Rauhut (2003: character 219).

2215. Os fibulare (calcaneum), tuberculum medialis (**new term**), forma:

a. small, often synostotic with os tibiale;

b. prominent;

x. noncomparable by absence of ossified element (most ratites).

Note.—Status in Neornithes confirmed only through study of early juveniles. See: Cracraft (1986:

appendix, character 38); Welles (1984); Sereno (1991a: appendix, ingroup-clades character 29), regarding basal Archosauria; Novas (1992: character 13), in converse terms of "concave proximal articular surface"; Russell and Dong (1994a [1993a]: table 2, character 57); Novas (1996: appendix, character 65), in reference to "posteroventral projection"; Novas (1997: appendix, character 66); Novas and Puerta (1997), see identical characters in Novas (1997); Azuma and Currie (2000: appendix 1, character 17); Holtz (2000 [1998]: appendix I, character 367).

2216. Os pretibiale, status:

a. present, synostotic at early stage with ossa fibulare et tibiale;

b. absent.

Note.—Status in Neornithes confirmed only through study of early juveniles. Codings consistent with those adopted by Rotthowe and Starck (1998: appendix, character 11). Polarity and presence in Theropoda based largely on classical work by Huxley (1870). McGowan (1984) discussed this small *Anlage* with respect to the ratites, and considered it to be ontogenetically associated with os tibiale, whereas L. D. Martin and Stewart (1985) inferred it to be associated more closely with os fibulare (especially tuberculum medialis). In either case, this ephemeral element is unlikely to be homologous with the "os intermedium" of other Tetrapoda (G. B. Müller, *fide* Baumel and Witmer 1993: 111, annotation 283).

Ossa Tarsi Distale

2217. Os tarsi distale proprius (**new term**), contribution to extremitas proximalis tarsometatarsus proprius (i.e., laminar, dorsal, subangular corona for termini proximales ossa tarsalia (**new term**), status definitivum and descendant structures:

a. present, limited to lamina described above, hypotarsus (if present) a neomorphic derivation of plantad-displaced extremitas proximalis metatarsi III;

b. present, contributes to both lamina et hypotarsus.

Note.—Appearance of hypotarsus in ratites results from relative plantar displacement of os metatarsale II without contribution of os tarsi distale. Examination of juveniles and adults of ratites, including moas, revealed that the unicristate conformation in the region occupied by hypotarsal elaborations in neognathous species was virtually identical to the quasi-cristate aspect provided by the plantar displacement of os metatarsale III proximally. Other ramifications of this metatarsal configuration in Neornithes include the proximal portion of the sulcus extensorius.

2218. Os tarsale distalis quartus (**new term**), status et forma (proximal perspective) proximodistalis (**unordered**):

a. present, deep and trapezoidal;

b. present, compressed and triangular;

c. absent.

Note.—Status in Neornithes confirmed only through study of early juveniles. See: Novas (1994 [1993]: appendix, character 23); J. A. Wilson and Sereno (1998: appendix, character 13), concerning retention of ossa tarsi distalia III et IV among Sauropoda; Hinchliffe (1977), McGowan (1985), G. B. Müller and Alberch (1990), regarding absence in Aves.

Ossa Metatarsalia

2219. Ossa metatarsalia, dorsoplantar depths relative to lateromedial widths at midpoint of shafts (**ordered**):

a. former less than or subequal to latter;

b. former approximately equal to latter;

c. former greater than latter.

Note.—See: Cracraft (1982: series 2, character 6); Cracraft (1988: series XI, character 11); Holtz (1994a: appendix 1, character 55); J. D. Harris (1998: appendix 2, character 143); Azuma and Currie (2000: appendix 1, character 82); Holtz (2000 [1998]: appendix I, character 371). Related to superficial character of facies plantaris et dorsalis, perhaps best to subdivide into two or more separate characters.

Os metatarsale I (primum)

2220. Ossa metatarsalia et trochleae metatarsalia propriae, numerus modalis (**ordered**):

a. four, retaining ossa metatarsalia et trochleae metatarsalia I–IV;

b. three, retaining ossa metatarsalia et trochleae metatarsalia II–IV;

c. two, complete, retaining ossa metatarsalia et trochleae metatarsalia III (tertius) et IV (quartus), with os metatarsale II (secundi) distally truncated approximately distal one-fifth corpus and trochlea lost or vestigial).

Note.—See: Cracraft (1974: 502, character 9, part); Bledsoe (1988: appendix, character 75); K. Lee et al. (1997: appendix 1, character 32).

2221. Os metatarsale I (primum), status modalis (**unordered**):

a. present, typically robust, retaining phalanges proximalis et ungualis;

b. present, vestigial, truncated, lacking torsion and tuberositates poorly defined;

c. present, vestigial, with phalanx vestigial or absent;

d. absent, also lacking phalanges.

Note.—Polymorphism in presence of hallux—ranging from typically manifest to vestigium to completely lacking—is not uncommon, occurring within some genera, e.g., *Ceyx*, *Alcedo* among Alcedinidae (W. DeW. Miller 1912), and within *Calidris* in Scolopacidae. Exceptional polymorphism within *Apteryx* renders state indeterminate for analytical purposes.

See: W. E. Clarke (1892); Coues (1927); Delacour (1951); Swierczewski and Raikow (1981: character 49); Raikow (1982: character 15, part); B. Campbell and Lack (1985); Raikow (1985a: table V); Gauthier (1986); J. D. Harris (1998: appendix 2, character 139); Holtz (2000 [1998]: appendix I, character 378), in which mere retention of element (status) was combined with relative length of appendage (see below); Bertelli et al. (2002: appendix 2, character 9); J. M. Clark et al. (2002b: appendix 2.1, character 205); G. Mayr (2003a: appendix I, character 50); Novas et al. (2004: appendix, character 28).

2222. Os metatarsale I (primum), length relative to ossa metatarsalia II–IV and situs articularis ossa metatarsalia, forma (**unordered**):

a. length comparable to that of ossa metatarsalia II–IV and participates in articulatio intertarsalis;

b. length moderate, fragmentiform, junctura limited to os metacarpale II;

c. length extremely truncated, corpus broadly triangular, junctura limited to extremitas distalis of os metacarpale II;

x. noncomparable in absence of element.

Note.—See: Gauthier (1986: text character 52); Cracraft (1988: series XX, character 4); J. D. Harris (1998: appendix 2, character 139); J. A. Wilson and Sereno (1998: appendix, character 16), pertaining to relative lengths among Sauropoda; Rauhut (2003: character 222).

2223. Os metatarsale I (primum), forma generalis (**unordered**):

a. sublinear, atorsionate;

b. hamulate ("J-shaped"), atorsionate;

c. sublinear, with variably pronounced torsion;

x. noncomparable in absence of element.

Note.—Form comprises proximodistal curvature and apparent torsion about axis majoris. See: Chiappe (1992: character B3); Chiappe (1993: character 5); Sanz et al. (1995: appendix 3, character 5); Varricchio and Chiappe (1995: legend for fig. 2); Chiappe et al. (1999), regarding superficially similar condition in *Confuciusornis* averred to be nonhomologous; Sereno (2000: table 4, character 8); Norell and Clarke (2001: appendix I, characters 194–195), treated similarly by J. A. Clarke (2002: appendix I, characters 194–195), J. A. Clarke and Norell (2002: appendix 2, characters 194–195), and J. A. Clarke (2004: appendix 1, characters 194–195); Chiappe and Walker (2002: appendix 11.1, character 33); Zhou and Zhang (2002: appendix III, characters 194–195); Ji et al. (2005: supplement, part I, characters 194–195).

2224. Os metatarsale I (primum), relative length and apparent torsion:

a. relatively elongate, torsion distinct;

b. truncate and rectanguloid, torsion obsolete;

x. noncomparable in absence of element.

Note.—Form comprises length relative to distal width and apparent torsion about axis majoris corporis.

2225. Os metatarsale I (primum), corpus metarsalis, forma generalis—(*i*) distinct reduction characterized by lateromedial and dorsoplantar narrowing, (*ii*) conformational change in which facies articularis tarsometatarsalis is subacuminate and distinctly narrower than trochlea, and (*iii*) morphoclinal reduction in general robustness (even presence) of os metatarsale I et digitus I—status (**ordered**):

a. absent;

b. present, os metatarsale et both phalanges digiti I conserved and semifunctional, tuberositates medialis et lateralis trochlearis asymmetrical;

c. present, os metatarsale et both phalanges digiti I conserved but vestigial, only one tuberositas trochlearis moderately developed;

d. present, os metatarsale vestigial or absent, and digitus I obsolete or absent;

x. noncomparable in absence of element.

Note.—Although listed under ossa metatarsalia, manner of reduction and loss of associated digit equally informative.

2226. Os metatarsale I (primum), facies syndesmosis intermetatarsalis hallucis, situs proximodistalis relative to adjacent segments of os tarsi distale et metatarsale secundi (II) (**ordered**):

a. "**proximal**," opposite proximal half os metatarsale II and forming articulatio accessoria with os tarsi distale;

b. "**intermediate**," opposite approximate midpoint of os metatarsale II;

c. "**distal**," opposite distal one-fourth of os metatarsale II;

x. noncomparable because of absence of part or all of included components (*Gallimimus*, *Struthiomimus*, ratites, Dromornithidae, Turnicidae, many Charadriiformes).

Note.—See: Gauthier (1986: 12, unindexed synapomorphy of Avialae, expanded); J. D. Harris (1998: appendix 2, character 138), described in terms of caudal *vs.* medial position; Holtz (2000 [1998]: appendix I, character 379); Xu et al. (2002a: supplement, character 169).

2227. Os metatarsale I (primum) et phalanges proximalis et ungualis, position with respect to axes proximodistales of ossa metatarsalia II–IV and planum spanned thereby (**ordered**):

a. medial, coplanar, and parallel—os metatarsale I and associated digitus parallel to ossa metatarsales II–IV and associated phalanges, i.e., with facies dorsales et plantares of all ossa metatarsales et phalanges digitorum pedis in parallel alignment;

b. distinctly plantar and parallel—os metatarsale I approximately parallel to ossa metatarsales II–IV, whereas digitus in opposition to ossa metatarsales II–IV and associated phalanges, i.e., combining plesiomorphic position of fossa metatarsi I on margo medialis of os metatarsale II with apomorphic curvature of os metatarsale I to effect functional opposition of digitus;

c. distinctly plantar and "reversed"—both os metatarsale I et digiti in virtual opposition to ossa metatarsales II–IV and associated phalanges, i.e., combining apomorphic position of fossa metatarsi I on facies plantaris of os metatarsale II with apomorphic diminishment of curvature and added torsion of os metatarsale I;

x. noncomparable in absence of element (see status).

Note.—See: G. Steinbacher (1935), concerning articulationes metatarsophalangeales pedis; Ostrom (1976a); Tarsitano (1981); Gauthier (1986: text character 66), emphasis on position relative to os metatarsale secundum (II); Sanz and Bonaparte (1992: character 19); Sanz and Buscalioni (1992: character 9); Sereno and Rao (1992); Chiappe et al. (1996: appendix 1, character 87); Norell and Makovicky (1997); Forster et al. (1998: supplement, character 108); J. D. Harris (1998: appendix 2, character 138); Xu et al. (1999b: character 79); De Klerk et al. (2000); Holtz (2000 [1998]: appendix I, character 380), relative to os metatarsale II; Sereno (2000: table 4, character 8); Xu et al. (2000: supplement, character 59); Zhou and Wang (2000); Zhou et al. (2000); Chiappe (2001a: appendix 1, character 163); Middleton (2001), regarding the morphological basis for the evolutionary shift in orientation of the hallux in Aves; Norell et al. (2001: appendix 1, character 203, part); Chiappe (2002: appendix 20.2, character 163); Chiappe and Walker (2002), regarding intermediacy of Euenatiornithes; J. M. Clark et al. (2002a: appendix 2.2, character 205, part); Sereno et al. (2002), regarding *Sinornis*; Xu (2002: suite II, character 224, part); Ji et al. (2003a: 24); Hwang et al. (2004: supplement, character 202); Xu and Norell (2004: supplement, character 202).

2228. Os metatarsale I (primum), processus articularis tarsometatarsalis, forma:

a. blunt, moderately broad, suborbiculate;

b. narrow, lateromedially compressed, sublinear;

x. noncomparable in absence of element.

2229. Os metatarsale I (primum), corpus ossis metatarsalis, facies plantaris, impressiones mm. extensores relative to impressiones phalangiorum digiti II–IV pedis, status:

a. obsolete or significantly less marked relative to other digiti pedis;

b. present, foveate, depth and distinctness comparable to latter;

x. noncomparable in absence of element.

Note.—Apomorphic condition features impressio of aspectus comparable to those of distinct foveae collateriae digitorum. Evidently related to rigorous abduction of element during locomotion and totipalmy.

2230. Os metatarsale I (primum), trochlea metatarsi I, width relative to that of trochleae metatarsalia II–IV, status:

a. smaller or subequal;

b. distinctly greater;

x. noncomparable in absence of element.

2231. Os metatarsale I (primum), facies dorsalis (interna), corpus metatarsalis trochlea metatarsi I immediately proximal to trochlea metatarsi I, foramina (pori) pneumatici, status:

a. absent; **b.** present;

x. noncomparable in absence of element.

2232. Os metatarsale I (primum), trochlea metatarsi I, diameter relative to that of trochleae metatarsalia II–IV, status:

a. approximately equal;

b. distinctly greater;

x. noncomparable in vestigial condition (most Procellariiformes, Sphenisciformes) or absence of element.

Note.—Functional alternative for enhanced perching ability, and perhaps for improved ancillary cursoriality.

2233. Os metatarsale I (primum), trochlea metatarsi I, tuberculum (tuberositas) lateralis, size of trochlea relative to trochleae digitorum II–IV pedis, and relative diameters of tuberculae lateralis et medialis, forma:

a. trochlea metatarsi I not distinctly larger than trochleae metatarsalia II–IV, and tuberculum lateralis not larger than tuberculum medialis;

b. trochlea metatarsi I distinctly larger than trochleae metatarsalia II–IV, and tuberculum lateralis larger than tuberculum medialis.

2234. Os metatarsale I (primum), trochlea metatarsi I, forma *sensu* subdivision into tuberositates (tuberculae) laterale et mediale:

a. absent, trochlea metatarsi et facies articularis metatarso-phalangealis sublaminate or uniglobular;

b. present, trochlea metatarsi et facies articularis metatarso-phalangealis bilobate;

x. noncomparable in vestigial condition or absence of element.

Note.—See: Norell et al. (2001: appendix 1, character 204); J. M. Clark et al. (2002a: appendix 2.2, character 206); Xu (2002: suite I, character 70; suite II, character 225) regarding "ball-like" facies articularis metatarsophalangealis (primus) I in Mesozoic forms; Xu et al. (2002a: supplement, character 170), worded so as to leave doubt as to whether character was in reference to processus articularis tarsometatarsalis or trochlea metatarsi I; Hwang et al. (2004: supplement, character 203); Xu and Norell (2004: supplement, character 203).

2235. Os metatarsale I, trochlea metatarsi I, tuberositas medialis, marked elongation relative to tuberositas lateralis trochlearis metatarsi I, status:

a. absent, trochlea metatarsi I unilobate or approximately evenly bilobate;

b. present, former markedly smaller than latter, appearing spurlike;

x. noncomparable in vestigial condition or absence of element.

Os metatarsale II (secundum)

2236. Os metatarsale II (secundum) aut III (tertium), facies dorsalis, tuberculum insertii m. tibialis cranialis, status, forma et situs (**ordered**):

a. absent;

b. present, distinct tuberculum, on approximate midpoint of facies dorsalis;

c. present, distinct subtabulate eminentia, on pars proximalis of facies dorsalis;

d. present, indistinct tuberositates or jugulae, on pars proximalis of facies dorsalis.

Note.—See: Ballmann (1969a); Brett-Surman and Paul (1985); Rowe (1989); Chiappe (1992: character B2); Chiappe (1993: character 4), with respect to "tubercle on dorsal face," averred to be a comparatively prominent and distal tuberculum insertii m. tibialis cranialis; Sanz et al. (1995: appendix 3, character 4) and Varricchio and Chiappe (1995: legend for fig. 2), with respect to "dorsal tubercle on metatarsal II"); Chiappe et al. (1999: 46–47), noting presence in *Confuciusornis* and myological likelihood; Hughes (2000: appendix 2, characters 68–70), after Seibel (1988: characters TM 27–29), in which proximodistal position relative to foramina vascularia proximalia was assessed; Chiappe (2001a: appendix 1, character 166); Norell and Clarke (2001: appendix I, character 196), treated similarly by J. A. Clarke (2002: appendix I, character 195) and J. A. Clarke and Norell (2002: appendix 2, character 195); Chiappe (2002: appendix 20.2, character 166); Zhou and Zhang (2002: appendix III, character 196); Ji et al. (2005: supplement, part I, character 196).

Os metatarsale III (tertium)

2237. Os metatarsale III (tertium), sectio intermedia, facies dorsalis, distinct transverse "convexity" (eminentia, tuberculum, or tumulus), status:

a. absent;

b. present, typically immediately distal to formina vascularia proximalia.

Note.—See: Chiappe (1992: character B4); Chiappe (1993: character 8); Chiappe and Calvo (1994: appendix II, character 20), "distinct knob for muscle attachment" listed as synapomorphy of Enantiornithes; Sanz et al. (1995: appendix 3, character 8); Varricchio and Chiappe (1995: legend for fig. 2); Chiappe and Walker (2002: appendix 11.1, character 35).

2238. Os metatarsale III (tertium), extremitas proximalis metatarsalis, robustness relative to adjacent segmenta of ossa metatarsalia secundum et tertium (**ordered**):

a. distinctly diminutive, smaller than ossa metatarsalia II et IV;

b. approximately equal in size to ossa metatarsalia II et IV;

c. distinctly robust, larger than ossa metatarsalia II et IV.

Note.—Character treats genuine differences in size as opposed to apparent reductions (dorsal view) related to positional peculiarities of os metacarpale III in taxa having "arctometatarsalian" aspect (Holtz 1994b). See: Gauthier (1986); Madsen (1976); Ostrom (1978); Welles (1984); Sanz et al. (1988); Wellnhofer (1988); Rowe (1989); Chiappe (1990); Chiappe (1991b); Bonaparte (1991); Chiappe (1992: character A2); Sereno et al. (1994: footnote 12); Holtz (2000 [1998]: appendix I, character 375); Xu (2002: suite I, characters 68–69; suite II, character 222); Turvey and Holdaway (2005), regarding ontogenetic evidence of arctometatarsal condition of Dinornithiformes.

2239. Os metatarsale III (tertium), extremitas proximalis metatarsalis (dorsal perspective), fragmentiform aspect (appears "splintlike," bilaterally compressed, or "hourglass-shaped") and plantar displacement relative to extremitates proximales of ossa metatarsalia II et IV (such that os metatarsale III excluded from "extensor surface"), status:

a. absent, ossa metatarsalia II–IV subequal in proximal position in planum spanned;

b. present, os metatarsale III compressed between ossa metatarsalia II et IV proximally, i.e., "arctometatarsalian" condition, presenting compressed aspect of former in dorsal perspective.

Note.—See: Holtz (1994a: appendix 1, character 66); Holtz (1994b); Russell and Dong (1994a [1993a]: table 2, character 58); Russell and Dong (1994b [1993b]: troödontid character 23; list A, character

14); Sereno et al. (1996); J. D. Harris (1998: appendix 2, characters 140–141); Makovicky and Sues (1998: appendix 1, character 94); Azuma and Currie (2000: appendix 1, characters 80–81); Holtz (2000 [1998]: appendix I, characters 373–374 [two dorsal aspects], 376 [plantar aspect], and 377); Norell et al. (2000: appendix 1, character 34); Holtz (2001a); Chiappe and Walker (2002: 256), regarding coplanarity in Euenantiornithes; Brochu (2003); Rauhut (2003: character 220).

Os metatarsale IV (quartum)

2240. Os metatarsale IV (quartum), status et size relative to ossa metatarsalia secundi (II) et tertii (III):

a. present, "short," subequal in length to that of os metatarsale II;

b. present, "long," longer than os metatarsale II and closer to length of os metatarsale III.

Note.—See: Gauthier (1986: text character 67, part); Chiappe (1992: character B1); Chiappe (1993: character 1); Chiappe and Calvo (1994: appendix II, character 19), as synapomorphy of Enantiornithes; Holtz (1994a: appendix 1, character 122); Russell and Dong (1994b [1993b]: troödontid character 24); Sereno et al. (1994: footnote 12); Varricchio and Chiappe (1995: legend for fig. 2); Sanz et al. (1995, 1997: character 80; appendix 3, character 1); De Klerk et al. (2000); Holtz (2000 [1998]: appendix I, character 374); Sereno (2000: table 4, character 10).

2241. Os metatarsale IV (quartum), robustness relative to os metatarsale II (secundum) and (to lesser degree) os metatarsale III (tertius):

a. subequal, producing approximate pedal symmetry;

b. "apparently" greater, producing marked pedal asymmetry.

Note.—See: Norell et al. (2000: appendix 1, character 36); Xu et al. (2000: supplement, character 88); Chiappe (2001a: appendix 1, character 164); Chiappe (2002: appendix 20.2, character 164); Chiappe and Walker (2002: appendix 11.1, character 34); J. M. Clark et al. (2002a: appendix 2.2, character 208); Xu (2002: suite I, character 68; suite II, character 222); Xu et al. (2002a: supplement, character 206), pertaining to symmetry of foot so produced; Hwang et al. (2004: supplement, character 205); Xu and Norell (2004: supplement, character 205), in terms of simple pedal symmetry.

2242. Os metatarsale IV (quartum), facies plantaris, longitudinally oriented linea or cristula, status:

a. absent; **b.** present.

Note.—This feature may represent a deepened distal segment of crista plantaris lateralis, serving to provide additional surface for origo m. adductor digiti IV, a muscle involved in closing the pedal digits (e.g., in capture of prey). See: Sereno (1991a); Norell and Makovicky (1997); Xu et al. (2000: supplement, character 87), with respect to "longitudinal ridge along the postomedial surface of metatarsal IV"; Xu (2002: suite II, character 48).

2243. Os metatarsale IV (quartum), lateromedial width relative to dorsoplantar depth or forma in planum transversus:

a. dorsoplantar dimension greater than lateromedial, element "thick" or round;

b. lateromedial dimension greater than dorsoplantar, element "flat" or distinctly rectangular.

Note.—See: Norell et al. (2001: appendix 1, character 202); J. M. Clark et al. (2002a: appendix 2.2, character 207); Xu (2002: suite II, character 258); Xu et al. (2002a: supplement, character 203); Hwang et al. (2004: supplement, character 207); Xu and Norell (2004: supplement, character 207).

Os metatarsale V (quintum)

2244. Os metatarsale V (quintum), status et forma (**ordered**):

a. present, commensurate with gradation in size among other ossa metatarsalia, with rounded trochlea metatarsi;

b. present, reduced to truncated vestigium, lacking trochlea metatarsi, deformed through transverse compression and dorsal curvature distad;

c. present, reduced to vestigium proximalis, lacking trochlea metatarsi;

d. absent.

Note.—See: Wiman (1937), regarding vestigia in Aepyorniformes and Dinornithiformes; Ostrom (1976a); Cracraft (1986: appendix, character 28); Gauthier (1986); Cracraft (1988: series II, character 12); Sereno (1991a); Chiappe and Calvo (1994: appendix I, character 70); Sereno and Arcucci (1994 [1993]: appendix, character 24); Chatterjee (1995: character 16); Chiappe (1995b: character 70); Elzanowski (1995: character O9); Sanz et al. (1995, 1997: character 68); Chiappe (1996b: character 64); Chiappe et al. (1996: appendix 1, character 63); Norell and Makovicky (1997: 13); Chiappe et al. (1998: character 89); Forster (1998: character 107); J. D. Harris (1998: appendix 2, character 142, size of os metacarpale V quantified by means of ratio with os metacarpale IV); Ji et al. (1998: supplement, character 89); Chatterjee (1999: appendix II, character 84); Holtz (2000 [1998]: appendix I, character 372); Chiappe (2001a: appendix 1, character 158); Norell and Clarke (2001: appendix I, character 189), treated similarly by J. A. Clarke (2002: appendix I, character 189), J. A. Clarke and Norell (2002: appendix 2, character 189), and J. A. Clarke (2004: appendix 1, character 189); Chiappe (2002: appendix 20.2, character 158); Vickers-Rich et al. (2002), concerning *Avimimus*; Xu (2002: suite I, character 19; suite II, character 50), regarding relative length, curvature, and midshaft expansion relative to os metatarsale IV; Zhou and Zhang (2002: appendix III, character 189); Xu et al. (2003); Rauhut (2003: character 223); Ji et al. (2005: supplement, part I, character 189).

Tarsometatarsus (Proprius)

Note.—Characters treated here are those optimally considered features of the united elements comprising the tarsometatarsal complex, as opposed to consideration under ossa tarsi distalia or under junctura tarsometatarsalia. Consequently, many tarsometatarsal characters pertinent to Aves were not comparable to more-basal Theropoda possessing separate ossa metatarsalia and lacking true hypotarsi, etc.

Extremitas proximalis tarsometatarsi

2245. Extremitas proximalis tarsometatarsi, cotylae lateralis et medialis, et area intercotylaris (i.e., “proximal articular surface”), dorsal inclination, status:
a. absent; **b.** present.
Note.—This generalized slanting not demonstrable in present survey, but provisionally assumed to be profound and distinct from comparatively subtle characters of orientation among Neornithes (below). See: Payne and Risley (1976: character 32), regarding unspecified “angulation” among Ardeidae; Chiappe (1993: character 7); Sanz et al. (1995: appendix 3, character 7); Varricchio and Chiappe (1995: legend for fig. 2); Chiappe and Walker (2002: appendix 11.1, character 34).

2246. Extremitas proximalis tarsometatarsi, area intercotylaris, fovea menisci lateralis, status et forma (**unordered**):
a. absent or obsolete, area intercotylaris subplanar;
b. present, moderately deep, subelliptical;
c. present, exceptionally deep.
Note.—See: Stolpe (1935a) for review, in which the meniscus lateralis is averred to be better developed generally than meniscus medialis; Baumel and Raikow (1993: annotation 168).

2247. Extremitas proximalis tarsometatarsi, facies plantaris, sulcus ligamentosus, status et forma (**ordered**):
a. absent or obsolete;
b. present, shallow; **c.** present, deep.
Note.—See: Bledsoe (1988: appendix, character 71); Baumel and Witmer (1993: annotation 286).

2248. Extremitas proximalis tarsometatarsi, cotyla lateralis, crista cotylaris lateralis (**new term**), forma *sensu* relative proximal elevation distinctly greater than cotyla medialis (**ordered**):
a. distinctly less; **b.** subequal;
c. distinctly greater.

2249. Extremitas proximalis tarsometatarsi, cotyla medialis, rima (facies) lateralis cotyli, medial prominence relative to facies lateralis corporis, status:
a. absent;
b. present, approaching lateromedial width of corpus.

2250. Extremitas proximalis tarsometatarsi, cotylae lateralis et medialis (dorsal perspective), relative proximal elevation (**ordered**):
a. cotyla lateralis distinctly distal to cotyla medialis;
b. cotyla lateralis subequal to cotyla medialis;
c. cotyla lateralis distinctly proximal to cotyla medialis.
Note.—Relative elevations of cristae cotylares medialis et lateralis typically follow in parallel. See: Bledsoe (1988: appendix, characters 69 and 72); K. Lee et al. (1997: appendix 1, character 29); Livezey (1998b: appendix A, character 332).

2251. Extremitas proximalis tarsometatarsi, cotylae lateralis et medialis, facies articulares, relative area:
a. cotyla lateralis approximately equally expansive as cotyla medialis;
b. cotyla lateralis distinctly less expansive than cotyla medialis.
Note.—See: Murray and Vickers-Rich (2004: table 9, character 38), regarding Dromornithidae.

2252. Extremitas proximalis tarsometatarsi, cotylae lateralis et medialis, forma superficialis:
a. both cotylae concave;
b. cotyla lateralis distinctly convex, whereas cotyla medialis concave.

2253. Extremitas proximalis tarsometatarsi, cotylae lateralis et medialis, rima cotylarum, sectio dorsalis, distinct diminishment and distal displacement, effecting dorsal slant of cotylae, status et forma (**unordered**):
a. absent;
b. present, approximately symmetrical;
c. present, margo dorsalis cotylae lateralis obsolete.

2254. Extremitas proximalis tarsometatarsi, cotyla medialis, eminentia intercondylaris, status:
a. absent or rudimentary; **b.** present.

Note.—See: Ligon (1967: table 7); Cracraft (1974: 503, character 13); Thulborn (1984: 126–127, character 23); Bledsoe (1988: appendix, character 70); Gauthier (1986: 14, part, unindexed synapomorphy of Ornithurae); Andors (1992: table 2, character 45); Chiappe and Calvo (1994: appendix I, character 72); Chiappe (1995b: character 72); Sanz et al. (1995, 1997: character 70); Chiappe (1996b: character 66); Chiappe et al. (1996: appendix 1, character 65); K. Lee et al. (1997: appendix 1, character 28); Chiappe (2001a: appendix 1, character 160); Norell and Clarke (2001: appendix I, character 191), treated similarly by J. A. Clarke (2002: appendix I, character 191), J. A. Clarke and Norell (2002: appendix 2, character 191), and J. A. Clarke (2004: appendix 1, character 191); Chiappe (2002: appendix 20.2, character 160); Zhou and Zhang (2002: appendix III, character 191); Ji et al. (2005: supplement, part I, character 191).

2255. Extremitas proximalis tarsometatarsi, impressio (tuberositas) ligamentum collateralis lateralis, forma (**unordered**):

a. impressio aut tuberositas, typically indistinct;

b. fossa aut fovea, craniodorsally angled on or proximate to rima dorsalis of cotyla lateralis;

c. tuberculum aut jugum, comparatively robust;

d. substantial fovea with prominent lateral laminar tuberculum.

Note.—See: Ligon (1967: table 1), regarding Cathartidae and Ciconiidae.

2256. Extremitas proximalis tarsometatarsi, areae parahypotarsales medialis et lateralis, forma:

a. depressiones, but depth variable;

b. facies lateralis et medialis hypotarsales planar, a condition related to extreme lateromedial compressio of corpus.

2257. Extremitas proximalis tarsometatarsi, fossa parahypotarsalis medialis, status et forma (**ordered**):

a. absent or indistinct, area without marked departure from general curvature of element;

b. present, small to moderately deep;

c. present, broad and deep, often manifesting distinct triangular terminus of impressio origii m. flexor hallucis brevis.

Note.—Fossa principally represents impressio origii m. flexor hallucis brevis (Vanden Berge and Storer 1995).

See: Livezey (1986: appendix 1, character 72); Livezey (1989: table 1, character 72); Livezey (1996a: appendix 1, character 71); Ericson (1997: table 2, character 45); Livezey (1997a: appendix 1, character 90; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, character 341); G. Mayr (2002a: legend fig. 9, node 4, character 3); G. Mayr (2003b: appendix I, character 15).

2258. Extremitas proximalis tarsometatarsi, fossa parahypotarsalis lateralis, status:

a. absent or indistinct, area without detectable departure from general curvature of element;

b. present, variably deep, margo lateralis typically distinct.

Note.—Fossa represents (*i*) impressio origii m. abductor digiti IV, (*ii*) accommodates passage distad of (*ii*) tendines insertiorum mm. flexor hallucis longus et gastrocnemius lateralis (Vanden Berge and Storer 1995: fig. 8), and (iii) insertio m. fibularis brevis. See: Livezey (1998b: appendix A, character 342).

2259. Extremitas proximalis tarsometatarsi, fossa infracotylaris dorsalis, status:

a. absent or indiscernable from facies dorsalis corporis et/aut sulcus extensorius;

b. present, typically a depressio ovalis distinct from facies dorsalis corporis et/aut sulcus extensorius.

Note.—See: G. Mayr and Ericson (2004: appendix I, character 76), in which relative dispersion of foramina assessed. Area in question is bounded medially by origii m. extensor hallucis, and laterally (as well as overlain dorsally) by origii m. brevis digiti IV (Hudson et al. 1959). Margo distalis of fossa infracotylaris dorsalis (as distinct from enclosed foramina vascularia proximales)—defined as margo proximalis of sulcus extensorius—is only vaguely discernable in some taxa. Assignment to states challenging for many Piciformes and Passeriformes. Typical of state "a" are Columbiformes.

2260. Extremitas proximalis tarsometatarsi, fossa infracotylaris dorsalis (aut fossa extensorius), tuberositas (area tuberculata tendinis) insertii m. tibialis cranialis, forma (**ordered**):

a. obsolete or small, subcircular tuberositas;

b. moderately elevated, tumulus aut area tuberculata tendinis;

c. prominent jugum, typically angling toward facies medialis corporis.

Note.—Extreme, angular jugum manifested in some larger Accipitridae. See: Norell and Makovicky (1997: 10–11); Livezey (1998b: appendix A, character 343); G. Mayr and Ericson (2004: appendix I, character 76, part), in which attempt made to encode variation in situs lateromedialis corporis.

2261. Extremitas proximalis tarsometatarsi, facies dorsalis, fossa infracotylaris dorsalis, foramina vascularia proximalia, diameters relative to that of fovea ligamentum collateralium trochlea digiti IV:

a. "small"—diameters distinctly less than that of fovea;

b. "large"—diameters equal or distinctly greater than that of fovea.

Note.—Foramina vascularia proximalia admit arteria metatarsalis dorsalis communis (Baumel 1993: annotation 70) and passing between the partes extremitates of ossa metatarsalia II et III, and III et IV, the arteria bifurcating distad into arteriae plantares superficiales medialis et lateralis (serving trochleae II–IV), as well as arteria metatarsalis plantaris (extending distad to extremitas distalis metatarsalis I). See: Ligon (1967: fig. 6), regarding Cathartidae and Ciconiidae.

2262. Extremitas proximalis tarsometatarsi, facies dorsalis, fossa infracotylaris dorsalis, translucentia infracotylaris medialis (**new term**), status et situs (**unordered**):

a. absent;

b. present, latus lateralis fossae;

c. present, latus medialis fossae.

Note.—See: Ford (1967).

2263. Extremitas proximalis tarsometatarsi, fossa infracotylaris dorsalis, foramina vascularia proximalia, status:

a. absent;

b. present, typically passing between adjacent couplets among ossa metatarsalia II–IV, sometimes with foramina accessoria.

Note.—See: Gauthier (1986: 14, unindexed synapomorphies of Ornithurae and Aves); Cracraft and Clarke (2001: appendix 2, character 31); Norell and Clarke (2001: appendix I, character 193), treated similarly by J. A. Clarke (2002: appendix I, character 193), J. A. Clarke and Norell (2002: appendix 2, character 193), and J. A. Clarke (2004: appendix 1, character 193); Zhou and Zhang (2002: appendix III, character 193); Ji et al. (2005: supplement, part I, character 193).

2264. Extremitas proximalis tarsometatarsi, facies dorsalis, fossa infracotylaris dorsalis, foramina vascularia proximalia (dorsal perspective), forma *sensu* situs, numerus modalis et forma (**unordered**):

a. one distal, medial foramen;

b. two (micro)foramina comprising distal pair, both lateral to midline;

c. two foramina comprising distal, bilateral pair;

d. three foramina comprising (*i*) proximal, medial, single foramen, and (*ii*) distal, lateromedially (sub) parallel pair.

Note.—See: Worthy (1988: 21–30); Hughes (2000: appendix 2, characters 66–67), after Seibel (1988: character TM 26).

2265. Extremitas proximalis tarsometatarsi, facies dorsalis, fossa infracotylaris dorsalis, foramina pneumatica suprasulciorum (**new term**), status:

a. absent; **b.** present.

Note.—Foramina in question qualitatively distinguishable, typically larger, foramina vascularia proximalia tarsometatarsi; latter typically immediately distal to or investing former. Also, augmentation of proximal pneumaticity on facies dorsalis typically associated with enlargement of foramina on facies plantaris.

2266. Extremitas proximalis tarsometatarsi, fossa infracotylaris dorsalis, tuberculum m. fibularis (peronei) brevis, status et forma:

a. absent or indistinct impressio or tumulus;

b. present, prominent processus.

2267. Extremitas proximalis tarsometatarsi, facies plantaris, fossa infracotylaris plantaris (**new term**), status:

a. absent; **b.** present.

Note.—New feature refers to *broad*, *conspicuous* depressio on facies plantaris tarsometatarsi between facies cotylaris et hypotarsus. See: Kurochkin (1995b: table 1, character 30), in reference to relative proximal extent of hypotarsus, likely the complement of present character.

Hypotarsus

Note.—Where hypotarsus verus (**new term**) is present, the structure comprises canales et/aut sulci accommodating tendines passing around aspectus plantaris (caudalis) of arthros tarsalis, and derives from both the plantar-displaced os metatarsale III and os tarsi distalis. Traditional use of primordial "calcaneum" in reference to definitive hypotarsus among Neornithes herein is considered nomenclaturally inappropriate. Primary sources for identification of homologous sulci et canales hypotarsalium, by a protocol modified from that used by Livezey (1998b) for Gruiformes, were: Hudson (1937), Berger (1956a), Harrison (1976, 1978), Hudson et al. (1959), Berger (1966), Ballmann (1969a), Cracraft (1971a), Jollie (1976), Strauch (1978), S. F. Simpson and Cracraft (1981: fig. 6), Berman and Raikow (1982), Rosser et al. (1982), Schulin (1987), and Baumel and Witmer (1993: annotation 288); Manegold et al. (2004: fig. 3). The scheme by Strauch (1978) served as primary source herein, with portals for tendines *through* or *on surface* of hypotarsus (i.e., sulci and canales) enumerated in that work being referred collectively as "passages."

Herein a scheme for characterization of hypotarsal variation was adopted that is based primarily on: (**a**) presence and ossification *vs*. (**b**) absence or cartilaginous condition of several fundamental lamina or septa. Secondarily, structures within the hypotarsus were conceptualized as: (*i*) basis hypotarsi; (*ii*) one or two horizontal (transverse) laminae; (*iii*) lateral, medial, and one or more intermediate vertical (perpendicular) laminae; and (*iv*) spinae aut cristae that the latter laminae may possess. The parsimonious and well-supported assumption that the same musculi et tendines pass through or over the hypotarsus is made, limiting the problem to devising a coherent system for description of homologous osseous passages for these muscular components. Where inferences of this kind are made, a passage transmitting a single tendo are termed a sulcus aut canalis simplexus (**new term**), whereas such transmitting two or more tendines flexores are termed a sulcus aut canalis complexus (**new term**). Various combinations of status and (to a lesser degree) extent or thickness of these laminae effectively determined the osseous features (cristae, [sub]sulci, canales, spinae, et facies) that collectively specify the form assumed by the hypotarsus avium.

2268. Extremitas proximalis tarsometatarsi, facies plantaris, hypotarsus ("calcaneum") proprius, status (**ordered**):

a. absent, neither hypotarsus proprius nor pseudohypotarsus (**new term**) indicated;

b. rudimentary or vestigial, including pseudohypotarsus (**new term**) produced by way of the caudally displaced, compressed extremitas proximalis of os metatarsale III typical of the "arctometatarsalian" configuration of the synostotic ossa metatarsalia II–IV, in ratites typically showing moderate elaboration of single crista plantaris metatarsale III;

c. present, a variably prominent hypotarsus proprius, comprising an eminentia plantaris and typically enclosing one or more sulci et/aut canales tendinorum.

Note.—See: Ostrom (1976a); C. A. Walker (1981); Cracraft (1982: series 3, character 3); Thulborn (1984: 126–127, character 25); Cracraft (1986: appendix, characters 26 and 38); Gauthier (1986: 14, unindexed synapomorphy of Aves); Cracraft (1988: series III, character 6); Elzanowski (1995: character N7); Chiappe (1991b); Chiappe (1992: character A3); Currie and Peng (1994 [1993]); Hou et al. (1996: character noted in legend for fig. 3); Norell and Makovicky (1997); Chatterjee (1999: appendix II, character 82); Norell et al. (2000: appendix 1, character 35); Chiappe (2001a: appendix 1, character 167); Cracraft and Clarke (2001: appendix 2, character 30); Norell and Clarke (2001: appendix I, character 192), treated similarly by J. A. Clarke (2002: appendix I, character 192), J. A. Clarke and Norell (2002: appendix 2, character 192), and J. A. Clarke (2004: appendix 1, character 192); Chiappe (2002: appendix 20.2, character 167); Vickers-Rich et al. (2002), concerning *Avimimus*; Zhou and Zhang (2002: appendix III, character 192); Manegold et al. (2004: fig. 3), regarding hypothesis of plesiomorphy for Passeriformes; Ji et al. (2005: supplement, part I, character 192).

The hypotarsus proprius (**new term**), a structure of comparatively late ontogenetic completion, is absent in ratites. Study of juveniles indicates that the comparatively nondescript structure quasi-hypotarsus is simply the plantad-displaced extremitas proximalis tarsometatarsale III that is characteristic of the "arctometatarsalian" condition. Juvenile neognathous birds are characterized by ossa tarsalia distalia that compose a proximal lamina for the ossa metatarsalia II–IV, one replete with rudimentary cristae clearly derived from os tarsale proximale.

2269. Hypotarsus, length relative to width (**ordered**):

a. length distinctly greater than width;

b. length subequal to width;

c. length distinctly less than width;

x. noncomparable (palaeognathous Neornithes, Dromornithidae).

Note.—See: Cracraft (1985: character 34); Andors (1992: table 2, character 46); Livezey (1997a: appendix 1, character 89; *corrigenda*, Livezey 1998a); G. Mayr (2002a: legend fig. 9, node 2, character 2); G. Mayr (2004b: appendix 1, character 46).

2270. Hypotarsus (proximal perspective), dorsoplantar position with respect to corpus (**ordered**):

a. entirely plantar to facies plantaris corporis, depth distinctly less than that of corpus;

b. entirely plantar to facies plantaris corporis, depth approximating that of corpus;

c. entirely plantar to facies plantaris corporis, depth at least as great as that of corpus, typically exceeding latter;

d. partly to largely dorsal to facies plantaris corporis, forming recessus hypotarsi corporis;

x. noncomparable by absence (palaeognathous Neornithes).

Note.—Recessus hypotarsi corporis (**new term**) refers to the dorsal invagination or extension of hypotarsus proprius (e.g., canales dorsales) dorsal to facies plantaris of corpus tarsometatarsi.

2271. Hypotarsus, cristae hypotarsalia (i.e., lateralis, intermediae, medialis, if present), approximate mean proximodistal length relative to mean for fossa parahypotarsalia lateralis et/aut medialis, forma (**ordered**):

a. at least majority of latter;

b. approximately one-half of latter;

c. significantly less than one-half of latter, termini proximoplantares extremely truncate;

x. noncomparable (palaeognathous Neornithes, Strigiformes).

Note.—Cristae propriae, not jugae extending distad, used for assessments. See: Hughes (2000: appendix 2, characters 58–63, in part), after Seibel (1988: character TM 13).

2272. Hypotarsus, crista lateralis hypotarsi, plantar prominence relative to adjacent surfaces of hypotarsus (including internum hypotarsi), status et forma (**ordered**):

a. absent;

b. present, extension plantad to basis hypotarsi modest or intermediate;

c. present, extension plantad to basis hypotarsi substantial;

x. noncomparable (palaeognathous Neornithes, Dromornithidae).

Note.—See: Payne and Risley (1976: figs. 22–23), regarding Ardeidae; Cracraft (1981a: 692); Cracraft (1988: series XII, character 5); Hughes (2000: appendix 2, characters 61–63), after Seibel (1988: character TM 13); G. Mayr and Ericson (2004: appendix I, character 75).

2273. Hypotarsus, crista lateralis hypotarsi, spina lateralis hypotarsi (**new term**):

a. absent or miniscule; **b.** present;

x. noncomparable (palaeognathous Neornithes, Dromornithidae).

Note.—New term refers to distally directed spina from crista lateralis. See: Holdaway (1991: appendix 5.1, character 249); Livezey (1998b: appendix A, character 333).

2274. Hypotarsus, crista intermedia(e) hypotarsi, plantar prominence relative to adjacent crista(e) of hypotarsus, status:

a. absent; **b.** present, distinct;

x. noncomparable (palaeognathous Neornithes, Dromornithidae).

Note.—Further subdivision of cristae by prominence declined because of confounding appearance imposed by surrounding hypotarsal structures; e.g., Columbiformes manifest prominent crista intermedia, modest crista medialis, and obsolete crista lateralis.

2275. Hypotarsus, crista intermedia hypotarsi, spina intermedia hypotarsi (**new term**), status:

a. absent;

b. present, in association with isolated, exceptionally prominent crista;

x. noncomparable (palaeognathous Neornithes, Dromornithidae).

Note.—New term refers to distally directed spina from crista intermedia. See: Holdaway (1991: appendix 5.1, character 250); Livezey (1998b: appendix A, character 334); G. Mayr (2003a: appendix I, character 39).

2276. Hypotarsus, crista medialis hypotarsi, plantar extension relative to adjacent surfaces of hypotarsus, status (**ordered**):

a. absent;

b. present, crista moderately plantar to basis hypotarsi;

c. present, crista substantially plantar to basis hypotarsi;

x. noncomparable (palaeognathous Neornithes, Dromornithidae).

Note.—See: Payne and Risley (1976: figs. 22–23), regarding Ardeidae; Livezey (1986: appendix 1, character 70); Cracraft (1988: series XIV, character 9); Livezey (1995c: appendix II, character 37); Livezey (1998b: appendix A, character 336), in reference to total *lamina* medialis (**new term**), including exposed crista, plantar to facies plantaris tarsometatarsi; Hughes (2000: appendix 2, characters 58–63, especially 61), after Seibel (1988: character TM 13).

2277. Hypotarsus, crista medialis hypotarsi, spina medialis hypotarsi (**new term**), status:

a. absent;

b. present, in some cases continuous distad forming distally extensive, prominent jugum with crista medianus plantaris, or uniting with facies plantaris corporis via ligamentum ossificans;

x. noncomparable (palaeognathous Neornithes, Dromornithidae).

Note.—New term refers to distally directed spina from crista medialis. See: Holdaway (1991: appendix 5.1, character 252); Livezey (1998b: appendix A, character 335); G. Mayr (2002a: legend fig. 9, node 2, character 2); G. Mayr (2003a: appendix I, character 40).

Sulci et canales tendinorum mm. flexores hypotarsi

Note.—Hypotarsal diversity was surveyed by Strauch (1978: figs. 29A–D) and S. F. Simpson and Cracraft (1981: fig. 6). With the exception of a minority of unique conformations of limited taxonomic distribution (detailed last), ossified tendinal passages (sulci, canales) are treated here as "absent or shallow sulcus" *vs.* "present as deep sulcus or canalis" in order to minimize intrataxonomic variation in closure of sulci. G. Mayr and Clarke (2003: appendix A, character 103) attempted binary coding of status of "well-developed cristae/sulci" of hypotarsi without tendinal associations. Herein, each primary passage is treated as a separate character with "presence or absence" being two primary states, to which a third state for conjoined primary passages is added where evident. Sulci are described as "majority-delimited" if sulcus delimits more than 180° of homologous canalis. Separate treatments were practical for mediodorsal tendinal passages—especially passages 1–3 of Strauch (1978)—whereas distinguishability and establishment of tendinal homologies became increasingly difficult with more lateral or plantar passages. The treatment by Strauch (1978: characters 64–70, fig. 29E) and employed by Livezey (1998b: appendix A, characters 332–339) conformed well with schemes by Zusi and Bentz (1978: fig. 7) and Vanden Berge and Storer (1995: fig. 8). This synthetic, idealized scheme formed the basis for homologies employed in the characterizations that follow.

Some details of relative position proved intractable here. See: Ligon (1967: table 7); Payne and Risley (1976: figs. 22–23); Strauch (1978: character 65), reanalyzed by Björklund (1994: appendix) and Chu (1995); Livezey (1998b: appendix A, character 337); Hughes (2000: appendix 2, characters 58 and 60), after Seibel (1988: character TM 13); Strauch (1978: character 70), reanalyzed by Björklund (1994: appendix) and Chu (1995); S. F. Simpson and Cracraft (1981: character 9); Hughes (2000: appendix 2, characters 58 and 60), after Seibel (1988: character TM 13).

2278. Hypotarsus, canales et/aut sulci hypotarsi—"tendinal passage 1" of Strauch (1978) or "anteromedial canal" of Stallcup (1954: fig. 6)—canalis tendinis insertii m. flexor digitorum longus (Vanden Berge and Storer 1995: fig. 8), status et forma modalis (**unordered**):

a. absent, indiscernable or shallow sulcus;

b. present, deep, majority-delimited sulcus or canalis;

c. present, conjoined with tendinal passage 2 of Strauch (1978), i.e., with canalis tendinorum (*i*) m. flexor perforatus digiti IV et (*ii*) m. flexor perforans et perforatus digiti II;

d. present, conjoined with tendinal passage 3 of Strauch (1978), i.e., with canalis tendinis m. flexor hallucis longus;

x. noncomparable (palaeognathous Neornithes, Dromornithidae).

Note.—See: Strauch (1978: character 64), reanalyzed by Björklund (1994: appendix) and Chu (1995); Strauch (1985: character 19); Vanden Berge and Storer (1995: fig. 8); Livezey (1998b: appendix A, character 337); Hughes (2000: appendix 2, characters 58 and 60), after Seibel (1988: character TM 13); G. Mayr (2003a: appendix I, character 38); G. Mayr and Clarke (2003: appendix A, character 105); G. Mayr et al. (2003: appendix 1, character 64); Dyke and van Tuinen (2004: appendix 1, character 74); G. Mayr (2004b: appendix 1, character 47); G. Mayr (2004d: appendix I, character 37); G. Mayr and Ericson (2004: appendix I, character 74); G. Mayr (2005a: appendix 1, character 38).

2279. Hypotarsus, canales et/aut sulci hypotarsi—"tendinal passage 2" of Strauch (1978) or "midmedial canal" of Stallcup (1954: fig. 6)—canalis tendinis insertii m. flexor perforatus digiti II (Vanden Berge and Storer 1995: fig. 8), status et forma modalis (**unordered**):

a. absent, indiscernable or shallow sulcus;

b. present, deep, majority-delimited sulcus or canalis;

c. present, conjoined with tendinal passage 4 of Strauch (1978), i.e., with canalis tendinis m. fibularis longus;

x. noncomparable (palaeognathous Neornithes, Dromornithidae).

Note.—See: Vanden Berge and Storer (1995: fig. 8); Livezey (1998b: appendix A, character 339); G. Mayr (2003a: appendix I, character 38).

2280. Hypotarsus, canales et/aut sulci hypotarsi—"tendinal passage 3" of Strauch (1978) or "anterolateral canal" of Stallcup (1954: fig. 6)—canalis tendinis insertii m. flexor hallucis longus (Vanden Berge and Storer 1995: fig. 8), status modalis:

a. absent, indiscernable or shallow sulcus;

b. present, deep, majority-delimited sulcus or canalis;

x. noncomparable (palaeognathous Neornithes, Dromornithidae).

Note.—See: Payne and Risley (1976: figs. 22–23), regarding Ardeidae; Strauch (1978: character 66), reanalyzed by Björklund (1994: appendix) and Chu (1995); Strauch (1985: character 19); Vanden Berge and Storer (1995: fig. 8); Livezey (1998b: appendix A, characters 338–339); Hughes (2000: appendix 2, characters 58 and 60), after Seibel (1988: character TM 13), for cuculiforms; G. Mayr (2002a: legend fig. 9, node 3, character 4); G. Mayr (2003a: appendix I, character 38); G. Mayr (2003b: appendix I, character 14); G. Mayr et al. (2003: appendix 1, character 63); G. Mayr (2004d: appendix I, character 38); G. Mayr and Ericson (2004: appendix I, character 73); G. Mayr (2005a: appendix 1, character 39).

2281. Hypotarsus, canales et/aut sulci hypotarsi—"tendinal passage 4" of Strauch (1978)—canalis tendinis insertii m. fibularis (peroneus) longus (Vanden Berge and Storer 1995: fig. 8), status modalis:

a. absent, indiscernable or shallow sulcus;

b. present, deep, majority-delimited sulcus or canalis, including minority conjoined with tendinal passage 2 of Strauch (1978), i.e., with canalis tendinorum (*i*) m. flexor perforatus digiti IV et (*ii*) m. flexor perforans et perforatus digiti II;

x. noncomparable (palaeognathous Neornithes, Dromornithidae).

Note.—See: Strauch (1978: character 67), reanalyzed by Björklund (1994: appendix) and Chu (1995), for charadriiforms; Vanden Berge and Storer (1995: fig. 8); Hughes (2000: appendix 2, characters 58 and 60), after Seibel (1988: character TM 13), for cuculiforms; G. Mayr and Clarke (2003: appendix A, character 106); Dyke and van Tuinen (2004: appendix 1, character 75).

2282. Hypotarsus, canales et/aut sulci hypotarsi—"tendinal passage 5" of Strauch (1978) or "posterolateral canal" of Stallcup (1954: fig. 6)—canalis tendinorum insertii (*i*) m. flexor perforatus digiti III, (*ii*) m. flexor perforatus et perforans digiti III, et/aut (*iii*) m. flexor perforatus digiti IV (Vanden Berge and Storer 1995: fig. 8)—status modalis:

a. absent, indiscernable or shallow sulcus;

b. present, deep, majority-delimited sulcus or canalis;

x. noncomparable (palaeognathous Neornithes, Dromornithidae).

Note.—See: Strauch (1978: character 69), reanalyzed by Björklund (1994: appendix) and Chu (1995); Vanden Berge and Storer (1995: fig. 8); Chu (1998: appendix 1, character 113); Hughes (2000: appendix 2, characters 58 and 60), after Seibel (1988: character TM 13) for cuculiforms. Tendo m. flexor hallucis longus may join with tendo m. flexor digitorum longus where hallux reduced.

2283. Hypotarsus, canales et/aut sulci hypotarsi—"tendinal passage 6" of Strauch (1978) or "posteromedial canal" of Stallcup (1954: fig. 6)—canalis tendinis insertii m. flexor perforans et perforatus digiti III (Vanden Berge and Storer 1995: fig. 8)—status et forma modalis (**unordered**):

a. absent, indiscernable or shallow sulcus;

b. present, deep, majority-delimited sulcus or canalis;

c. present, conjoined partly or completely with tendinal passages 1–5 of Strauch (1978), i.e., with two or more other canales tendinorum mm. flexores;

x. noncomparable (palaeognathous Neornithes, Dromornithidae).

Note.—See: Strauch (1978: character 68), reanalyzed by Björklund (1994: appendix) and Chu (1995); Strauch (1985: character 19); Vanden Berge and Storer (1995: fig. 8). Infrequently, two canales are present, apparently a confluence of this tendo with that of (displaced) m. flexor digitorum longus; Hughes (2000: appendix 2, characters 58 and 60), after Seibel (1988: character TM 13) for condition of cuculiforms.

2284. Hypotarsus, canales et/aut sulci hypotarsi, status generalis:

a. present, variable with respect to both sulci et canales;

b. absent, aspectus hypotarsi rectanguloid;

x. noncomparable (palaeognathous Neornithes, Dromornithidae).

Note.—Local polarity predicated on exclusion of palaeognathous Neornithes as lacking hypotarsi verae (and thereby sulci aut canales). See: Berger (1960b: table 4, character 3), regarding two and one canales hypotarsalia in Cuculidae and Musophagidae, respectively; Payne and Risley (1976: figs. 22–23), regarding Ardeidae; Cracraft (1974: 502, character 10); Strauch (1978: 64–70); S. F. Simpson and Cracraft (1981: characters 8, 11, and 16); Bledsoe (1988: appendix, characters 66–68, and 73); Prum (1988: character 27); Kurochkin (1995b: table 1, character 29); K. Lee et al. (1997: appendix 1, character 27); Livezey (1998b: appendix A, characters 337–340); Hughes (2000: appendix 2, character 59), after Seibel (1988: character TM 13); J. A. Clarke and Chiappe (2001: character 72); G. Mayr (2002a: legend fig. 9, node 1, character 4); Norell and Clarke (2001: appendix I, character 192), treated similarly by J. A. Clarke and Norell (2002: appendix 2, character 192). Some authorities simply enumerated sulci et canales, without respect for inferred tendinal homologies, an approach avoided here.

2285. Hypotarsus, canalis complexus hypotarsi lateralis (**new term**)—i.e., laterally displaced, enlarged passage evidently enclosing two or more tendines, presumptively comprising tendinal passages 3 (m. flexor hallucis longus) and 5 (m. flexor perforatus digiti IV) of Strauch (1978), status:

a. absent; **b.** present.

Note.—See: Livezey (1998b: appendix 2, characters 337–339).

2286. Hypotarsus (plantar perspective), sulci et/aut canales magnus hypotarsi (**new term**), status et lamina(e) limitates (**unordered**):

a. absent, hypotarsus either imperforate or includes one or more small sulci aut canales tendinorum;

b. present, bounded asymmetrically by lamina medialis;

c. present, bounded symmetrically (bilaterally) by laminae medialis et lateralis, defining single sulcus magnus hypotarsi;

d. present, bounded symmetrically (bilaterally) by laminae medialis et lateralis that are joined by margines plantares, thereby enclosing a homologous canalis magnus hypotarsi;

e. present, divided by single lamina paramediana;

x. noncomparable (palaeognathous Neornithes, Dromornithidae).

Note.—See: G. Mayr and Clarke (2003: appendix A, character 104); G. Mayr et al. (2003: appendix 1, character 62); Dyke and van Tuinen (2004: appendix 1, character 73); G. Mayr (2004a: appendix 1, character 57); G. Mayr (2004d: appendix I, character 39, part); G. Mayr (2005a: appendix 1, character 40). Sulcus magnus hypotarsi (**new term**) refers to single, large passage that occupies most or virtually all of the area delimited for hypotarsus and which transmits multiple tendines flexores. As indicated below, smaller, more typical passages are distinguished herein using traditional terms of sulci et canales hypotarsi, and typically (like their corresponding canales) transmit but one or two tendines flexores.

Corpus tarsometatarsi

2287. Corpus tarsometatarsi, marked lateromedial compression of corpus such that dorsoplantar depth exceeds lateromedial width, status:

a. absent; **b.** present.

Note.—See: Cracraft and Mindell (1989: series XI, character 11); Holtz (1994a: appendix 1, character 67), limited incomparably to nonavialian theropods; Livezey (1997b: appendix 1, character 88); Chu (1998: appendix 1, character 115); Livezey (1998b: appendix A, character 344); Xu (2002: suite I, character 67.

2288. Corpus tarsometatarsi, margo medialis, pars proximalis, forma:

a. rounded, similarly conformed as rest of corpus;

b. dorsoplantad compressed, margo medialis comparatively thin.

Note.—In large part a reflection of the depth and expanse of fossa parahypotarsalis medialis. See: Ericson (1997: table 1, character 70).

2289. Corpus tarsometatarsi, margo (crista) lateralis (especially pars distalis), forma (dorsal perspective):

a. concave, distally curving smoothly to facies lateralis of trochlea digiti IV, typically effecting approximate symmetry with margo medialis;

b. (sub)linear, oriented (virtually) directly distad to margo lateralis trochlearis digiti IV, typically effecting distinct asymmetry with margo medialis.

Note.—See: Livezey (1986: appendix 1, character 76); Livezey (1995c: appendix II, character 39).

2290. Corpus tarsometatarsi, margo (crista) medialis (interna), dorsoplantar compression rendering sublaminate forma, status:

a. absent; **b.** present.

Note.—Evidently related to hypertrophy of mm. abductor et adductor digiti II.

2291. Corpus tarsometatarsi, facies subcutanea medialis, concavitas marginalis (evidently enlarged impressio m. extensor hallucis longus), extending obliquely distoplantad from fossa infracotylaris dorsalis toward os metatarsale I pedis, status:

a. absent or obsolete;

b. present and prominent.

2292. Corpus tarsometatarsi, facies dorsalis, margines medialis (interna) et lateralis (externa), relative dorsal prominence (**ordered**):

a. medial distinctly less prominent than lateral;

b. medial and lateral essentially equally prominent;

c. medial distinctly more prominent than lateral, especially proximally.

Note.—Facies medialis tarsometatarsi typically serves as situs origii m. extensor hallucis longus (proximally) and m. abductor digiti III (distally). Inequality of dorsal prominence of margines (especially if differential varies proximodistad), produces apparent torsion of corpus about axis majoris ossis. See: Cracraft (1982: series 4, character 6); Livezey (1986: appendix 1, character 75); Cracraft (1988: series XI, character 12); Livezey (1995a: appendix 1, character 13); Livezey (1995c: appendix II, character 38); Livezey (1996b: appendix 1, character 39); Livezey (1996c: character 14); Hughes (2000: appendix 2, characters 64–65), after Seibel (1988: characters TM 16 and 17).

2293. Corpus tarsometatarsi (ossa metatarsalia II–IV), facies dorsalis, foramina (fenestrae) intertarsometatarsalia lateralis et medialis (**new terms**), forma (**unordered**):

a. small, limited to pars proximalis metatarsalia as small foramina parahypotarsalia (**new term**) that entail variable degrees of internal and dorsal obstruction;

b. medium, in some foramen medialis is twice the size of lateral counterpart and bounded medially by narrow, columnar os metatarsale IV;

c. large, fenestrae extending majority of lengths of bordering ossa metatarsalia, foramina vascularia proximalia enclosed within termina proximales fenestralia as partitioned (medialis) or common (lateralis) ostia.

Note.—Also associated with this feature is the distinctness of the composite ossa metatarsalia, and the generality that fenestra intermetatarsalia III et IV is completely dorso-plantad whereas that between ossa metatarsalia is sometimes occluded on facies plantaris by membrana ossificans. See: Stephan (1979), a comprehensive atlas of Spheniscidae.

2294. Corpus tarsometatarsi, facies plantaris, forma (**unordered**):

a. essentially flat or marked subtly by cristae et sulci longitudinales;

b. distinctly angular-convex, variably but typically well marked by cristae et sulci, often declining in prominence distad longitudinales.

Note.—See: Cracraft (1974: 502, character 11); Bledsoe (1988: appendix, character 74); Sanz et al. (1995: appendix 3, character 3); K. Lee et al. (1997: appendix 1, character 31); Norell and Makovicky (1997).

2295. Corpus tarsometatarsi, facies plantaris, sulcus m. fibularis (peronei) longi, forma:

a. weakly or moderately defined, typically truncated impressio;

b. strongly defined by peripheral cristulae intermusculares, typically deeply recessed, distally extensive fossa.

2296. Corpus tarsometatarsi, facies plantaris, sulcus flexorius, crista plantaris medialis, eminentia:

a. distinct, often prominent;

b. absent or indistinct.

2297. Corpus tarsometatarsi, facies plantaris, sulcus flexorius, crista plantaris lateralis, eminentia:

a. absent or indistinct; **b.** prominent.

Note.—See: G. Mayr (2004d: appendix I, character 39); G. Mayr (2005a: appendix 1, character 40).

2298. Corpus tarsometatarsi, facies plantaris, sulcus flexorius, crista medioplantaris, status:
a. absent;
b. present, variably prominent;
x. noncomparable (palaeognathous Neornithes, Dromornithidae).

Note.—See: G. Mayr et al. (2003: appendix 1, character 61); G. Mayr (2004d: appendix I, character 36); G. Mayr (2005a: appendix 1, character 37). Feature considered synonymous with "crista plantaris medialis," and its proximal genesis is extremitas distalis of crista medialis hypotarsi. Pseudo-hypotarsi of ratites may resemble this crista, but plantar displacement of os metatarsale III contributes much or all of the apparent crista in ratites, hypotarsae verae actually lacking.

2299. Corpus tarsometatarsi, facies plantaris, sulcus flexorius, crista medioplantaris, extension proximal to cotylae medialis et lateralis, status:
a. absent; **b.** present.

Note.—Apomorphic taxa comprise ratites in which a true hypotarsus is lacking. Apomorphic state may result from synostosis of terminus proximalis cristae with os sesamoideum intertarsale, and related to hypertrophy of m. adductor digiti II.

2300. Corpus tarsometatarsi, facies plantaris, sulcus flexorius, crista medioplantaris, situs lateromedialis:
a. approximately mediad on facies plantaris;
b. shifted distinctly laterad throughout, underlying (in part) the virtually complete concavity of facies plantaris tarsometatarsi.

2301. Corpus tarsometatarsi, facies plantaris, sulcus flexorius, crista plantaris medianus, synostosis with aponeurosis (tendo origii) ossificans m. gastrocnemiali, status:
a. absent;
b. present, typically with lacuna(e) infracristalis (**new term**).

Note.—Typically restricted to those taxa having multiple ligamenta et/aut tendines ossificantes along the tarsometatarsus or elsewhere in the membri pelvici. This osseus complex forms a septum enclosing (in part) tendines flexores longa of ossa digitorum pedis, and in males of some Galliformes, pars intermedia septi contributes to bases processi calcaris.

2302. Corpus tarsometatarsi, facies plantaris, sectio proximalis medial to axis proximodistalis, jugum origii m. adductor digiti II pedis, forma:
a. moderate or absent, typically smooth, generally continuing parallel to crista medioplantaris distal to approximate midpoint of element;
b. prominent, typically rugose, converging with crista medioplantaris at approximate midpoint of element.

2303. Corpus tarsometatarsi, facies plantaris, sulcus parahypotarsalis lateralis (**new term**), a distinct extension of fossa parahypotarsalis lateralis distad to facies lateralis trochlearis metatarsale IV, status:
a. absent, indistinct, or proximally truncated;
b. present.

Note.—Characterized primarily by delineation and extent for virtually entire corpus tarsometatarsale as opposed to depth, sulcus reflects distal robustness of m. flexor perforatus digiti IV (Owre 1967).

2304. Corpus tarsometatarsi, facies plantaris, processus calcaris, status definitivum (typically adult males) et forma (**unordered**):
a. absent;
b. present, singular at basis, afurcate distally;
c. present, two or more separately based processes.

Note.—See: Davison (1985) and Dyke et al. (2003: appendix 1, character 86). Some members of Phasianidae lack calcares, including polymorphism of status within Odontophorinae, Phasianinae, and Numidinae. Some taxa possessing processus present variable expression in females or multiple calcares (polymorphism), the last state apparently limited to some male Phasianidae (e.g., *Acryllium*). Presence of this processus implies parallel development of integumentary "calcar metatarsale" (not coded under INTEGUMENTUM to avoid redundancy). Osteologically, the processus calcaris tarsometatarsi extends plantad from a distal extension and plantar deepening of crista medioplantaris.

2305. Corpus tarsometatarsi, facies dorsalis, sulcus extensorius, status et forma (**ordered**):
a. absent or present, shallow to approximate midpoint, diminishing distad, thereby effecting distal extension of fossa infracotylaris dorsalis;
b. present, and delimited moderately well by both cristulae subcutaneae lateralis et medialis (**new term**), and typically extending distad the majority of length of corpus tarsometatarsi;
c. present, deep to cavernous, both cristulae subcutaneae lateralis et medialis (**new terms**) bounding cavitas extensorius (**new term**), and typically extending distad virtually the entirety of corpus tarsometatarsi.

Note.—See: Cracraft (1974: 503, character 12) and K. Lee et al. (1997: appendix 1, character 30), regarding ratites; Cracraft (1982: series 2, character 7) regarding "gaviomorphae"; Livezey (1998b: appendix A, characters 346–347), regarding gruiforms. Also termed "anterior metatarsal groove," principally serves as situs origii m. extensor brevis digiti

IV, and in those taxa in which sulcus extends distad, situs origii m. extensor proprius digiti III.

2306. Corpus tarsometatarsi, facies dorsalis, sulcus extensorius, impressiones retinaculi extensorii, ruga medialis sulci (**new term**) distinct in absence of ruga lateralis sulci (**new term**), status:

a. absent;

b. present, accentuated by comparatively wide, deep sulcus adjacent to ruga, and minimally raised tuberositas m. tibialis cranialis.

Note.—Aspect produced is proximal extension of broad, deep sulcus extensorius on facies dorsalis of corpus tarsometatarsi.

2307. Corpus tarsometatarsi, facies dorsalis, sulcus extensorius, impressiones retinaculi extensorii, dorsal prominence of rugae (especially medialis) et solum sulci, status:

a. absent; **b.** present.

2308. Corpus tarsometatarsi, facies dorsalis, sulcus extensorius, arcus extensorius, status:

a. absent, intrinsic mm. extensorii restrained by an ansa ligamentosa;

b. present, ansa restraining intrinsic mm. extensorii ossified as arcus shortly distal to cotylae tarsometarsalia.

Note.—Polymorphism characterized by homologous rudimenta manifested as jugular impressiones retinaculi extensorii medialis et/aut lateralis.

See: Sibley and Ahlquist (1972: table 4), noted absence in Tytonidae and presence in Strigidae; Chu (1998: appendix 1, character 114); Livezey (1998b: appendix A, character 345); G. Mayr et al. (2003: appendix 1, character 65); G. Mayr (2004d: appendix I, character 35); G. Mayr (2005a: appendix 1, character 36). Arcus represents homologue of retinaculum ossificans extensorium tarsometatarsalium.

2309. Corpus tarsometatarsi, facies plantaris, sulcus flexorius (plantar perspective), status et forma (**ordered**):

a. absent or obsolete, medial narrowing and decreased depth imposed either by (*i*) convex facies plantaris or (*ii*) enlarged crista medioplantaris;

b. present, moderately distinct;

c. present, deep.

Note.—Sulcus flexorius largely obviated if crista medioplantaris prominent and extensive; critical to distinguish from fossa (sulcus) parahypotarsialis lateralis in some taxa (e.g., Columbiformes). Prominence of cristae plantares medialis et lateralis broadly corresponds with distinctness of delimited sulcus flexorius.

See: Livezey (1998b: appendix A, character 348); Chiappe (2001a: appendix 1, character 165); Chiappe (2002: appendix 20.2, character 165), in reference to "plantar surface . . . excavated." Norell and Makovicky (1997) presented evidence that this feature may have occurred in at least some dromaeosaurids; G. Mayr (2004d: appendix I, character 36), with respect to fossa parahypotarsalis medialis in Piciformes and Passeriformes; G. Mayr (2005a: appendix 1, character 37).

2310. Corpus tarsometatarsi, medial angulation and associated marginal asymmetry of distal four-fifths of corpus, status:

a. absent;

b. present, angulation in accord with distal obsolescence of os metatarsale II.

Note.—Associated with vestigial trochlea metatarsi et digitus II pedis.

2311. Corpus tarsometatarsi (principally os metatarsale IV), facies plantaris, margo lateralis, crista origii m. extensor brevis digiti IV (**new term**), status:

a. absent or only rudimentary;

b. present, a prominent septum osseum musculorum.

Note.—See: G. Mayr (2004d: appendix I, character 42); G. Mayr (2005a: appendix 1, character 40), regarding "crista plantaris lateralis."

2312. Corpus tarsometatarsi, facies plantaris aut medialis, pars distalis (typically or principally associated with os metatarsale II), fossa metatarsi I (primus, hallucis), status et forma (**ordered**):

a. absent or indiscernable;

b. present, vague impressio;

c. present, fovea or distinct fossa;

x. noncomparable in taxa lacking os metatarsale I (see character treating status) aut synostosis intermetatarsalis (Phaethontidae, Haematopodidae).

Note.—See: Livezey (1986: appendix 1, character 71); Livezey (1989: table 1, character 71); Livezey (1996a: appendix 1, character 72); Ericson (1997: table 2, character 47); Livezey (1997a: appendix 1, character 91; *corrigenda*, Livezey 1998a); Norell and Makovicky (1997), who averred that subtle depressiones in this area have been mistaken for this fossa; Norell and Clarke (2001: appendix I, character 197), treated similarly by J. A. Clarke (2002: appendix I, character 196), J. A. Clarke and Norell (2002: appendix 2, character 196), and J. A. Clarke (2004: appendix 1, character 196); Zhou and Zhang (2002: appendix III, character 197); Ji et al. (2005: supplement, part I, character 197).

2313. Corpus tarsometatarsi, facies plantaris, fossa metatarsi I (primus, hallucis), situs proximodistalis relative to basis trochlearis of os metatarsale III (**ordered**):

a. proximal—facies plantaris fossae os metatarsalia immediately mediodistal to hypotarsus;

b. subproximal—facies plantaris fossae os metatarsalia at approximate midpoint of corpus;

c. subdistal—facies plantaris fossae os metatarsalia approximately one-quarter of length of corpus proximal to terminus;

d. distal—fossae os metatarsalia proximal to terminus tarsometatarsi by approximate length of one trochlea or less;

x. noncomparable in taxa lacking os metatarsale I.

Note.—See: Norell et al. (2001: appendix 1, character 203); J. M. Clark et al. (2002a: appendix 2.2, character 205); Xu (2002: suite II, character 224), all of which confounded status, proximodistal and lateromedial positions (characters treated separately herein); Hwang et al. (2004: supplement, character 202); Xu and Norell (2004: supplement, character 202).

2314. Corpus tarsometatarsi, facies plantaris, fossa metatarsi I (primus, hallucis), situs dorsoplantaris relative to trochlea metatarsale II:

a. medial, situated on margo medialis metatarsale II;

b. plantar, some with minor medial component;

x. noncomparable in taxa lacking os metatarsale I.

Extremitas distalis tarsometatarsi

2315. Extremitas distalis tarsometatarsi, foramen vasculare distale, status (**ordered**):

a. absent, among Neornithes related to absence of distal, delimiting pons;

b. present and complete, situated at variably proximodistal positions between ossa metatarsalia III et IV, and possessing both ostia foraminis dorsalis et plantaris;

c. present but occluded, situated distally between ossa metatarsalia III et IV, and lacking ostium foraminis plantaris.

Note.—*Casuarius* typically retains vestigia of bases lateralis et medialis pontis, the absence of latter underlying the absence of foramen; indicative of secondary loss are the vestigial foramina et foveae in the incisura intertrochlearis, possibly related to absent canalis interosseus (intertrochlearis) tendineus distalis.

See: Payne and Risley (1976: character 33), regarding "distal metatarsal foramen" among Ardeidae; Cracraft (1986: appendix, character 27); Gauthier (1986: 14, unindexed synapomorphy of Aves); Cracraft (1988: series II, character 11); Houde (1988: table 27, character 50); S. L. Olson and Hasegawa (1979, 1985, 1996); Stephan (1979); S. L. Olson (1980); Chiappe and Calvo (1994: appendix I, character 73); Chiappe (1995a: legend for fig. 1); Chiappe (1995b: character 73); Elzanowski (1995: character N'3); Sanz et al. (1995, 1997: character 71); Chiappe (1996b: character 67); Chiappe et al. (1996: appendix 1, character 66); Norell and Makovicky (1997); Forster et al. (1998: supplement, character 113); Livezey (1998b: appendix A, character 349); Chiappe (2001a: appendix 1, character 161); Chiappe (2002: appendix 20.2, character 161); G. Mayr (2004b: appendix 1, character 48); Murray and Vickers-Rich (2004: table 9, character 37), concerning variable delimitation in Dromornithidae.

2316. Extremitas distalis tarsometatarsi, facies dorsalis, foramen vasculare distale, forma *sensu* diameter (mean of ostia dorsalis et plantaris) relative to lateromedial width of incisura intertrochlearis metatarsalia III et IV (**ordered**):

a. distinctly smaller; **b.** subequal;

c. distinctly larger;

x. noncomparable (Casuariiformes, Sphenisciformes).

Note.—See: Murray and Vickers-Rich (2004: table 9, character 39; fig. 140E), concerning related assessment of relative widths of incisurae intertrochleares metatarsalia II–III et III–IV in Dromornithidae.

2317. Extremitas distalis tarsometatarsi, foramen vasculare distale, forma *sensu* dorsoplantar orientation relative to axis majoris of corpus tarsometatarsi (**ordered**):

a. subperpendicular, essentially directly dorsoplantad, unobstructed perpendicular line of sight;

b. oblique, distinctly ventrodistal, obstructed perpendicular line of sight;

c. subparallel, ostium distalis oriented virtually proximodistad;

x. noncomparable (Casuariidae, Sphenisciformes, Bucerotidae).

Note.—See: Payne and Risley (1976: character 33), "distal metatarsal foramen" among Ardeidae; Livezey (1986: appendix 1, character 77); Livezey (1989: table 1, character 77); Livezey (1996a: appendix 1, character 74); Andors (1992: table 1, character 25); Ericson (1997: table 2, character 46); Livezey (1997a: appendix 1, character 92; *corrigenda*, Livezey 1998a).

2318. Extremitas distalis tarsometatarsi, foramen vasculare distale (dorsal perspective), dorsoplantar orientation and proximodistal positions of ostia distalis et proximalis (respectively) for canalis interosseus (intertrochlearis) tendineus distalis and foramen vascularia propria, forma (**unordered**):

a. only ostia proximalis of canalis dorsalis visible;

b. ostia moderately separated proximodistad and both visible in dorsal perspective;

c. ostia considerably separated proximodistad and exposed in dorsal perspective;

x. noncomparable (Casuariidae, Sphenisciformes).

Note.—Canalis interosseus (intertrochlearis) tendineus distalis conducts tendo m. extensor brevis digiti IV, ostium efferens for which opens in vertex of incisura intertrochlearis lateralis tarsometatarsi.

2319. Extremitas distalis tarsometatarsi, foramen vasculare distale, septum vasculo-tendineus foraminis (**new term**), status:

a. absent; **b.** present;

x. noncomparable (Casuariidae, Sphenisciformes).

Note.—Appears (dorsal perspective) as fine transverse pons within foramen vasculare distale, and evidently separates tendo extensor digiti IV (passing distad to septum) from vascular components (passing proximad).

2320. Extremitas distalis tarsometatarsi, foramen vasculare distale, situs in which foramen perforates tarsometatarsus relative to approximate axis majoris tarsometatarsi:

a. lateral; **b.** central;

x. noncomparable (Struthionidae, Casuariidae, Sphenisciformes).

Note.—Both foramen vasculare distale and canalis interosseus (intertrochlearis) tendineus distalis pass between ossa metatarsalia III et IV, but apparent position within composite tarsometatarsus varies. See: Payne and Risley (1976: character 33), regarding position of "distal metatarsal foramen" among Ardeidae.

2321. Extremitas distalis tarsometatarsi, foramen vasculare distale, ostium foraminis dorsale (dorsal perspective), situs proximodistalis:

a. distal—approximately parallel to margines proximales trochleares (especially that of os metatarsale IV), typically within terminus of sulcus intertrochlearis metatarsalia III et IV;

b. proximal—distinctly proximal to trochlea, extreme conditions proximal to margo proximalis of sulcus intertrochlearis metatarsalia III et IV;

x. noncomparable (Casuariidae, Sphenisciformes).

Note.—See: Murray and Vickers-Rich (2004: table 9, character 37).

2322. Extremitas distalis tarsometatarsi, foramen vasculare distale, positioned at terminus distalis of sulcus extensorius such that ostium foraminis dorsalis is concealed (dorsal perspective), status:

a. absent; **b.** present;

x. noncomparable (Casuariidae, Sphenisciformes).

2323. Extremitas distalis tarsometatarsi, foramen vasculare distale (dorsal perspective), ostium foraminis dorsalis (**new term**), forma:

a. continued proximad by essentially smooth bone or shallow sulcus;

b. continued proximad by deep, distinctly emarginated sulcus;

x. noncomparable (Casuariidae, Sphenisciformes).

Note.—See: G. Mayr (2003c: appendix, character 25); G. Mayr (2005b: appendix A, character 44).

2324. Extremitas distalis tarsometatarsi, foramen vasculare distale (plantar perspective), ostium foraminis plantaris (**new term**), forma (**unordered**):

a. not continued distad by distinct sulcus intermetatarsalis to incisura intertrochlearis lateralis;

b. continued distad by distinct sulcus intermetatarsalis to incisura intertrochlearis lateralis;

c. emerging well distad, within distinct sulcus intermetatarsalis;

x. noncomparable (Palaeognathidae exclusive of Tinamiformes, Sphenisciformes).

Note.—See: Holdaway (1991: appendix 5.1, character 263); Livezey (1998b: appendix A, character 350). Taxa lacking solum plantaris foraminis (e.g., *Centropus*, *Aegotheles*, *Brachypteracias*) included by default in "a."

2325. Extremitas distalis tarsometatarsi, canalis aut sulcus interosseus (intertrochlearis) tendineus distalis (foramen tendinis m. extensor brevis digiti IV), forma dorsalis (**ordered**):

a. foramen continued distad by *dorsoventrally exposed* sulcus tendineus, including taxa lacking foramen distale;

b. foramen continued distad by *complete canalis* tendineus;

c. foramen continued distad (obliquely, proximodorsal to distoplantar) by *ventrally exposed* sulcus tendineus.

Note.—*Apteryx* and Sphenisciformes retain fovea at homologous situs for ostium efferens canalis interosseus distalis, supporting hypothesis of secondary loss; tendo m. extensor brevis digiti IV—retained in both Apterygidae (McGowan 1979; Vanden Berge 1982) and Spheniscidae (Schreiweis 1982)—passes through incisura intertrochlearis dorsalis, as in other Neornithes lacking canalis interosseus distalis. Ostium efferens (distalis) of canalis is within incisura intertrochlearis III–IV; some diving anatids show secondary reduction of lamina dorsalis canalis (Livezey 1986, 1995b).

See: Siegel-Causey (1988: character 136); Livezey (1986: appendix 1, character 69); Andors (1992: table 1, character 24); Livezey (1995b: appendix 1, character 20); Livezey (1995c: appendix II, character 36); Livezey (1996c: character 13); Norell and Makovicky (1997); Norell and Clarke (2001: appendix I, character 201), treated similarly by J. A. Clarke (2002: appendix I, character 200), J. A. Clarke and Norell (2002: appendix 2, character 200), and J. A. Clarke (2004: appendix 1, character 200); Zhou and Zhang (2002: appendix III, character 201); G. Mayr and Clarke (2003: appendix A, character 107); G. Mayr et al. (2003: appendix 1, character 66); Dyke and van Tuinen (2004: appendix 1, character 76); G. Mayr (2004d: appendix I, character 43); G. Mayr (2005a:

appendix 1, character 44); Ji et al. (2005: supplement, part I, character 201).

2326. Extremitas distalis tarsometatarsi, canalis aut sulcus interosseus (intertrochlearis) tendineus (foramen tendinis m. extensor brevis digiti IV), forma plantaris *sensu* distal extent relative to that of margo incisurae intertrochlearis lateralis:
a. ostium foraminis tendinis et margo incisurae intertrochlearis lateralis approximately equally distal;
b. foramen tendinis emergent distinctly proximad to margo incisurae intertrochlearis lateralis, former continued to latter by irregularly delimited sulcus.

2327. Extremitas distalis tarsometatarsi, canalis aut sulcus interosseus (intertrochlearis) tendineus (foramen tendinis m. extensor brevis digiti IV), forma plantaris *sensu* trochlea accessoria forms solum plantaris of passage, status:
a. absent; **b.** present.
Note.—Apomorphic state requires presence of *Sehnenhalter*.

2328. Extremitas distalis tarsometatarsi, facies dorsalis, sulcus musculi extensorius brevis digiti IV (Ballmann 1969a: 161)—sharply defined, comparatively deep sulcus proximal to foramen vascularis distale—status:
a. absent or indistinct;
b. present and distinct.
Note.—The nonstandardized but logical term of Ballmann (1969a) employed above also was adopted by Andors (1988: 245).

2329. Extremitas distalis tarsometatarsi (plantar perspective), fossa supratrochlearis plantaris, status:
a. absent or indistinct;
b. present, distinctly concave.
Note.—See: Chiappe (1993: character 3). Apparent depth of this fossa (plantar perspective) can be distorted by confounding curvature among positions of trochleae (e.g., simply plantar displacement of trochlea metatarsi II) with true concavity of area intertrochlearis.

2330. Extremitas distalis tarsometatarsi (plantar perspective), trochleae metatarsalia II–IV, termini proximales, sharp, subparallel emargination bordered proximad by distinctly depressed regiones (i.e., a "steplike" aspect), status:
a. absent, trochleae grading variably smoothly with facies plantares tarsometatarsi;
b. present; **x.** noncomparable (*Struthio*).

2331. Extremitas distalis tarsometatarsi, facies dorsomedialis, sulcus m. extensor digitorum longus (ramus medialis), passing distad through incisura intertrochlearis medialis, status:
a. absent or indiscernable; **b.** present.
Note.—See: Wilcox (1952).

Extremitas distalis tarsometatarsi, trochleae metatarsalia

Note.—Following treatments are organized in ascending numerical sequence by ossa metatarsalia involved (thereby permitting application of characters codable for a given specimen), beginning with: (*i*) presence or absence of ossa metatarsalia; (*ii*) conformational characters *among* trochleae (e.g., incisurae intertrochleares), wherein it is noted that some striking, apparently unified characters (e.g., multicolinearity among trochleae digiti II–IV in Mesitornithidae, *Menura*) are parsed into several different characters; (*iii*) conformational aspects of the trochleae relative to the corpus tarsometatarsalis (e.g., status and relative sizes of eminentiae dorsoplantares, lateromediales, and proximodistales); and (*iv*) conformational details of individual trochleae *per se*, whether unique to one or more ossa metatarsalia.

Qualitative characteristics of individual trochleae metatarsalia

2332. Extremitas distalis tarsometatarsi, trochleae accessoriae group I (i.e., primarily or solely involving trochlea metatarsi I, with secondary implications for trochleae II et IV), trochlea accessoria (*Sehnenhalter*) metatarsi I (primus), status et forma (**ordered**):
a. absent, associated with anisodactyly;
b. present, moderately developed and limited to os metatarsi I, functionally associated with rudimentary propamprodactyly;
c. present, well developed and accompanied by changes in trochleae metatarsalia II et IV, functionally associated with pamprodactyly proprius.
Note.—Associated with pamprodactyly in trochiliform digital subtypus and pamprodactyly proprius of Apodidae. Condition of Trochilidae comprises distal truncation and rounding of os metatarsi I in conjunction with strictly lateromedially aligned trochleae metatarsalia II–IV (G. Steinbacher 1935: fig. 9), whereas in Apodidae condition involves asymmetrical lobation of os metatarsi I in conjunction with proximodistally oblique but lateromedially aligned trochleae metatarsalia II–IV (G. Steinbacher 1935: fig. 10). See: Ingram (1955, 1958, 1972).

2333. Extremitas distalis tarsometatarsi, trochleae accessoriae group II (i.e., primarily or solely involving plantar torsion of trochlea metatarsi II), trochlea accessoria (*Sehnenhalter*) metatarsi II (secundus), status:
a. absent, associated with anisodactyly;
b. present without trochleae accessoriae metatarsalia I et/aut IV, associated with heterodactyly.
Note.—Apomorphic state of this typus among *Sehnenhalteren* involves lateromedially expanded trochleae accessoriae and lateromedial ankylosis be-

tween trochleae metatarsalia I et IV, as well as plantar hemi-rotations of trochleae metatarsalia I et IV (resulting in opposition with trochleae metatarsalia II et III), effecting a quadrangular arrangement of opposing pairs of trochelae (G. Steinbacher 1935: figs. 12–13).

2334. Extremitas distalis tarsometatarsi, trochleae accessoriae group III, trochleae accessoriae (*Sehnenhalteren*) metatarsalia II (secundus) et IV (quartus), i.e., primarily or solely involving differential modifications of trochleae metatarsalia II et IV and infrequently also trochlea metatarsale I, status et typus (**unordered**):

a. absent, associated with anisodactyly;

b. present, typus "falconiformis"—comprising a distinct bilobation of trochlea os metatarsi I, and subsymmetrical, variably prominent, aliform eminentiae plantares trochleares metatarsalia II et IV;

c. present, typus "strigiformis"—comprising a deep sulcus trochlearis metatarsi I and symmetrical plantar displacements of trochleae metatarsalia II et IV, with primary modification being a prominent, aliform eminentia plantaris trochlearis metatarsi IV;

d. present, typus "psittaciformis"—comprising a medial tuberculum trochlearis metatarsi I in articulation with eminentia medialis trochlea metatarsi II, and expanded lobus lateralis and approximately 90° plantar rotation of trochlea metatarsi IV;

e. present, typus "cuculiformis"—comprising a deep fossa supratrochlearis plantaris (perforated by comparatively large, distal foramen vasculare distale), a jugum separating fossa metatarsale I from basis trochlearis metatarsale II, extreme medial displacement and hamulate shape of trochlea metatarsi II (e.g., *Centropus*), a variably plantomediad-oriented spinus trochlearis metatarsi IV, and associated with a form of zygodactyly;

f. present, typus "galbuliformis"—comprising a lateromedially expanded, bilobate trochlea metatarsi IV in which part is rotated plantad in virtual opposition to essentially typically conformed trochleae metatarsalia II et III and immediately lateral to trochlea metatarsi I, and associated with a form of zygodactyly;

g. present, typus "piciformis"—comprising a prominent, broadly lamellar, well-differentiated subtrochlea plantaris (**new term**) metatarsi IV variably separated from trochlea propria, associated with a form of zygodactyly.

Note.—*Sehnenhalteren*, detailed by G. Steinbacher (1935), less frequently involve trochleae metatarsalia I et/aut II in the absence of apomorphies of trochlea metatarsi IV (treated separately). Associated with digital reversibility (*Wendezehen*) in Coliidae, Leptosomatidae, Musophagidae, and Strigiformes. "Typus falconiformis" applicable to Falconidae and Pandionidae, but only approached by Accipitridae *sensu* rudimentary eminentiae plantares trochleares metatarsalia II et IV. Similarly, pamprodactyl Coliidae may be interpretable as precursory with respect to "cuculiformis" or "apodiformis" trochlear states, being limited to notably deep sulci trochleares metatarsalia II et IV (G. Steinbacher 1935: figs. 6–7). Typus psittaciformis associated with dorsolateral broadening of sulcus intertrochlearis III–IV as well as sulcus tendinis m. flexor perforatus digiti IV (G. Mayr 2002d: fig. 7), treated analytically by Dyke and van Tuinen (2004: appendix 1, character 80), but considered redundant here.

See: Forbes (1882e); Richardson (1942); G. Mayr (1998a–b); pedal anatomy for Psittaciformes (Virchow 1931), *Opisthocomus* (Banzhaf 1929), and Piciformes (Burt 1930); Cracraft (1971a: fig. 13), detailing Coraciiformes; Jollie (1976: figs. 123–141); S. F. Simpson and Cracraft (1981: characters 3 and 7); Cracraft (1988: series XIX, character 3); Hughes (2000: appendix 2, character 75), after Seibel (1988: character TM 21); G. Mayr and Clarke (2003: appendix A, character 109), treating spinous form of trochlea metatarsale IV in zygodactyl cuculids; Dyke and van Tuinen (2004: appendix 1, character 79).

2335. Extremitas distalis tarsometatarsi, trochleae accessoriae group III, trochleae accessoriae (*Sehnenhalteren*) metatarsalia II (secundus) et IV (quartus), sulcus intertrochlearis between trochleae accessoria et metatarsale IV, status:

a. absent, associated with anisodactyly, except other taxa with *Sehnenhalteren*;

b. present.

Note.—See: G. Mayr (2002d: fig. 7); Dyke and van Tuinen (2004: appendix 1, character 80); G. Mayr (2004d: appendix I, character 42), with whom disagreement exists regarding apomorphy of Bucconidae (*Semnornis*); G. Mayr (2005a: appendix 1, character 43).

2336. Extremitas distalis tarsometatarsi, trochleae metatarsalia II, III, et/aut IV, synostosis dorsalis intertrochlearis rendering obsolete or absent corresponding incisurae intertrochleares, status:

a. absent; **b.** present.

Note.—Coraciiformes generally characterized by close lateromedial juxtaposition of trochlea metatarsalia and obsolete incisurae intertrochleares. Apomorphic condition also apparently associated with typically wide, distal foramen vasculare distale. In Galbulidae, coincidence with essentially singly-rimmed trochlea metatarsi IV results in articulatio rimae trochlearis metatarsale III with both digiti III et IV pedis.

2337. Extremitas distalis tarsometatarsi, trochlea metatarsi II, reduction to unirimulate condition related to lateromedial compression of extremitas tarsometatarsi, status:

a. absent; **b.** present.

Note.—Note that Passeriformes have reduced trochleae tarsometatarsalia II et IV (others coded separately).

2338. Extremitas distalis tarsometatarsi, sectio corporis supratrochlearis, facies medioplantaris, facies articularis hallucis:

a. absent; **b.** present.

Note.—The facies articularis hallucis as elaborated under pamprodactyly.

See: G. Mayr (2004d: appendix I, character 44); G. Mayr (2005a: appendix 1, character 45).

2339. Extremitas distalis tarsometatarsi, trochlea metatarsi II, sulcus trochlearis (**new term**), especially facies dorsalis, status (**unordered**):

a. absent or obsolete, latter manifested by plantar segment or truncated sulcus on facies medialis trochlearis;

b. present, essentially complete rudimentum aut vestigium, exceptionally shallow and variably defined;

c. present, distinct and virtually circumcentrally positioned throughout.

Note.—New term in reference to narrow groove between rimae lateralis et medialis trochleariorum, as distinct from trochlea *in toto*. Obsolescence by oblique medial shift of sulcus evidently underlies truncate, medial condition. Absence closely associated with loss of crista trochlearis (**new term**) on facies articularis of basis phalangis proximalis digiti II.

See: Livezey (1986: appendix 1, character 74); Livezey (1989: table 1, character 74); Livezey (1996a: appendix 1, character 76); Ericson (1997: table 2, character 49); Livezey (1998b: appendix A, character 354); Dyke and Gulas (2002: appendix 1, character 47), emphasis being on plantar separation; Murray and Vickers-Rich (2004: table 9, characters 34–36), concerning reduction relative to trochlea metatarsi IV in Dromornithidae.

2340. Extremitas distalis tarsometatarsi, trochlea metatarsi II, facies plantaris, pronounced plantar displacement and partial clockwise angulation, such that sulcus trochlearis (**new term**) approaching subdiagonality with axis majoris corporis, status:

a. absent; **b.** present;

x. noncomparable (Struthionidae).

Note.—See: G. Mayr (2004d: appendix I, character 40) regarding possibly associated spina plantaris of rima medialis of trochlea metatarsale II; G. Mayr (2005a: appendix 1, character 41).

2341. Extremitas distalis tarsometatarsi, trochlea metatarsi II, distinct plantomedial angulation initially evident comparatively proximal on corpus tarsometatarsi (i.e., immediately distal to fossa articularis metatarsale I), status:

a. absent; **b.** present;

x. noncomparable (Struthionidae).

2342. Extremitas distalis tarsometatarsi, trochlea metatarsi II (secundi), facies lateralis trochlearis, foveae ligamentorum collateralium, status et forma *sensu* depth and width relative to that of associated trochlea (**ordered**):

a. present, prominent fovea;

b. present, variable, shallow to moderately distinct depressio;

c. essentially absent;

x. noncomparable by absence or modification of trochlea (*Struthio*, Psittaciformes).

Note.—Fovea alternatively referable as *umbilicus trochlearis* medialis (**new term**; cf. Livezey 1997a). Trinary character basically comprising two extreme states with an intermediate class for a diversity of other conditions.

2343. Extremitas distalis tarsometatarsi, trochlea metatarsi II (secundi), facies et rima medialis trochlearis, processus medioplantaris (**new term**), status:

a. absent or subtle;

b. present, prominent and subrectangular;

x. noncomparable (*Struthio*).

Note.—New feature restricted to columnar processus of falconiform taxa, distinct from the more widely distributed subcircular alar rima in same locus of some taxa (e.g., galliform birds; e.g., G. Mayr 2004b: appendix I, character 40).

2344. Extremitas distalis tarsometatarsi, trochlea metatarsi III, dorsoplantar position relative to (*i*) those of trochleae metatarsalia II et IV and (*ii*) that of corpus tarsometatarsi at midpoint (**ordered**):

a. comparable, subparallel;

b. moderately elevated dorsally, subequal to that of corpus;

c. prominently elevated dorsally, distinctly greater than that of corpus and trochleae metatarsalia II et IV almost in articulation plantad to trochlea metatarsale III.

Note.—See: Varricchio and Chiappe (1995: legend for fig. 2); Sereno (2000: table 4, character 9), as synapomorphy for Enantiornithes; Bledsoe (1988: appendix, character 77); Chiappe et al. (2002: fig. 4.29); Dyke and van Tuinen (2004: appendix 1, character 78), combining both relative dorsoplantar depth and sulcus trochlearis of trochlea digiti III pedis; Murray and Vickers-Rich (2004: table 9, character 40).

2345. Extremitas distalis tarsometatarsi, trochleae metatarsalia II–IV, foveae ligamentorum collateralium, exceptional depth and subcircular forma, typically enclosing pori pneumatici, and extending distolaterad to produce incisura (fovea) trochlearis metatarsale II (**new term**), status:

a. absent; **b.** present.

Note.—In *Balaeniceps*, incisura assumes extreme, lateral form of a fovea set within central circus of trochlea.

2346. Extremitas distalis tarsometatarsi, trochlea metatarsi III (tertii), facies lateralis trochlearis, foveae ligamentorum collateralium, status:
a. essentially absent;
b. present, shallow to moderate depressio;
c. present, very deep, typically with margo distalis concave and in some enclosing pori neurovascularia;
x. noncomparable (Psittaciformes).
Note.—See: Hughes (2000: appendix 2, character 72), after Seibel (1988: character TM 20); Dyke and Gulas (2002: appendix 1, character 46). Fovea synonymous with umbilicus trochlearis lateralis (**new term**), the latter preferred where scroll-like termina are not associated with ancora ligamentosa.

2347. Extremitas distalis tarsometatarsi, trochlea metatarsi IV (quarti), lateroplantar torsion producing dorsoplantar, oblique splaying of sulcus trochlearis and obsolescence of fovea ligamentorum collateralium, status:
a. absent; **b.** present.

2348. Extremitas distalis tarsometatarsi, trochlea metatarsi IV (quarti), reduction to unirimulate condition related to lateromedial compression of extremitas tarsometatarsi, status:
a. absent; **b.** present.
Note.—Note that passerines show reduction to unirimulate state in both trochleae metatarsalia II et IV (other coded separately).

2349. Extremitas distalis tarsometatarsi, os metatarsale IV (quarti), trochlea metatarsi quarti (IV), foveae ligamentorum collateralium, status et forma *sensu* depth and width relative to that of associated trochlea (**ordered**):
a. present, deep fovea;
b. present, shallow to moderate depressio;
c. essentially absent;
x. noncomparable (Psittaciformes, Cuculiformes, Coraciiformes).
Note.—See: Andors (1992: table 1, character 23), in reference to "helical" form of trochlea; Chiappe (1993: character 6); Sanz et al. (1995: appendix 3, character 6); Varricchio and Chiappe (1995: legend for fig. 2). Originally termed "medial concavity," and synonymous with umbilicus trochlearis lateralis (**new term**).

2350. Extremitas distalis tarsometatarsi, trochleae metatarsalia III (tertii) et/aut IV (quarti), depressiones supracondylares trochleares (**new term**), status (**unordered**):
a. absent;
b. present, moderately deep, trochlea metatarsale IV only;
c. present, small but distinct fovea, trochlea metatarsal III only;
d. present, moderately deep, trochleae metatarsalia III et IV.
Note.—Notable that most conspicuously developed fossa observed in a large, flightless, graviportal anserinae *Geochen rhuax* (Livezey 1996a: appendix 1, character 73).

2351. Extremitas distalis tarsometatarsi, os metatarsale secundi (II), rima medialis trochlearis, incisura laterodistalis, status:
a. absent;
b. present, effecting medial interruption of trochlea in distal perspective, typically accompanied by opposing lateral incisura trochlearis IV;
x. noncomparable (Struthionidae).
Note.—Suggestive rudimenta of such incisurae indicated in some Procellariformes. Potentially confusable with superficially incisuralike inflection associated with eminentiae plantares in trochleae of some taxa.

2352. Extremitas distalis tarsometatarsi, trochlea metatarsi (secundi) II, eminentia (medio)plantaris (**new terms**), status et forma (**unordered**):
a. obsolete or indistinctly differentiated, including taxa having obliquely formed trochlea or effect of simple torsion or intratrochlear slant;
b. present, variably and subsymmetrically developed;
c. present, conspicuously enlarged;
x. noncomparable (Struthionidae).
Note.—Apomorphies associated with trochleae accessoriae excluded here, treated elsewhere; e.g., lateral spinae plantares of trochlea metatarsi II in Cuculidae. See: Houde (1988: table 27, character 53); Livezey (1998b: appendix A, character 351); Hughes (2000: appendix 2, character 76), after Seibel (1988: character TM 25), who simultaneously treated relative curvature of distal trochlear rim in assessment of eminentiae in general; Hughes (2000: appendix 2, character 73), after Seibel (1988: character TM 24), who compared eminentiae lateroplantaris et medioplantaris.

2353. Extremitas distalis tarsometatarsi, os metatarsale tertii (III), trochlea metatarsi tertii (III), margo medialis, eminentia (medio)plantaris (**new term**), status:
a. present, prominent; **b.** absent.
Note.—See: Chiappe (1993: character 2); Russell and Dong (1994b [1993b]: troödontid character 25); Chiappe and Calvo (1994); Varricchio and Chiappe (1995); Sanz et al. (1995: appendix 3, character 2); Chiappe and Walker (2002: appendix 11.1, character 32).

2354. Extremitas distalis tarsometatarsi, trochlea metatarsi IV (quarti), eminentia (latero)plantaris (**new term**), status et forma (**ordered**):

a. absent or aspect wholly or largely the result of differential positions of rimae trochleares;

b. present and moderately developed;

c. present and conspicuously enlarged.

Note.—Apomorphies associated with trochleares accessoriae excluded here and treated elsewhere. See: Livezey (1998b: appendix A, character 356); G. Mayr (2002a: fig. 5; legend fig. 9, node 2, character 3), in which trochlea metatarsalia IV shows marked medial orientation and eminentia plantaris; G. Mayr et al. (2003: appendix 1, character 68); G. Mayr (2004d: appendix I, character 42); G. Mayr and Ericson (2004: appendix I, character 78); G. Mayr (2005a: appendix 1, character 43).

2355. Extremitas distalis tarsometatarsi, ossa metatarsalia II–IV, trochleae metatarsalia, forma *sensu* relative lateromedial breadths of individual trochlea (**unordered**):

a. trochlea metatarsi II ≤ trochlea metatarsi III ≥ trochlea metatarsi IV;

b. trochlea metatarsi II > trochlea metatarsi III ≥ trochlea metatarsi IV;

c. trochlea metatarsi II < trochlea metatarsi III ≤ trochlea metatarsi IV;

x. noncomparable (Struthionidae).

Note.—See: Strauch (1985: character 20); Livezey (1986: appendix 1, character 73); Andors (1992: table 1, character 21; table 2, character 47); Chiappe (1993: character 10); Sanz et al. (1995, 1997: character 81; appendix 3, character 10); Varricchio and Chiappe (1995: legend for fig. 2); Livezey (1997a: appendix 1, character 93; *corrigenda*, Livezey 1998a); Sereno (2000: table 4, character 9); Norell and Clarke (2001: appendix I, characters 199–200), treated similarly by J. A. Clarke (2002: appendix I, characters 198–199), J. A. Clarke and Norell (2002: appendix 2, characters 198–199), and J. A. Clarke (2004: appendix 1, characters 198–199); Sereno (2000: table 4, character 9); Chiappe (2001a: appendix 1, character 162); Chiappe (2002: appendix 20.2, character 162); Chiappe and Walker (2002: appendix 11.1, character 30); Zhou and Zhang (2002: appendix III, characters 199–200); Ji et al. (2005: supplement, part I, characters 199–200).

2356. Extremitas distalis tarsometatarsi, ossa metatarsalia secundi (II) et quartus (IV), forma *sensu* breadth relative to that of trochlea metatarsi III and definition of sulci trochleares (**unordered**):

a. breadths of trochleae metatarsalia II et IV comparable to that of trochlea metatarsi III and typically possessing, at least dorsally, sulcus trochlearis;

b. breadths of trochleae metatarsalia II et IV comparable to that of trochlea metatarsi III and possessing well-defined sulci throughout complete circus of rimae trochleares;

c. breadths of trochleae metatarsalia II (if present) et IV approximately one-half that of trochlea metatarsi III;

d. breadth of trochlea metatarsi IV conspicuously more narrow (typically approximating one-half breadth) and with sulcus obsolete or absent entirely, whereas trochlea metatarsi II essentially typical;

e. breadths of trochleae metatarsalia II et IV conspicuously more narrow (typically approximating one-half breadth) and with sulcus obsolete or absent entirely;

x. noncomparable (Struthionidae).

Note.—Where trochlea are reduced to single rimae, respective phalanges proximales engage in ancillary articulationes marginales (**new term**) with adjacent trochleae, typically (at least among Passerines) involving relatively enlarged ossa cuneata (commonly comprising dorsal and plantar pairs in the cavitates articulares metatarsophalangeales II–IV.

2357. Extremitas distalis tarsometatarsi, os metatarsale secundus (II), facies plantaris, basis trochlearis, proximally narrowing triangulo-cuneate eminentia to point opposite to foramen vasculare distale, ostium plantaris, status:

a. absent or only vague, irregular;

b. present, distinctly formed;

x. noncomparable (Struthionidae).

Lateromedial characteristics relating trochleae tarsometatarsalia

2358. Extremitas distalis tarsometatarsi, trochleae metatarsalia II–IV, "splaying" or lateromedial breadth of extremitas distalis tarsometatarsi (extremitas trochlearis) relative to that of extremitas proximalis et corpus tarsometatarsi, status et forma (**unordered**):

a. typically expansive (i.e., comparable to lateromedial spread of extremitas proximalis) and bilaterally symmetrical with respect to axis majoris tarsometatarsi;

b. strongly reduced medially (i.e., by profound displacement of trochlea metatarsi II) and thereby strongly asymmetric, with margo medialis tarsometatarsi sublinear;

c. moderately reduced laterally (i.e., by displacement of trochlea metatarsi IV) and thereby asymmetric;

d. both trochleae metatarsalia II et IV distinctly, symmetrically divergent;

x. noncomparable (Struthionidae).

Note.—Lateromedial "splaying" of trochleae is generally comparatively invariant and difficult to assess in repeatable fashion in Neornithes. Instead, states were defined on the basis of the most informative component—relative lateral displacement of trochlea metatarsi II et/aut medial displacement of trochlea metatarsi IV (similar to assessments of widths of incisurae intertrochleares), with magnitude relative to that of extremitas proximalis tarsometatarsi and symmetry by comparative (curvi)linearities of margines. In the absence of extraordinary modifications of trochlear form, spread reflected by angulae of incisurae intertrochleares.

See: Strauch (1978: character 63), reanalyzed by Björklund (1994: appendix) and Chu (1995); Cracraft (1982: series 2, character 8); Livezey (1986: appendix 1, character 73); Cracraft (1988: series XI, character 13); Andors (1992: table 1, characters 19–20); Varricchio and Chiappe (1995: legend for fig. 2); Livezey (1997a: appendix 1, character 93; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, character 355); Sereno (2000: table 4, character 9); Chiappe and Walker (2002: appendix 11.1, character 36), concerning medial inflection; G. Mayr et al. (2003: appendix 1, character 67).

2359. Extremitas distalis tarsometatarsi, trochleae metatarsalia II et IV, plantaromedial torsion (II laterad and IV mediad) relative to trochlea metatarsale III, status:

a. absent or indistinct;

b. present and pronounced;

x. noncomparable (Struthionidae).

Note.—See: Strauch (1978: character 81).

2360. Extremitas distalis tarsometatarsi, trochlea metatarsale II, prominent distomedial extent (relative to trochleae metatarsalia III–IV), defining by linear prominence a distinct, asymmetrical angulus with margo medialis tarsometatarsi (**ordered**):

a. absent; **b.** present;

c. present, extremely developed, with angulus medialis occupied by proximally articulating, elongated os metatarsale I having relatively enlarged trochlea.

Proximodistal characteristics relating trochleae tarsometatarsalia

2361. Extremitas distalis tarsometatarsi, ossa metatarsalia II–IV, trochleae metatarsalia II–IV, forma *sensu* relative distal extents (**unordered**):

a. trochlea metatarsi II < trochlea metatarsi III > trochlea metatarsi IV, *and* trochlea metatarsi II ≤ trochlea metatarsi IV or trochlea metatarsi II << trochlea metatarsi IV;

b. trochlea metatarsi II < trochlea metatarsi III > trochlea metatarsi IV, *and* trochlea metatarsi II << trochlea metatarsi IV;

c. trochlea metatarsi II < trochlea metatarsi III ≥ trochlea metatarsi IV, *and* trochlea metatarsi II > trochlea metatarsi IV;

d. trochlea metatarsi II < trochlea metatarsi III < trochlea metatarsi IV;

e. trochlea metatarsi II > trochlea metatarsi III ≥ trochlea metatarsi IV;

x. noncomparable (Struthionidae).

Note.—Use of double inequalities (<<, >>) implies difference in proximodistal position is at least length of one trochlea in magnitude. See, many of whom compared trochleae in pairwise manners: Holman (1964: character 16); Strauch (1978: character 61), reanalyzed by Björklund (1994: appendix) and Chu (1995); Cracraft (1982: series 3, character 2); Livezey (1986: appendix 1, character 68); Bledsoe (1988: appendix, character 76); Livezey (1989: table 1, character 68); Andors (1992: table 1, character 21; table 2, character 47); Chiappe (1992: character B5); Varricchio and Chiappe (1995: legend for fig. 2); Livezey (1996a: appendix 1, character 75); Ericson (1997: table 2, character 48); Livezey (1997a: appendix 1, character 94; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, character 353); Hughes (2000: appendix 2, character 74), after Seibel (1988: character TM 21), who compared distal extent of trochlea metatarsi IV [quarti] relative to incisura inter-trochlearis medialis; J. A. Clarke (2002: appendix I, characters 201–202); J. A. Clarke (2002: appendix I, characters 201–202); J. A. Clarke and Norell (2002: appendix 2, characters 201–202); Dyke and Gulas (2002: appendix 1, character 45); Maryanska et al. (2002: appendix 1, character 192); G. Mayr and Clarke (2003: appendix A, character 108), limited to relative distal extents of trochleae metatarsalia II et IV; J. A. Clarke (2004: appendix 1, characters 201–202); Dyke and van Tuinen (2004: appendix 1, characters 77 and 82), pertaining to relative lengths of trochlea digitorum II et IV pedis, respectively; G. Mayr (2004a: appendix 1, character 58), relating distal extents of trochleae metatarsalia II et IV; G. Mayr (2004b: appendix 1, character 49); G. Mayr (2004d: appendix I, character 41); G. Mayr (2005a: appendix 1, character 42).

2362. Extremitas distalis tarsometatarsi, os metatarsale II, corpus proximal to trochlea metatarsale II, status:

a. present, comparable to ossa metatarsalia III–IV;

b. absent or obsolete;

x. noncomparable (Struthionidae).

Dorsoplantar characteristics relating trochleae tarsometatarsalia

2363. Extremitas distalis tarsometatarsi, trochleae metatarsalia II–IV (distal perspective), relative dorsal elevations (**unordered**):

a. trochlea metatarsi II < trochlea metatarsi III > trochlea metatarsi IV, *and* trochlea metatarsi II ≃ trochlea metatarsi IV;

b. trochlea metatarsi II < trochlea metatarsi III ≥ trochlea metatarsi IV, *and* trochlea metatarsi II < trochlea metatarsi IV;

c. trochlea metatarsi II << trochlea metatarsi III ≥ trochlea metatarsi IV;

d. trochlea metatarsi II ≃ trochlea metatarsi III ≃ trochlea metatarsi IV;

e. trochlea metatarsi II < trochlea metatarsi III < trochlea metatarsi IV;

x. noncomparable (Struthionidae).

Note.—Reflects dorsoplantar positions of center of mass of trochlea, i.e., equivalent to assessment independent of torsion of trochlea with respect to that of corpus tarsometatarsi. Use of double (proper) inequalities (<<, >>) implies difference in dorsal position is at least depth of one trochlea in magnitude. See: Marsh (1880: pl. XVII); Jollie (1976: figs. 123–141); Andors (1992: table 1, character 22); Livezey (1998b: appendix A, character 352); J. A. Clarke (2004: fig. 17).

2364. Extremitas distalis tarsometatarsi, trochleae metatarsalia II–IV (distal perspective), forma in which trochleae (*i*) virtually coplanar dorsoventrally and (*ii*) equal in distal extent, status:

a. absent;

b. present, trochleae typically also closely juxtaposed.

Note.—Arrangement of trochleae diagnosed here is generally incompatible with *Sehnenhalteren*.

2365. Extremitas distalis tarsometatarsi, trochlea metatarsale III, dorsal elevation relative to trochleae metatarsalia II et IV such that (lateral perspective) fovea ligamentorum collaterium et rima exposed dorsal to other trochleae, status:

a. absent; **b.** present.

Note.—In part an extreme form of state "a" in previous character.

2366. Extremitas distalis tarsometatarsi, trochlea metatarsi IV (quarti), conspicuous counterclockwise torsion (distal perspective) relative to counterparts of other trochleae (including metatarsale II), status:

a. absent; **b.** present.

Note.—See: Stephan (1979: fig. 48).

2367. Extremitas distalis tarsometatarsi, trochlea metatarsi IV (quarti), rima medialis trochlearis, prominent dorsoproximal elevation relative to counterparts of other trochleae, status:

a. absent; **b.** present.

2368. Extremitas distalis tarsometatarsi, os metatarsale II (secundum), trochlea metatarsi, ventral torsion (rotation) of facies medialis trochlearis about axis proximodistalis of corpus tarsometatarsi (including distal extension through trochlea metatarsi III), status (**ordered**):

a. absent or limited to conformity with widespread, modest dorsal convexity of trochleae;

b. present, moderate, trochlea oblique with respect to corpus;

c. present, pronounced, trochlea subperpendicular with respect to corpus;

x. noncomparable (Struthionidae).

Note.—See: Strauch (1978: character 63), reanalyzed by Björklund (1994: appendix) and Chu (1995), with respect to bilateral aggregate of torsion; Chiappe (1993: character 9); Sanz et al. (1995: appendix 3, character 9), with respect to strong medial curvature of trochlea; Chu (1998: appendix 1, character 116); G. Mayr and Ericson (2004: appendix I, character 77).

2369. Extremitas distalis tarsometatarsi, os metatarsale IV (quartus), trochlea metatarsi, ventral torsion (rotation) of facies lateralis trochlearis about axis proximodistalis of corpus tarsometatarsi (including distal extension through trochlea metatarsi III), status:

a. absent or indistinct, trochlea at most subdiagonal with respect to corpus;

b. present, pronounced, trochlea subperpendicular with respect to corpus.

Note.—See: Strauch (1978: character 63), reanalyzed by Björklund (1994: appendix) and Chu (1995), with respect to bilateral aggregate of torsion; Livezey (1997a: appendix 1, character 95; *corrigenda*, Livezey 1998a), in terms of relative dorsal elevation of rimae trochleares metatarsi III.

Ossa Digitorum Pedis

Digiti completae

2370. Ossa digitorum pedis, numerus digitorum cum phalanges (**ordered**):

a. five; **b.** four;

c. three (tridactyly), hallux lacking;

d. two (didactyly), hallux et digitus secundus (with associated os metacarpalis I et trochlea digiti II) absent.

Note.—Transient retention among Neornithes of plesiomorphic pentadactyly substantiate the reductive evolutionary trend of digiti pedis in Aves (Sieglbauer 1911; Lutz 1942). In taxa lacking hallux, variation exists concerning parts of the digit (i.e., os metatarsale I et/aut phalanges) are lost. Depressio in purportedly tridactyl Aepyornithidae may be fossa metatarsi I, suggesting retention of hallux.

See: Andrews (1894: pl. XIV); Coues (1927); Cracraft (1974: 502, character 9, part); Strauch (1978: character 62), reanalyzed by Björklund (1994: appendix) and Chu (1995); B. Campbell and Lack

(1985); Bledsoe (1988: appendix, character 75); Houde (1988: table 27, character 51); Currie (1995: appendix, character 26), regarding functional didactyly in Dromaeosauridae; Ericson (1997: table 1, character 71); K. Lee et al. (1997: appendix 1, character 32); Chu (1998: appendix 1, character 117); Livezey (1998b: appendix A, character 357); J. A. Wilson and Sereno (1998: appendix, character 57), with respect to digitus IV pedis among Sauropoda; Chiappe (2002: fig. 13.25); Maryanska et al. (2002: appendix 1, character 191); Sereno et al. (2002: fig. 8.5); G. Mayr and Clarke (2003: appendix A, character 110); Dyke and van Tuinen (2004: appendix 1, character 81).

2371. Digiti II–IV pedis, forma *sensu* relative total lengths (**ordered**):

a. digitus III > digitus II > digitus IV;
b. digitus III > digitus IV > digitus II;
c. digitus IV > digitus III > digitus II.

Note.—For a substantial majority of Neornithes, this character reduces to relative lengths of digiti II *vs*. IV (excluding digitus I); for most modern taxa, exclusion of ungues does not alter rankings of digital lengths.

See: Bock (1956) in reference to Ardeidae, specifically digitus II being shorter than digitus IV in Ardeinae, with opposite inequality characteristic of Botaurinae; Bledsoe (1988: appendix, character 80), discounted by K. Lee et al. (1997: appendix 2), regarding relative lengths of phalanges proximales digitorum pedis among ratites; Holtz (1994a: appendix 1, character 32); Russell and Dong (1994b [1993b]: list B, character 17); Sues (1997: appendix 1, character 47); J. A. Wilson and Sereno (1998: appendix, character 57), with respect to size or loss among Sauropoda; Xu et al. (1999a: character 84); Holtz (2000 [1998]: appendix I, character 381); Rauhut (2003: character 221).

2372. Digiti II–IV pedis, phalanges proximales et intermediae, narrowing of middle portion of corpora relative to extremitates proximales et distales phalangiorum (“waisting” or “dumbell-shaping”), status:

a. present, variably distinct;
b. absent (exclusive of minimal basal inequality of some phalanges proximales), resulting in simple, cylindrical or “peglike” phalanges lacking diametric heterogeneity of extremitates proximales aut distales relative to corpus.

2373. Digiti II–IV pedis, phalanges non-unguales, facies laterales et mediales, pronounced (subtubercular) lateromedial expansion immediately proximal to foveate ligamentorum collaterales, status:

a. absent; **b.** present.

Note.—Evidently related to robust insertiones tendinorum of musculi flexorum pedis; large-bodied, nonexemplar relatives of *Accipiter* also show apomorphic state.

Phalanges Digitorum Pedis

Note.—Modal counts of digiti pedis exclude atypical polydactyly (e.g., R. M. Chandler 1992).

Digitus I (primus) pedis aut hallux

2374. Digitus I pedis (hallux), phalanges digiti (including phalanx ungualis), numerus modalis (**ordered**):

a. three; **b.** two; **c.** two, vestigial;
d. one; **e.** zero, absent.

Note.—See: Bledsoe (1988: appendix, character 79), regarding ratites; Andrews (1894: pl. XIV); Chiappe (2002: fig. 13.25); Sereno et al. (2002: fig. 8.5), regarding *Sinornis*; G. Mayr (2004a: appendix 1, character 59).

2375. Digitus I pedis (hallux), forma *sensu* robustness and length relative to that of other digiti pedis (**ordered**):

a. present, functional, comparable in proportion to other digiti pedis;
b. vestigial, phalanges short and feeble;
c. absent.

Note.—*Menura*, *Aphelocoma*, and *Parus* approach qualitatively elongation of hallux. See: Carlsson (1884), concerning aquatic specializations of hallux; Scharnke (1930, 1931), pertaining to loss of the hallux; Raikow (1985a: table V) regarding “size”of hallux; Livezey (1998b: appendix A, character 569); Rotthowe and Starck (1998: appendix, character 36); Sereno et al. (2002: fig. 8.5), regarding *Sinornis*; G. Mayr and Clarke (2003: appendix A, character 110); G. Mayr and Ericson (2004: appendix I, character 79).

2376. Digitus I pedis (hallux), phalanx proximalis, basis phalangis et cotyla articularis phalangis, lateromedial width relative to proximodistal length:

a. comparatively narrow;
b. comparately broad, semiovate, medial extremity expanded for insertio m. flexor hallucis brevis.

Note.—Apomorphic breadth functionally related to strength and positional flexibility of hallux during grasping (e.g., pedal capture of prey).

2377. Digitus I pedis (hallux), phalanx proximalis, length relative to that of phalanges (unguales) distales digitorum II–IV:

a. former proximalis at least as long as latter;
b. former distinctly shorter than latter;
x. noncomparable in taxa lacking hallux (see status).

Note.—Equivalent to comparison of phalangeal proportions within digitus. See: Bledsoe (1988: appendix, character 80), regarding ratites.

2378. Digitus I pedis (hallux), phalanx proximalis, length relative to phalanx (ungualis) distalis digiti I:
a. proximalis at least as long as distalis;
b. proximalis distinctly shorter than distalis;
x. noncomparable in taxa lacking hallux (see status).
Note.—Consult Hopson (2001) regarding ecofunctional implications of phalangeal proportions of diverse Theropoda.

2379. Digitus I pedis (hallux), phalanx proximalis, basis phalangis disproportionate breadth, status:
a. absent; **b.** present;
x. noncomparable in taxa lacking hallux (see status).
Note.—G. Mayr (2002a: legend fig. 9, node 5, character 5); G. Mayr et al. (2003: appendix 1, character 69); G. Mayr (2004d: appendix I, character 45); G. Mayr (2005a: appendix 1, character 46).

2380. Digitus I pedis (hallux), forma *sensu* length of phalanges proximalis et ungualis relative to digitus III pedis, phalanx proximalis:
a. greater, halluces elongate;
b. subequal;
x. noncomparable in taxa lacking hallux (see status).
Note.—See: Raikow (1982: 438–443), in which elongate, incumbent hallux (and associated robustness of mm. flexor hallucis brevis et extensor hallucis longus) were averred to support monophyly of Passeriformes; Gauthier (1986: 12, unindexed synapomorphy of Avialae); Chiappe (1995a: legend for fig. 1); Hou et al. (1996: character 27); Sereno et al. (1996); Livezey (1997a: appendix 1, character 96; *corrigenda*, Livezey 1998a); Azuma and Currie (2000: appendix 1, character 87); Holtz (2000 [1998]: appendix I, character 382); G. Mayr and Clarke (2003: appendix A, character 110); G. Mayr (2004d: appendix I, character 46); G. Mayr (2005a: appendix 1, character 47).

2381. Digitus I pedis (hallux), phalanx proximalis, corpus phalangis, facies plantaris, curvature distinctly marked relative to that of phalanges proximales digitorum II–IV, status:
a. absent or obsolete;
b. present, distinct;
x. noncomparable in taxa lacking hallux (see status).

2382. Digitus I pedis (hallux), phalanx distalis (ungualis), elongate and falchionate forma relative to other phalanges distales (unguales), status:
a. absent; **b.** present;
x. noncomparable in taxa lacking hallux (see status).
Note.—See: Raikow (1982: character 17); Vanden Berge and Storer (1995: table 7); Livezey (1997a: appendix 1, character 116; *corrigenda*, Livezey 1998a); G. Mayr and Clarke (2003: appendix A, character 110).

Digitus II (secundus) pedis

2383. Digitus II (secundus) pedis, phalanges digiti (including digitus ungualis), status et numerus modalis (**ordered**):
a. present, four; **b.** present, three;
c. absent, zero.
Note.—Loss of digitus II pedis occurs rarely in *Alcedo* and *Ceyx* of Alcedinidae. See: Cracraft (1974: 502, character 9, part); Rich (1979: table 5); Raikow (1985a: table V); Bledsoe (1988: appendix, characters 75 and 79), regarding ratites; K. Lee et al. (1997: character 32); Chiappe (2002: fig. 13.25); Sereno et al. (2002: fig. 8.5), regarding *Sinornis*.

2384. Digitus II (secundus) pedis (all phalanges), hypertrophy relative to other digiti pedis and associated hyper-extensibility, status:
a. absent; **b.** present;
x. noncomparable (Struthionidae).
Note.—See: Ostrom (1969); Holtz (1994a: appendix 1, character 39); Makovicky and Sues (1998: appendix 1, character 95); Holtz (2000 [1998]: appendix I, character 383); Xu et al. (2002a: supplement, character 168); Rauhut (2003: character 224), in which Aves were coded as variable.

2385. Digitus II (secundus) pedis, distinctly truncated total length (optimally compared in articulation) relative to lengths of digiti III et IV pedis (if present), status:
a. absent; **b.** present.

2386. Digitus II (secundus) pedis, ordination of lengths of phalanges within homologous digitus, in which phalanges within digitus (lettered proximodistally *"a,"* *"b,"* . . . , *"u"*) are sequenced in order of descending length, and virtual equalities were resolved by assignment of greater rank to more-proximal of pair:
a. $a > b$; **b.** $b > a$;
x. noncomparable (Struthionidae).
Note.—Uncertainties concerning digital association of ungues and imprecision stemming from residual integument, wear, and breakage, and nature of measurement (chord for variably curvilinear shape) prompted the exclusion of the digitus ungualis ("*u*") from states based on rankings.

See: Bledsoe (1988: appendix, character 80), regarding ratites; Russell and Dong (1994b [1993b]: troödontid character 26, part), combined with troödontid characters of abbreviated facies articulares distales phalangiorum intermedia ("II-2") et distalis ("II-3"); J. A. Wilson and Sereno (1998: appendix, character 55), pertaining to lengths of "penultimate phalanges" relative to phalanges proximales digitorum II–IV among Sauropoda; Norell et al. (2000: appendix 1, character 37); Xu et al. (2000: supplement, character 89). Consult Hopson (2001) regarding ecofunctional implications of phalangeal proportions of diverse Theropoda.

2387. Digitus II (secundus) pedis, phalanges proximalis, intermediae et ungualis, forma *sensu* length and robustness relative to corresponding elements in digiti III et IV pedis (if present):

a. phalanges of magnitudes broadly comparable to digiti III–IV;

b. phalanges (especially ungualis et proungualis) digiti II substantially enlarged relative to other digiti, with phalanx ungualis digiti II hyperdeveloped into large, supra-extensible digit possessed of an exceptionally enlarged, semicircular armament;

x. noncomparable (Struthionidae).

Note.—See: Gauthier (1986: text character 24); Holtz (1994a: appendix 1, character 32); Forster et al. (1998: supplement, character 110); Xu et al. (1999b: character 81); Xu et al. (2000: supplement, character 61); Norell et al. (2001: appendix 1, character 205); J. M. Clark et al. (2002a: appendix 2.2, character 204); Maryanska et al. (2002: appendix 1, character 193); Xu (2002: suite I, character 71; suite II, character 223); Hwang et al. (2004: supplement, character 201); Xu and Norell (2004: supplement, character 201).

2388. Digitus II (secundus) pedis, phalanx proximalis, basis phalangis, facies dorsolateralis, tuberculum extensorium (tuberculum insertii m. abductor digiti II), status:

a. absent or minute;

b. present, prominent;

x. noncomparable (Struthionidae).

Note.—In at least some taxa with apparently enlarged tuberculi, this boss may serve both as situs insertii m. abductor digiti II, but as expanded facies articularis for facies lateralis phalanx proximalis digiti I.

2389. Digitus II (secundus) pedis, phalanx proximalis, basis phalangis, cotyla articularis lateralis, lateromedially compressed, bipartite facies articulationes cotylae to accommodate trochleae metatarsalia II et III, status:

a. absent; **b.** present.

Note.—Associated with modification (notably narrowing and obsolescence of sulcus) of trochlea digiti II pedis. Both features apply to lesser degree to digitus IV pedis and articulating phalanx proximalis in some of same taxa.

2390. Digitus II (secundus) pedis, phalanx proximalis, basis phalangis, cotyla articularis lateralis, facies lateralis, distinct but variably extensive cavitas articularis interphalangealis (**new term**), status et forma (**ordered**):

a. absent;

b. present, moderately deep;

c. present, deep, extensive.

Note.—Associated with narrowing of trochlea metatarsale digiti II and lateromedial compression of trochleae et bases phalangiorum pedis related to syndactyly.

2391. Digitus II (secundus) pedis, phalanx proximalis, basis phalangis, facies medialis, tuberculum insertii m. flexor perforatus digiti II, status:

a. absent or minute;

b. present, prominent;

x. noncomparable (Struthionidae).

Note.—Evidently involves tuberculum ligamentosum with facies lateralis of phalanx proximalis digiti III pedis, a potential contributing factor to size of tuberculum. If instead involving facies plantaris, would be in reference to tuberculum flexorium.

2392. Digitus II (secundus) pedis, phalanx distalis (ungualis), forma *sensu* corpus (size) et apex phalangis (shape):

a. proportionate to other phalanges distales;

b. disproportionately elongate and acuminate relative to other phalanges distales, falchionate.

Note.—See: Strauch (1985: character 21); Livezey (1998b: appendix A, character 570).

Digitus III (tertius) pedis

2393. Digitus III (tertius) pedis, phalanges digiti (including phalanx ungualis), status et numerus modalis:

a. present, five; **b.** present, four.

Note.—Evidently invariant among Archosauromorpha (Romer 1956; Weishampel et al. 1990). See: Rich (1979: table 5); Bledsoe (1988: appendix, character 79), regarding ratites; Chiappe (2002: fig. 13.25); Sereno et al. (2002: fig. 8.5), regarding *Sinornis*.

2394. Digitus III (tertius) pedis, ordination of lengths of phalanges within homologous digitus, in which phalanges within digitus (lettered proximodistally—"*a*," "*b*," . . . , "*u*") are sequenced in order of descending length, wherein equalities were awarded to more-proximal phalanx (**unordered**):

a. $a > b > c$; **b.** $a > c > b$;

c. $b > c > a$; **d.** $c > b > a$;

e. $c > a > b$.

Note.—Uncertainties concerning digital association of ungues and imprecision stemming from residual integument, wear, and breakage, and nature of measurement (chord for variably curvilinear shape) prompted the exclusion of the digitus ungualis ("*u*") from states based on rankings.

See: Gauthier (1986: text characters 24 and 84); Bledsoe (1988: appendix, character 80), regarding ratites; Livezey (1998b: appendix A, character 358), regarding length of phalanx (secundus) intermedius relative to that of phalangis tertii (subungualis); Hopson (2001) regarding ecofunctional implications of digital proportions of Theropoda.

2395. Digitus III (tertius) pedis, phalanx proximalis, length relative to that of corpus tarsometatarsi (**ordered**):

a. former distinctly less than one-third of latter;

b. former approximately one-third of latter;

c. former distinctly greater than one-third of latter.

Note.—Score for *Archaeopteryx* based solely on Eichstätt specimen.

2396. Digitus III (secundus) pedis, phalanx proximalis, basis phalangis, facies dorsomedialis, tuberculum insertii m. extensor brevis digiti III, status:

a. absent or indistinct;

b. present, prominent.

Note.—Ligamentum evidently joined tuberculum with facies lateralis of phalanx proximalis digiti III pedis, a potential contributing factor to size of tuberculum. If instead in reference to facies plantaris, would pertain to tuberculum flexorium.

2397. Digiti III et IV, partial, principally basal synostosis between adjacent surfaces of bases of respective phalanges proximales (indicated osteologically), status:

a. absent; **b.** present.

Note.—Variable at least within Bucerotidae. See: G. Mayr (2003b: appendix I, character 16); G. Mayr (2004d: appendix I, character 48); G. Mayr (2005a: appendix 1, character 49).

Digitus IV (quartus) pedis

2398. Digitus IV (quartus) pedis, phalanges digiti (including phalanx ungualis), numerus modalis (**unordered**):

a. six; **b.** five;

c. four, evidently by synostosis phalangiorum proungualis et ungualis;

d. four, evidently by synostosis phalangiorum (prounguales) intermediae.

Note.—Synostosis underlying apparent reductions indicated by "doubling" of tuberculae flexoria on facies ventralis and subterminal terminus ventralis of sulcus neurovascularius (Struthionidae–Rheidae). Reduction of digitus IV pedis to a single phalanx is unique to a single passeriform, *Cholornis* (Bock and Miller 1959). See: Forbes (1882e); Rich (1979: table 5); Raikow (1982: character 15); Raikow (1985a: table V); Andors (1988); Bledsoe (1988: appendix, character 79), regarding ratites (both at least partly erroneous); Chiappe (2002: fig. 13.25); Sereno et al. (2002: fig. 8.5), regarding *Sinornis*. Apomorphic "loss" of one phalanx intermedius in state "c" evidently the result of ontogenetic means as yet undetermined, and may not reflect (as provisionally assumed) the loss of homologous phalanges in all affected lineages. Synostosis of phalanges digitorum pedis in some other Neornithes, in some taxa appearing as phalangeal loss—e.g., some Falconiformes (*Ichthyophaga*), Caprimulgidae, Apodidae—suggests that early union of phalangeal primordia may be involved, although simple terminus and catalysis of primordium may be the simple ontogenetic mechanism of underlying deletion (Jollie 1977a). Single passeriform *Paradoxornis paradoxa* possesses vestigial digitus IV.

2399. Digitus IV (quartus) pedis, ordination of lengths of phalanges within homologous digitus, in which phalanges within digitus (lettered proximodistally—"*a*," "*b*," . . . , "*u*") are sequenced in order of descending length, wherein equalities were resolved by assigning first position to the most-proximal element (**unordered**):

a. $a > b > c > d$; **b.** $c > d > \{a \vee b\}$;

c. $a > b > d > c$;

x. noncomparable by loss of (presumably proungual) phalanx (Dromaiidae, Dromornithidae).

Note.—Uncertainties concerning digital association of ungues, imprecision stemming from residual integument, differential wear, and breakage, and nature of measurement (chord for variably curved shape) prompted the exclusion of the digitus ungualis ("*u*") from rankings.

Phalanges digiti IV pedis for *Dromaius* and Dromornithidae, each having only four phalanges digiti IV, are ranked: "*a*, *b*, *u*, *c*." See: Gauthier (1986: text characters 24 and 84); Bledsoe (1988: appendix, character 80); Hesse (1990, 1992); Ericson (1997: table 2, character 50); Livezey (1998b: appendix A, character 359); Hopson (2001); Xu (2002: suite II, character 49); G. Mayr and Ericson (2004: appendix I, character 80).

2400. Digitus IV (quartus) pedis, phalanges II et III shorter than phalanges I et IV, such that length of either of former approximating no more than one-half of that of latter, status:

a. absent; **b.** present.

Note.—Coraciiformes, at least in part, approach state "b" in possessing short digiti II et III, but not to the degree required for compliance with apomorphy. See: G. Mayr (2004d: appendix I, character 47); G. Mayr (2005a: appendix 1, character 48).

Digitus V (quintus) pedis

Note.—A transient primordium for digitus V pedis was observed in embryonic *Apteryx* by T. J. Parker (1891), described as a truncated cartilago attached proximally to os fibulare. Similar ontogenetic indications have been observed in some neognathous birds (Pycraft 1900).

2401. Digitus V (quintus) pedis, numerus modalis (**ordered**):

a. five; **b.** four;
c. three, diminutive or vestigial;
d. two; **e.** one, vestigial;
f. zero, digitus absent.

Note.—Unless otherwise indicated, proportions typical. Lineages possessing phalanges digiti V represent a subset of those taxa that possess os metatarsale V (quintus); alternative treatment includes placing all taxa lacking os metatarsale V as noncomparable for digitus V.

See: Gauthier (1986: 14, unindexed synapomorphy of Ornithurae); Benton (1990a: 25), listed "digit V of the foot reduced to a small metatarsal with no phalanges" as a synapomorphy of Ornithischia, while he (1990a: 21) listed profound reduction of digitus V pedis as synapomorphic of Theropoda; Currie and Peng (1994 [1993]), regarding presence in troödontid *Saurornithoides*; Norell and Makovicky (1997), regarding dromaeosaurids.

Phalanges et/aut partes phalangiorum digitorum

2402. Digiti II–IV pedis, phalanges proximales, intermediae, et distales, basis phalangis, tuberculum extensorium, tuberculum insertii m. extensor digitorum longus, forma *sensu* dorsoproximal prominence relative to cotyla articularis phalangis (**unordered**):

a. obsolete;
b. weakly developed, rudimentary;
c. moderately developed;
d. well developed proximad, negligibly developed dorsad;
e. prominently developed both proximad and dorsad.

Note.—See: Bledsoe (1988: appendix, character 81).

2403. Digitus III pedis, phalanx proximalis, basis phalangis, tuberculum flexorium, distinctly bilobate form, status:

a. absent or indiscernable, tuberculum subacuminate;
b. present, tuberculum distinctly bilobate.

Note.—See: G. Mayr (2002c: fig. 4), regarding virtually cylindrical phalanges possessing medial facies articulares interphalangiales, variably unusual tuberculae flexoriae, and subconical phalanges unguales pedis in fossil procellariform.

2404. Digitus IV pedis, phalanx proximalis, basis phalangis, tuberculum flexorium, prominently symmetrical bilobation (proximal perspective), status:

a. absent or indistinct;
b. present, tuberculum typically bilobate.

2405. Digiti III–IV pedis, phalanges exclusive of phalanges unguales, hypertruncate, discoid phalanges ("platy-phalangiformy")—characterized by maximal width being at least twice the length of the phalanx and foveae ligamentorum collaterium obsolete—status et forma digitorum et phalangiorum (**unordered**):

a. absent;
b. present, digitus IV (phalanges intermediae), significant;
c. present, digitus IV (phalanges intermediae), moderate to extreme;
d. present, digitus IV (phalanges proximalis et one–two intermediae), moderate;
e. present, digitus III (phalanx proximalis, lesser degree) et digitus IV (phalanges proximalis et two intermediae), substantial;
f. present, digiti II (phalanx proximalis), III (phalanges proximalis et intermedia), et IV (phalanges proximalis et two intermediae), significant.

Note.—See: G. Mayr et al. (2003: appendix 1, character 70); G. Mayr (2004d: appendix I, character 47); G. Mayr (2005a: appendix 1, character 48).

2406. Digiti II–IV pedis, phalanges distales, basis phalangis, tuberculum flexorium, situs relative to margo proximalis of facies plantaris phalangis:

a. proximate to or virtually coincident with margo;
b. distinctly distal to margo, approaching midpoint of facies plantaris of phalanx ungualis.

2407. Digiti II–IV pedis, phalanges intermediae (non-unguales), corpus phalangis, combination of virtually planar facies dorsalis et conspicuously concave facies plantaris (latter tending to increase distad), status:

a. absent; **b.** present.

2408. Digiti II–IV pedis, phalanx proximalis, capitulum phalangis, trochlea articularis, foveae ligamentorum collateralium, forma *sensu* depth:

a. absent or only moderately distinguished;
b. present, deep.

Note.—Depth of foveae typically declines proximodistad within phalanges of most taxa. *Aptornis* is unique, with foveae sulcus-shaped, elongate proximad.

2409. Digiti II–IV pedis, phalanges proximales et intermediae, basis phalangis, cotyla articularis, forma:

a. deep, curved; **b.** shallow, flattened;
x. noncomparable (Struthionidae).

Note.—See: Bledsoe (1988: appendix, character 82).

2410. Digiti II–IV pedis, forma phalangiorum characterized by (*i*) elongate, subcylindrical corpora; (*ii*) phalanges proximales with facies articulares interphalangeales, comparatively prominent tuberculae flexoriae, and modest torsion; and (*iii*) phalanges unguales subconical and variably elongate, status:

a. absent; **b.** present.

Note.—See: G. Mayr (2002c: fig. 4), regarding virtually cylindrical phalanges possessing medial facies articulares interphalangiales, variably unusual tuberculae flexoriae, and subconical phalanges unguales pedis in a purportedly fossil procellariform, whereas the taxon (if association of elements valid) also possessed a sulcus flexorius unique among Neornithes.

2411. Digiti II–IV pedis, phalanges proximales et intermediae, basis phalangis, cotyla articularis, apparent torsion of phalanges around axis proximodistalis (majoris) such that cotyla articularis of digitus III is oriented obliquely relative to axis perpendicular (normal) to axis majoris, necessitating dextrosinistral alignment of phalanges to effect proper articulationes, status:

a. absent; **b.** present;

x. noncomparable (Struthionidae).

2412. Digiti II–IV pedis, phalanges proximales (especially) et intermediae, capitulum phalangis, trochlea articularis, facies dorsalis phalangis, fovea subtrochlearis (**new term**), status:

a. absent or indistinct;

b. present, sharply emarginate, conspicuously deep.

Note.—New feature in reference to subcircular depressio evidently in accommodation of tuberculum extensorium during extension of phalanges, i.e., to the dorsoproximal terminus of the sulcus articularis phalangis distalis.

2413. Digiti II–IV pedis, phalanges proximales et intermediae, capitulum phalangis, fovea ligamentum collateralis, status et forma (**ordered**):

a. indistinct impressiones;

b. moderately deep, distinct fovea;

c. very deep, conspicuous concavitates.

2414. Digiti II–IV pedis, phalanges proximales et intermediae, extremitates distales phalangiorum, facies plantares, foveae flexores (**new term**), foramina pneumaticae, status:

a. absent; **b.** present.

Note.—Foveae in question typically serve as respective ancorae tendinorum insertii mm. flexores perforates digitorum II–IV.

2415. Digiti II–IV pedis, phalanges unguales, "raptorial modifications" (i.e., robustness, moderate truncation, and curvature), status:

a. absent; **b.** present;

x. noncomparable (Struthionidae).

Note.—See: Gauthier (1986: 14).

2416. Digiti II–IV pedis, phalanges unguales, forma *sensu* proportional length:

a. short or of intermediate proportion;

b. elongate (approaching or exceeding length of phalanx proungualis) and relatively slender.

Note.—See: Bledsoe (1988: appendix, character 83); Hou et al. (1996: character 28); Livezey (1998b: appendix A, characters 360–361).

2417. Digiti II–IV pedis, phalanges distales (ungualis), corpora phalangiorum, facies plantaris, size and concavitas plantaris, status:

a. present, variably pronounced and incorporated into diverse forms;

b. absent, phalanges unguales variably dorsoplantar compressed and diminutive, rendered euconical by unguis integumentum, lacking distinct curvature plantaris, diameter (width) less than that of subtending phalanges prounguales;

x. noncomparable by obfuscating, general dorsoplantar compression and subplanarity (Hesperornithiformes, Gaviiformes, Podicipediformes).

Note.—Ungues, including integumentary component, diminutive and evidently only large enough to protect apices digitorum, while being small enough to not extend beyond margines telae pedis (in some cases apparently enclosed within these margines apicales). Sublaminar extreme of osseous phalanx ungualis reminiscent to limited extent of those of Podicipedidae.

2418. Digiti I–IV pedis (especially digitus I), phalanx ungualis (terminalis), basis phalangis, tuberculum flexorium, status et forma (**ordered**):

a. absent or obsolete, facies ventralis ungualis essentially continuous with facies ventralis of basis phalangis;

b. present, tuberculum of intermediate depth, depth composing up to one-half depth of phalanx proprius;

c. present, prominent, tuberculum approximately as deep (dorsoplantad) as phalanx proprius, typically accompanied by substantial, lateromedial angularities.

2419. Digiti I–IV pedis, phalanx ungualis (terminalis), basis phalangis, tuberculum flexorium, extremely prominent form in which margo plantaris tuberculae is semicircular with distal concavity, status:

a. absent; **b.** present.

Note.—Evidently tuberculum uniquely enlarged to serve both raptorial flexure of phalanges pedis, as well as to protect the apex ungualis from excessive wear during highly cursorial locomotion of *Sagittarius*.

2420. Digiti I–IV pedis, phalanx ungualis (terminalis), basis phalangis, tuberculum flexorium, relatively great proximodistal extent and ventral rugosity, status et proximodistal extent (**unordered**):
a. absent;
b. present (especially digitus I), essentially limited to proximal half;
c. present, extending virtually over entire facies.

2421. Digitus II pedis, phalanx ungualis, forma relative to phalanges unguales digitorum III et IV pedis:
a. approximately conformal;
b. markedly distinct by elongated, crescentiform ("sickle-shaped") or falchionate ("bladelike") aspect.
Note.—See: Holtz (1994a: appendix 1, character 32, part); Holtz (2000 [1998]: appendix I, characters 385–386); Norell et al. (2000: appendix 1, character 36).

2422. Digitus III pedis, phalanx ungualis, forma relative to phalanges unguales digitorum II et IV pedis:
a. approximately conformal;
b. distinctly, exceptionally elongated, straight, and hyperacuminate, phalanx ungualis exceeding in length more-proximal phalanges.
Note.—Disproportionality cited in spite of general elongation of phalanges pedis of Jacanidae.

2423. Digiti I–IV pedis, phalanges unguales, pronounced diminution in robustness and length with curvature negligible, status:
a. absent; **b.** present.
Note.—Distinct from uniquely reduced formae characterizing Podicipedidae, Gaviidae, and Phoenicopterygidae.

2424. Digiti II–IV pedis, phalanges unguales (terminales), forma (planum transversus):
a. (sub)trianguloid;
b. subovoid with axis majoris aligned dorsoventrally, combined with variably planar facies plantaris.
Note.—See: Russell and Dong (1994a [1993a]: table 2, character 59), possibly equivalent to character descriptive of curvature; Holtz (2000 [1998]: appendix I, character 384).

2425. Digiti II–IV pedis, phalanges proximales et intermediae, corpus phalangis, facies dorsalis, forma:
a. corpus subcylindrical, with subparallel extremitates proximales et distales, latter at most one-third wider than corpus at midpoint;
b. corpus subcylindrical, with distinctly divergent extremitates proximales et distales.
Note.—See: G. Mayr (2002c: fig. 4), regarding virtually cylindrical phalanges possessing medial facies articulares interphalangiales, variably unusual tuberculae flexoriae, and subconical phalanges unguales pedis in fossil procellariform.

2426. Digiti III–IV pedis, phalanx proximalis, corpus phalangis, facies plantaris (lateral perspective), curvature (relative to other ungues), status:
a. absent or modest;
b. present, pronounced.
Note.—Curvature, where present, typically accompanied by curvature of phalanx subungualis and most pronounced in digitus IV.

2427. Digiti II–IV pedis, phalanges prounguales, corpus immediately proximal to cotylae articulares, facies plantaris, angulus protrochlearis plantaris (**new term**)—sharp vertex (*contra* simple curvature) effecting a ventral angularity with articulatio interphalangealis proungularis (**emended term**)—status:
a. absent; **b.** present.
Note.—New feature most evident in lateral perspective.

2428. Digiti II–IV pedis, phalanges prounguales, cotylae articulares, rimae laterales et mediales, hyperorbiculate forma—i.e., dorsoventral dimension at least as great as conphalangeal facies articularis proximalis—status:
a. absent; **b.** present.

2429. Digiti II–IV pedis, phalax ungualis, corpus phalangis, facies dorsolateralis, sulcus neurovascularis, status:
a. present; **b.** absent.

2430. Digiti II–IV pedis, phalanges proximales et intermedia, corpus et capitulum phalangis, facies plantaris, fossa infratrochlearis plantaris (**new term**), forma:
a. comparatively shallow or moderately defined;
b. comparatively deep and subcircular.
Note.—Associated with functionally related feature of trochlea, rima plantaris, in which latter is comparatively circular and expanded. See: Novas (1997: fig. 31E), regarding *Patagonykus*.

2431. Digiti II–IV pedis, phalanx ungualis (terminalis), basis et facies dorsolateralis phalangis, sulci aut canali neurovasculariae (paries bilaterales) if present, typus:
a. sulcus;
b. canalis, foramina in facies proximalis of tuberculum flexorium;
x. noncomparable (Phoenicopterygiformes).
Note.—See: G. Mayr et al. (2003: appendix 1, character 72).

2432. Digiti II–IV pedis, phalanges unguales, corpus phalangis, facies dorsolateralis, sulcus aut canalis neurovascularis (if present), forma *sensu* modal proximodistal extent:

a. extending majority to virtually entire length of element;
b. extending (at least exposed) between a minority to one-half of element;
x. noncomparable by absence of homologous sulci (Podicipedidae, *Phoenicopterus*) or canales (Falconiformes, including Cathartidae; Strigiformes).
Note.—See: Dyke and Gulas (2002: appendix 1, character 48), in reference to galliforms.

2433. Digiti II–IV pedis, phalanx ungualis (terminalis), basis et facies dorsolateralis phalangis, sulci aut canali neurovasculariae (bilaterally paired), numerus per latus et forma (**unordered**):
a. one;
b. two, sulci throughout, rami dorsoventrally separated basally and converging distally to unite immediately proximal to apex in lateromedial perspective;
c. two, sulci except where ramus plantaris passes through arcus proximally, both rami uniting distad;
x. noncomparable (Podicipedidae, Phoenicopterygiformes).
Note.—See: G. Mayr and Clarke (2003: appendix A, character 113); Dyke and van Tuinen (2004: appendix 1, character 113), inferring that ostia are part of canalis transversus.

2434. Digiti II–IV pedis, bases phalangiorum, tuberculae extensoriae, proximal elongation such that virtually entire tuberculum extends proximad to facies articularis phalangis, status:
a. absent; **b.** present.
Note.—Most conspicuous in phalanges prounguales.

2435. Digiti II–IV pedis, phalanges unguales, dorsoventral compression of corpus and spatulate lateromedial conformation of apex, status (**unordered**):
a. absent, apices variably acuminate;
b. present, apices subcircular and blunt, dorsoventral compression of corpus intermediate;
c. present, apices broadly rounded or transversely sublinear.
Note.—Apomorphic state "c" evidently a refinement for propulsion in aquatic medium.

Juncturae Membri Pelvici

Note.—See: Shimada (1922), Ametov (1971).

2436. Junctura (articulatio) tibiofibularis, os fibulare (calcaneum), status definitivum (**ordered**):
a. present, distinguishable from tibia et fibula by persistent sutura or synchondrosis;
b. present, typically synostotic with os tibiale;
c. absent by failure of os fibulare to ossify.
Note.—See: G. B. Müller and Alberch (1990); Baumel and Witmer (1993: annotation 283).

2437. Junctura (articulatio) tibiofibularis, os fibulare (calcaneum) and definitive homologue, caudal buttressing of os fibulare by caudolateral expansion of os tibia, status definitivum:
a. absent, "buttress" not discernable;
b. present, junctura accompanied cranioproximally by expansion of "buttress."
Note.—See: J. D. Harris (1998: appendix 2, character 132), respect to "distal end of tibia backs calcaneum"; Holtz (2000 [1998]: appendix I, character 352), citing Sereno et al. (1996).

2438. Junctura (articulatio) tibiotibialis, status definitivum:
a. articulatio aut synostosis incompletus, ossa tibia et tibiale remain discernably separate;
b. synostosis, ossa tibia et tibiale united.

2439. Synostosis tibio-tibialis et synostosis fibulofibularis, i.e., combination of specific subtypus of juncturae tibiofibularis et tibiotibialis—synostosis of terminus distalis tibiae propriae with the ossa proximalia tarsi (tibiale or astragalus, and fibulare or calcaneum—to form the unified extremitas distalis tibiotarsi, status et typus (**ordered**):
a. absent;
b. incomplete, suturae distinguishable;
c. present, suturae indistinguishable.
Note.—Character emphasizes synostosis tibiotarsus (fusion of ossa tibia, tibiale [astragulus], and fibulare [calcaneum]). With respect to diagnoses, it is important to distinguish the phylogenetic and ontogenetic variation in these synostoses with histological variation—i.e., distinctness of cartilago epiphysialis or epiphysis from diaphysis ossificans and intervening metaphysis—deriving from growth in ossa longa (Romanoff 1960).

See: Ostrom (1976a); Cracraft (1986: appendix, character 22); Sanz and Bonaparte (1992: character 17, part); Sanz and Buscalioni (1992: character 6); Currie and Peng (1994 [1993]); Chiappe and Calvo (1994: appendix I, character 62); Russell and Dong (1994b [1993b]: troödontid character 22, part); Sereno and Arcucci (1994 [1993]: appendix, character 15); Chiappe (1995a: legend for fig. 1); Chiappe (1995b: character 62); Sanz et al. (1995, 1997: character 60); Chiappe (1996b: character 57); Chiappe et al. (1996: appendix 1, character 56); Forster et al. (1996); Forster et al. (1998: supplement, character 103); Chiappe et al. (1998: character 83, modified); J. D. Harris (1998: appendix 2, character 133); Ji et al. (1998: supplement, character 83); Rotthowe and Starck (1998: appendix, character 11); Xu et al. (1999b: character 76, modified); Holtz (2000 [1998]: appendix I, character 368); Xu et al. (2000: supplement, character 57, modified); Chiappe (2001a: appendix 1, character 146); Norell and Clarke (2001: appendix I, character 177), treated similarly by J. A. Clarke (2002: appendix I, character 177), J. A.

Clarke and Norell (2002: appendix 2, character 177), and J. A. Clarke (2004: appendix 1, character 177); Norell et al. (2001: appendix 1, character 196, part); Chiappe (2002: appendix 20.2, character 146); J. M. Clark et al. (2002a: appendix 2.2, character 198, part); Xu (2002: suite II, character 217, part); Zhou and Zhang (2002: appendix III, character 177, part); Hwang et al. (2004: supplement, character 195); Xu and Norell (2004: supplement, character 195); Ji et al. (2005: supplement, part I, character 177).

2440. Syndesmosis tibialo-fibularis (**new term**), i.e., synostosis *between* ossa proximalia tarsi—tibiale et fibulare, status (**ordered**):

a. absent; **b.** present, partial;

c. present, complete.

Note.—An additional center of ossification—“os pretibiale”—evidently not homologous with the intermedium of other tetrapods (considered to be lost in birds) also may be involved (L. D. Martin and Stewart 1985; McGowan 1985; Baumel and Witmer 1993: annotation 283). In basalmost Archosauria, this junctura is considered critical by some for differentiation of two major basal lineages—Ornithosuchia and Crocodylotarsi—on the basis of conformation of gomphosis beween ossa fibulare et tibiale (Sereno 1991a).

See: Cracraft (1986: appendix, character 38); Gauthier (1986: 14, unindexed synapomorphy of Ornithurae; 12), unindexed synapomorphy of Avialae; Cracraft (1988: series I, character 3; series VI, character 3); Cracraft and Mindell (1989: table 1, character 22); Currie and Peng (1994 [1993]); Russell and Dong (1994b [1993b]: troödontid character 22, part); L. D. Martin and Stewart (1985); McGowan (1985); G. B. Müller and Alberch (1990); Hou et al. (1996: character 21), in reference to “pretibial bone”; Forster et al. (1998: supplement, character 104, modified); J. D. Harris (1998: appendix 2, character 133); Makovicky and Sues (1998: appendix 1, character 92, part); Xu et al. (1999b: character 77, modified); Azuma and Currie (2000: appendix 1, character 17, part); Currie and Carpenter (2000: appendix 1, character 107); Holtz (2000 [1998]: appendix I, characters 366 and 368, part); Xu et al. (2000: supplement, character 58); Cracraft and Clarke (2001: appendix 2, character 28), with reference to os fibulare and processus ascendens, and McGowan (1984, 1985); Norell et al. (2001: appendix 1, character 196, part); J. M. Clark et al. (2002a: appendix 2.2, character 198, part); Xu (2002: suite II, character 217, part); Xu et al. (2002a: supplement, character 162); Zhou and Zhang (2002: appendix III, character 177, part); Hwang et al. (2004: supplement, character 195); Xu and Norell (2004: supplement, character 195).

2441. Junctura (syndesmosis) tibiofibularis, proximity of elements exclusive of regio syndesmosis, reflected principally by breadths of the spatium tibiofibularis proximalis (**new term**) et spatium tibiofibularis distalis (**new term**) and lateromedial breadth of the intervening crista fibularis tibiotarsalis, forma:

a. well separated;

b. closely appressed throughout.

Note.—See: Holtz (1994a); Livezey (1998b: appendix A, character 320), employing slightly different nomenclature; Holtz (2000 [1998]: appendix I, character 353).

2442. Junctura (syndesmosis) tibiofibularis distalis (i.e., junctura between spina fibulae et margo lateralis tibiotarsi—typus III, see below), typus (**ordered**):

a. articulatio, in basal members typically within fossa in margo proximalis of os fibulare;

b. syndesmosis retaining discernable limits;

c. synostosis, firm and lacking discernable limits.

Note.—Critical to assess using specimens having complete fibulae and representative juncturae following preparation; rare instances of truly free spinae encoded in relative lengths. Three juncturae tibiofibulares occur, involving: typus I (proximal)—caput fibulae; typus II (intermediate)—crista corporis fibulae; et typus III (distal)—spina fibulae. See: Holtz (2000 [1998]: appendix I, character 361).

2443. Articulatio fibulotarsalis (fibulo-calcaneus) (**new term**), status:

a. present, distal extent of fibula comparatively great;

b. absent, distal extent of fibula comparatively reduced.

Note.—See: Cracraft (1986: appendix, character 21); Cracraft (1988; series II, character 9); Chiappe and Calvo (1994: appendix I, character 66); Holtz (1994a: appendix 1, character 2); Chiappe et al. (1996: appendix 1, character 60); Novas (1996: appendix, character M23, part); Chiappe et al. (1998: character 87); Forster et al. (1998: supplement, character 102); Ji et al. (1998: supplement, character 87); Xu et al. (1999b: character 75); Chatterjee (1999: appendix II, character 80); Holtz (2000 [1998]: appendix I, character 359); Zhou and Wang (2000); Zhou et al. (2000); Chiappe (2001a: appendix 1, character 155); Chiappe (2002: appendix 20.2, character 155); Sereno et al. (2002), regarding *Sinornis*; Vickers-Rich et al. (2002), concerning *Avimimus*.

2444. Synostosis tarsometatarsalis *sensu lato*, comprising (*i*) synostoses tarsometatarsalis *sensu stricto* (between os tarsi distale et ossa metatarsalia II–IV), et (*ii*) intermetatarsalia proximales et distales (among ossa metatarsalia II–IV, extremitates proximales et distales treated separately), status et typus (**ordered**):

a. synostosis tarsometatarsalis *sensu lato* absent;

b. synostosis tarsometatarsalis present;

c. synostoses tarsometatarsalis et intermetatarsalia proximales present;

d. synostoses tarsometatarsalis et intermetatarsalia proximales et distales present.

Note.—State "a" comprises potentially ordered substates "incompletely synostotic" and "completely (imperceptibly) synostotic" (Cracraft 1986: appendix, characters 23–25). Synostosis among the ossa tarsalia distales, and that between the ossa tarsalia distales and ossa metatarsalia may be distinguishable, separate character suites; the latter (synostosis intermetatarsalis) is the major part of the complete fusion producing the element in avian adults (i.e., synostosis tarsometatarsalis). With respect to practical diagnoses, it is important to distinguish the phylogenetic and ontogenetic variation in these synostoses with gross-histological variation (i.e., distinctness of cartilago epiphysialis or epiphysis from ossified diaphysis and intervening metaphysis) deriving from typical growth in ossa longa avium (Romanoff 1960).

See: Ostrom (1976a); L. D. Martin (1983a–b); Thulborn (1984: 126–127, character 22); Cracraft (1986: appendix, characters 23–24); Cracraft (1988: series I, character 4; series II, characters 1 and 10); Houde (1988: table 27, character 49); Sanz and Bonaparte (1992: character 17, part); Sanz and Buscalioni (1992: character 8); Chiappe and Calvo (1994: appendix I, characters 67–68); Chiappe (1995a: legend for fig. 1); Chiappe (1995b: characters 67–68); Elzanowski (1995: character N6); Sanz et al. (1995, 1997: characters 65–66); Chiappe (1996b: characters 62–63); Chiappe et al. (1996: appendix 1, characters 62–63); Hou et al. (1996: characters 26–27); Norell and Makovicky (1997); Chiappe et al. (1998: character 88); Forster et al. (1998: supplement, character 105); J. D. Harris (1998: appendix 2, character 144); Ji et al. (1998: supplement, character 88); Makovicky and Sues (1998: appendix 1, character 93, part); Chatterjee (1999: appendix II, character 83); Xu et al. (1999b: character 78); Chiappe (2001a: appendix 1, character 157); Norell and Clarke (2001: appendix I, character 188), treated similarly by J. A. Clarke (2002: appendix I, character 188), J. A. Clarke and Norell (2002: appendix 2, character 188), and J. A. Clarke (2004: appendix 1, character 188); Norell et al. (2001: appendix 1, character 197); Chiappe (2002: appendix 20.2, character 157); J. M. Clark et al. (2002a: appendix 2.2, character 199); Maryanska et al. (2002: appendix 1, characters 187–188); Xu (2002: suite II, character 218); Xu et al. (2002a: supplement, character 163); Zhou and Zhang (2002: appendix III, character 188); Hwang et al. (2004: supplement, character 196); Xu and Norell (2004: supplement, character 196); Ji et al. (2005: supplement, part I, character 188).

2445. Junctura intermetatarsalis, ossa metatarsalia I (primum) et II (secundum), typus modalis definitivum:

a. articulatio, constrained by ligamenta;

b. syndesmosis aut synostosis;

x. noncomparable in taxa lacking hallux et/aut os metatarsale I.

2446. Synostosis intermetatarsalis II–IV, status et modus (**ordered**):

a. absent;

b. present, apparently incomplete, limited to segmenta proximales or ontogenetically progresses proximodistally;

c. present, definitively incomplete, *sensu* retention of sulci intermetatarsalia throughout length and rudimentary closure of foramina intermetatarsalia proximales et distales;

d. present, definitively complete, evidently progresses ontogenetically from partes intermediae of ossa metatarsalia II–IV toward both extremitates proximalis et distalis (sectio proximalis, i.e., immediately distal to hypotarsus last), although some averred this a manifestation of ontogenetic progression of synostosis distoproximad.

Note.—This character treats synostosis *among ossa metatarsalia* as distinct from synostosis *between ossa tarsalia distales et ossa metatarsalia*, extremitates proximales metatarsalium, thereby separating characters of directionality (polarity) of synostosis to ossa metatarsalia. The typical progression for Neornithes evidently is initiated in middle regions (where juncturae most developed in nonavialian Theropoda), and to continue thereafter toward both extremitates (Hamilton 1952; Baumel and Raikow 1993: annotation 173), but inference remains controversial with respect to Enantiornithes, and confounded by some Neornithes, including Dromornithiformes suggesting ontogenetic progression proximodistad. Another possible trend concerns loss of ossa tarsi proximalia et distalia, which appears to characterize some of the most basal Archosauria, including Crocodylomorpha (Buscalioni et al. 1997).

See: Gilmore (1920); Ostrom (1976a); Stephan (1979); L. D. Martin (1983a–b); Cracraft (1986: appendix, character 25); Gauthier (1986: 14, unindexed synapomorphy of Ornithurae); Kurzanov (1987); Cracraft (1988: series I, character 5; series II, characters 1 and 10); Wellnhofer (1988); Rowe (1989); Chiappe (1992: character A1); Sanz and Bonaparte (1992: character 18); Sereno and Rao (1992); Chiappe and Calvo (1994: appendix I, character 69); Holtz (1994a: appendix 1, character 7); Chiappe (1995b: character 69); Sanz et al. (1995, 1997: character 67); Chiappe et al. (1996: appendix 1, character 61); Hou et al. (1996: character 25); Forster et al. (1998: supplement, character 106); Makovicky and Sues (1998: appendix 1, character 93, part); Holtz (2000 [1998]: appendix I, character 370); Chiappe (2001a: appendix 1, character 156); Norell et al.

(2001: appendix 1, character 198); Chiappe (2002: appendix 20.2, character 156); J. M. Clark et al. (2002a: appendix 2.2, character 200); Sereno et al. (2002), regarding *Sinornis*; Maryanska et al. (2002: appendix 1, character 190); Xu (2002: suite II, character 219); Xu et al. (2002a: supplement, character 164); Zhou and Zhang (2002: appendix III, character 179); Hwang et al. (2004: supplement, character 197); Xu and Norell (2004: supplement, character 197).

2447. Synostosis intermetatarsalis, ossa metatarsalia secundi (II) et quarti (IV), forma *sensu* contribution to articulatio intertarsalis (tibiotarsotarsometatarsalis) relative to that by os metatarsale tertii (III) and positional corollaries (**ordered**):

a. "archaeotarsalian."—ossa metatarsalia II–IV approximately equal or coplanar, with displacement of os metatarsale III not evident, extremitas proximalis of os metatarsale III discernable between those of ossa metatarsalia II et IV;

b. "(pro)arctometatarsalian."—ossa metatarsalia II–IV considerably dorsal to os metatarsale III, extremitas proximalis of the latter remaining robust and uncompressed lateromedially;

c. "(eu)arctometatarsalian."—ossa metatarsalia II–IV considerably dorsal to os metatarsale III, extremitas proximalis of the latter compressed, diminished in size, and displaced plantad, proximally ossa metatarsalia II et IV in articulation dorsal to os metatarsale III but all ossa metatarsalia II–IV involved in articulatio tarsometatarsalis;

d. "hyper-arctometatarsalian."—ossa metatarsalia II–IV considerably dorsal to os metatarsale III, the latter variably compressed and displaced plantad, proximally ossa metatarsalia II et IV in articulation dorsal to os metatarsale III but all ossa metatarsalia II–IV involved in articulatio tarsometatarsalis, os metatarsale III not extending proximad to articulatio tarsometatarsalis.

Note.—See: M. C. Wilson and Currie (1985); Gauthier (1986: 14, unindexed synapomorphy of Ornithurae); Gauthier (1986: text character 51); Currie and Peng (1994 [1993]); Chiappe and Calvo (1994: appendix I, character 71); Holtz (1994a: appendix 1, characters 62 and 66); Holtz (1994b); Chiappe (1995b: character 71); Sanz et al. (1995, 1997: character 69); Chiappe (1996: character 65); Chiappe et al. (1996b: appendix 1, character 64); Sereno et al. (1996: footnote 45, characters 20–21); Sues (1997: appendix 1, character 46), with respect to "arctometatarsal configuration"; Chiappe et al. (1998: character 90); Forster et al. (1998: supplement, character 109); Ji et al. (1998: supplement, character 90); Makovicky and Sues (1998: appendix 1, character 94); Xu et al. (1999a: character 83); Xu et al. (1999b: character 80); Holtz (2000 [1998]: appendix I, characters 373–375, and 377), regarding distoplantar contact and arctometatarsalian condition, respectively); Xu et al. (2000: supplement, character 60); Chiappe (2001a: appendix 1, character 159); Holtz (2001a); Norell and Clarke (2001: appendix I, character 190), treated similarly by J. A. Clarke (2002: appendix I, character 190), J. A. Clarke and Norell (2002: appendix 2, character 190), and J. A. Clarke (2004: appendix 1, character 190); Norell et al. (2001: appendix 1, character 201); Chiappe (2002: appendix 20.2, character 159); J. M. Clark et al. (2002a: appendix 2.2, character 203); Maryanska et al. (2002: appendix 1, character 189); Xu (2002: suite I, character 69; suite II, character 222); Xu et al. (2002a: supplement, character 167); Zhou and Zhang (2002: appendix III, character 190); Hwang et al. (2004: supplement, character 200); Xu and Norell (2004: supplement, character 200); Ji et al. (2005: supplement, part I, character 190).

2448. Articulationes metatarso-phalangeales (especially those for ossa metatarsalia II et III), typus:

a. articulatio sellaris;

b. articulatio trochlearis.

Note.—Contrary to interpretations by some—e.g., Norell and Makovicky (1997), Norell and Clarke (2001: appendix I, character 198), and J. M. Clark et al. (2001: appendix 2.2, characters 201–202)—articulationes involving trochleae metatarsalia in general or os metatarsale II in particular do not form a "ginglymus," synonymous with a zona flexoria (Baumel and Witmer 1993). Instead these are articulationes synoviales—plesiomorphically sellares, apomorphically trochleares (**new term**).

See: Sanz and Buscalioni (1992: character 7); Norell and Makovicky (1997); Norell et al. (2001: appendix 1, characters 199–200), treating ossa metatarsalia II et III, respectively; J. A. Clarke (2002: appendix I, character 197); J. A. Clarke and Norell (2002: appendix 2, character 197); J. M. Clark et al. (2002a: appendix 2.2, characters 201–202), treating ossa metatarsalia II et III, respectively; Xu (2002: suite I, character 77; suite II, characters 220–221), treating ossa metatarsalia II et III, respectively; Xu et al. (2002a: supplement, characters 165–166), treating ossa metatarsalia II et III, respectively, referring to "smooth, not ginglymoid" distal ends of ossa metatarsalia; Zhou and Zhang (2002: appendix III, character 198); J. A. Clarke (2004: appendix 1, character 197); Hwang et al. (2004: characters 198–199); Xu and Norell (2004: supplement, characters 198–199); Ji et al. (2005: supplement, part I, character 198).

2449. Juncturae interphalangeales longitudinis digiti II–III pedis, status et typus definitivum (**unordered**):

a. absent, articulationes interphalangeales present throughout pedis;

b. present, synostoses interphalangeales proximalis et intermedia digiti II pedis;

c. present, prosynostosis phalangiorum proximales et intermedia digitorum III–IV apparent by extreme truncation and reduced mobility of articulationes (Hemiprocnidae, Apodidae), in some confamilials perhaps leading to apparent loss of one or more phalanges.

Note.—See: Forbes (1882e); Zehltner (1890), who inferred phalanges involved in synostoses within digiti III et IV in *Cypselus melba* by embryological study; Jollie (1977a: fig. 181), pertaining to Falconiformes; Holdaway (1991: appendix 5.1, character 271); S. L. Olson (1982), who confirmed character only in some kites (*Milvus*), sea eagles (*Haliastur*, *Halieaetus*, *Ichthyophaga*), and variably in *Busarellus*. Condition functionally related to forma pachyphalangealis of many phalanges proximales et intermediae digitorum.

2450. Juncturae (synostosis) interphalangeales digiti IV, status:

a. absent;

b. present, evidently by union of phalanges proungualis et ungualis (*Struthio*, *Rhea*, *Dromaius*) or two phalanges intermediae.

Note.—See related character for numerus modalis phalangiorum digiti IV.

2451. Juncturae (articulationes) interphalangeales digitorum pedis (**new term**), status:

a. absent or minimal, incidental;

b. present, elaborated by tuberculae, between bases of phalanges proximales digiti III and that (those) of one or both of digitus II et (especially) digitus IV.

Note.—Articulatio indicated structurally by distinct tuberculae on facies medialis et/aut lateralis of basis digiti III.

Myologia

TERMINI MUSCULORUM

Throughout descriptions of myological characters, we considered the typical musculus skeleti to comprise: (*i*) origo(iones), comprising one or more capita; (*ii*) corpus ("belly" or venter), the sectio muscularis comprising *contractile* fibers and comprising one or more partes; (*iii*) insertio(nes); and (*iv*) typically one or more tendines (including aponeuroses) in one or more origiones et/aut insertiones. Less common components include raphes, vaginae tendinorum, vinculae tendinium, et manicae flexoriae (Vanden Berge and Zweers 1993).

MYOLOGICAL CHARACTERS

Musculi Nonstriati Dermatis

Note.—"Smooth" muscles comprise two principal types in birds: (*i*) musculi (subcutanei) pennarum et (*ii*) musculi apterylae (Berger 1960a, 1966; Vanden Berge 1970, 1975; A. M. Lucas and Stettenheim 1972). A member of the first group is m. expansor secundariorum, a musculus antebrachium having corpus positioned caudal to cubitus and possessed of variable tendines origiorum et insertiorum (Berger 1956c; Vanden Berge 1970). This musculus is treated under musculi alae. Other examples of musculi nonstriati avium include m. orbicularis palpebrarum (Vanden Berge and Zweers 1993) and m. adductor retricium (Baumel 1988). The former example acts upon the bulbus oculus in concert with a subset of musculi (striati) capitis, mm. bulbi oculii (Bubien-Waluszewska 1981; L. D. Martin 1985; Elzanowski 1987).

Musculi Mandibulae

Note.—Nomenclature of muscles follows Vanden Berge and Zweers (1993); terminology of subdivisions of muscles is new or follows sources noted under character descriptions. For comparisons with Reptilia, see: Edgeworth (1907); Adams (1919); Lakjer (1926); and Dzerzhinsky and Yudin (1982). For treatment of multiple orders see: D. Starck (1940); Hofer (1950); Barnikol (1952, 1953); D. Starck and Barnikol (1954); Ziswiler (1965, 1967); Schumacher (1973); Van Drongelen and Dullemeijer (1982); Zusi (1985); Cracraft (1988: series XV, character 11). See Lebedinsky (1913, 1919, 1921, 1929) for discussion of ligaments. Other publications of interest are: Dzerzhinsky (1983) and Elzanowski (1987) on **Tinamiformes**; Dzerzhinsky (1999) on **ratites**; Burggraaf (1954), Burggraaf and Fuchs (1954, 1955), A. Fuchs (1954a–b, 1955), Fujioka (1963), Sandoval (1964), Dzerzhinsky and Belokurova (1972), Dzerzhinsky (1974, 1980), and Weber (1996) on **Galliformes**; Davids (1952), Goodman and Fisher (1962), Zweers (1974), Dzerzhinsky (1982), and Zusi and Livezey (2000) on **Anseriformes**; Bams (1956), Zusi and Storer (1969), Korzun (1980), and Fjeldså (1981, 1982) on **Podicipediformes**; Korzun and Dzerzhinsky (1975) on **Gaviiformes**; Dzerzhinsky and Korzun (1977) on **Sphenisciformes**; Dzerzhinsky and Yudin (1979) and Sokolov (1990) on **Procellariiformes**; Balthasar (1935), Böker (1939), Dullemeijer (1951a–c, 1952), and Owre (1967) on **Pelecaniformes**; Bas (1954, 1955b, 1957) on **Ciconiiformes** (including *Balaeniceps*); Fisher and Goodman (1955), Karkhu and Dzerzhinsky (1985), and Marceliano et al. (1997) on **Gruiformes**; Marinelli (1928), Kozlova (1961), Yudin (1961, 1965), Zusi (1962), Burton (1974a), and Dzerzhinsky and Potapova (1974) on **Charadriiformes**; Fiedler (1951) and Hull (1991) on **Falconiformes**; Barnikol (1953) on **Cuculiformes** and *Opisthocomus*; Möller (1932), Homberger (1986), and Zusi (1993) on **Psittaciformes**; Rooth (1953), Merz (1963), Burton (1974b), Bhattacharyya (1982, 1985, 1987, 1989), and Van Gennip (1986) on **Columbiformes**; Bühler (1970) on **Caprimulgiformes**; Möller (1930), Rawal (1971), Morioka (1974), and Zusi and Bentz (1984) on **Apodiformes**; Burton (1974b) on **Coliiformes**; D. Starck (1940), Rawal (1970), Rawal and Bhatt (1974), Burton (1984: 370–371), Korzun (1988), and Flausino et al. (1999) on **Coraciiformes**; Burton (1984), Höfling and Gasc (1984), and Donatelli (1996b) on **Piciformes**; Fiedler (1951), Beecher (1953), Bock (1963b), Malhotra (1972), L. P. Richards and Bock (1973), Bhattacharyya (1982), Bock (1985b), and Dzerzhinsky and Mottozh (1989) on **Passeriformes**.

M. Adductor Mandibulae

Note.—See: Burton (1984: 370–371); Cracraft (1988: series XV, character 11); Prum (1988: character 8).

2452. Mm. adductor mandibulae externus, pseudotemporalis superficialis, et pterygoideus, tendo insertii *ossificans*, status (**ordered**):

a. absent, entirely without ossification;

b. present, ossification limited to m. pseudotemporalis superficialis;

c. present, ossification including both mm. adductor mandibulae externus, pseudotemporalis superficialis et pterygoideus.

Note.—Ossification of tendons typified by moderate ontogenetic variation. *Phoenicopterus* lacks tendinal ossification but is characterized by extreme development of aponeuroses in musculi mandibulae.

2453. M. adductor mandibulae externus, pars coronoidea, area origii, primary limitation to facies rostrodorsalis of processus zygomaticus, status:

a. absent; **b.** present.

Note.—"Pars coronoidea" follows Weber (1996) and Zusi and Livezey (2000), and is synonymous with "pars rostralis" of Vanden Berge and Zweers (1993). In *Apteryx*, origo includes rostral portion of fossa musculorum temporalium. See also: Hofer (1950).

2454. M. adductor mandibulae externus, pars coronoidea, origo, limitation primarily to facies caudoventralis of processus postorbitalis and adjacent fossa musculorum temporalium, status:

a. absent; **b.** present.

Note.—See: Zusi and Livezey (2000).

2455. M. adductor mandibulae externus, pars coronoidea, caput temporale, origo, situs calvarii (**ordered**):

a. rostral, restricted;

b. primarily lateral, moderately restricted;

c. lateral and dorsal or caudal, extensive;

x. noncomparable by absence of pars (palaeognathous taxa, Anseriformes).

Note.—"Caput temporale" is synonymous with "AME (adductor mandibulae externus) rostralis temporalis" of L. P. Richards and Bock (1973) and Burton (1984), and with "pars profunda rostralis" of Elzanowski (1987). Os (cartilago aut aponeurosis) nuchale serves as situs insertii m. adductor mandibulae. Origo of Podicipedidae includes raphus nuchalis et musculi cervicales. See: Lakjer (1926); Barnikol (1953); Zusi (1962); Fujioka (1963); Owre (1967); Zweers (1974); Bühler (1981); Dzerzhinsky and Yudin (1982); Zusi and Bentz (1984); van Gennip (1986); Vanden Berge and Zweers (1993: annotation 18).

2456. M. adductor mandibulae, pars externus, pars coronoidea, caput temporale, insertio, limitation primarily to facies medialis of ramus mandibulae, status:

a. absent; **b.** present.

Note.—See: Zusi and Livezey (2000).

2457. M. adductor mandibulae externus, pars coronoidea, caput mediale, origo, limitation to paries caudolateralis orbitae, status et situs (**ordered**):

a. absent; **b.** present, small;

c. present, large.

Note.—"Caput mediale" synonymous with "AME rostralis medialis" of L. P. Richards and Bock (1973) and Burton (1984). See: Zusi and Livezey (2000: 182), for relation to "postorbital lobe" of Burton (1984).

2458. M. adductor mandibulae externus, pars coronoidea, caput mediale, origo, situs primarily limited to paries caudalis orbitae between processes postocularis et postorbitalis, status:

a. absent; **b.** present.

2459. M. adductor mandibulae externus, pars coronoidea, caput mediale, origo, corpus postorbitalis (**new term**), status et forma (**ordered**):

a. absent; **b.** present, unipennate;

c. present, multipennate.

Note.—See: Burton (1984) under "postorbital lobe" of adductor mandibulae externus; Zusi and Livezey (2000).

2460. M. adductor mandibulae externus, pars superficialis, status et situs origii (**ordered**):

a. absent or rudimentary;

b. present, primarily processus postorbitalis;

c. present, processus zygomatica et/aut aponeurosis zygomatica.

Note.—"Pars superficialis" follows Elzanowski (1987), and is synonymous with "AME rostralis lateralis" of L. P. Richards and Bock (1973) and Burton (1984).

2461. M. adductor mandibulae externus, pars zygomatica, status et forma insertii:
a. absent or restricted;
b. present, extensive.

Note.—"Pars zygomatica" follows Weber (1996) and Zusi and Livezey (2000), and is synonymous with "AME pars media" of Elzanowski (1987) and "AME ventralis" of L. P. Richards and Bock (1973) and Burton (1984).

2462. M. adductor mandibulae externus, caput zygomaticus, origo, inclusion of arcus suborbitalis et arcus jugalis, status:
a. absent; **b.** present.

Note.—See: Hofer (1950); Zusi (1993).

2463. M. adductor mandibulae externus, pars articularis, caput externa, status:
a. absent or rudimentary; **b.** present.

Note.—"Pars articularis" follows Weber (1996) and Zusi and Livezey (2000). "Pars articularis" is synonymous with: "AME pars profunda" of Vanden Berge and Zweers (1993), "pars profunda caudalis" of Elzanowski (1987), and "AME caudalis" of Burton (1984). "Caput externa" is synonymous with "AME caudalis b" of L. P. Richards and Bock (1973).

2464. M. adductor mandibulae externus, pars articularis, caput externa, origo, situs calvarii (**ordered**):
a. extends rostrad on aponeurosis zygomatica to processus postorbitalis and adjacent calvaria;
b. restricted to region of processus zygomatica and proximal portion of aponeuorosis zygomatica;
c. extends caudal to processus zygomatica ventral to fossa musculorum temporalium;
x. noncomparable by absence of caput externus (palaeognathous taxa, Procellariiformes, Apodiformes).

2465. M. adductor mandibulae externus, pars articularis, caput externa, partes origii ossis aut raphus nuchalus, status:
a. absent or vestigial; **b.** present.

2466. M. adductor mandibulae externus, pars articularis, caput interna, status et forma (**ordered**):
a. absent or vestigial;
b. present, moderately to poorly developed;
c. present, well developed.

Note.—"Caput interna" is synonymous with "AME caudalis a" of L. P. Richards and Bock (1973).

2467. M. adductor mandibulae ossis quadrati, status:
a. absent; **b.** present.

Note.—This muscle synonymous with: "adductor mandibulae caudalis" of Weber (1993); "adductor mandibulae posterior" of Lakjer (1926), Hofer (1950), D. Starck and Barnikol (1954), L. P. Richards and Bock (1973), and Elzanowski (1987); and "adductor posterior" of Burton (1984).

2468. M. adductor mandibulae ossis quadrati, insertio, situs including facies lateralis mandibulae, status:
a. absent; **b.** present.

M. Pseudotemporalis

Note.—See: Prum (1988: character 8).

2469. M. pseudotemporalis superficialis, pars lateralis, caput temporale, origo, status:
a. present, typically including variable area fossae musculorum temporalium;
b. absent.

Note.—"M. pseudotemporalis superficialis" is synonymous with "m. pseudotemporalis" of Hofer (1950) and Elzanowski (1987). "Pars lateralis" is synonymous with "dorsal orbital portion," and "caput temporale" is synonymous with "temporal portion," both of Elzanowski (1987). A third state for this character—present, occupying all or at least half of fossa temporalis musculorum—was omitted here inadvertently. As described by Hofer (1950) and Elzanowski (1987), this state would apply only to ratites and Tinamiformes. The other taxa coded here under state "a" would then be described as: present, but limited to less than half of fossa temporalis musculorum (rostral portion). This potential state is pertinent to the conclusions of Rich et al. (1995), who interpreted the superficial jaw muscles of a rehydrated, mummified moa, *Megalapteryx didinus*, as representing m. adductor mandibulae externus, pars coronoidea (their "rostralis") and m. adductor mandibulae externus, pars articularis, caput externa (their "caudalis"). Given the relationship of these muscles to processus zygomaticus, they more likely represent m. pseudotemporalis superficialis, pars lateralis, caput temporale, and m. adductor mandibulae externus, pars coronoidea, caput temporale, respectively. The latter interpretation is consistent with a pattern found only in ratites (see: Hofer 1950; Weber 1996); the interpretation of Rich et al. (1995) is consistent with a pattern found only in some neognathous birds (Zusi and Livezey 2000). See also characters 2453 and 2463.

2470. M. pseudotemporalis superficialis, pars lateralis, caput orbitale (**new term**), origo, situs (**ordered**):

a. area extends to dorsal half of paries orbitalis;
b. restricted to ventral half of paries orbitalis;
c. substantially reduced or absent.
Note.—"Pars lateralis, caput orbitale" is synonymous with "dorsal orbital" and "ventral orbital" portions of Elzanowski (1987).

2471. M. pseudotemporalis superficialis, pars lateralis, caput orbitale, corpus, forma:
a. trianguloid or ovoid;
b. elongate-rectanguloid ("strap-shaped").

2472. M. pseudotemporalis superficialis, pars lateralis, tendo insertii, relative to tendo insertii m. adductor mandibulae externus (pars coronoidea), situs (**unordered**):
a. adjacent or coincident;
b. caudoventromedial;
c. ventral.

2473. M. pseudotemporalis superficialis, pars lateralis, caput subtemporale, status:
a. absent; **b.** present.
Note.—"Caput subtemporale" synonymous with "caput absconditum" of Hofer (1950) and "ventral temporal portion" of Elzanowski (1987: 83). The narrow tendo insertii crosses and joins tendo majoris in the Phalacrocoracidae, but corresponding tendines cross but remain distinct in the Sulidae. See Hofer (1950: 469–475) for descriptions of various taxa.

2474. M. pseudotemporalis superficialis, pars lateralis, caput intramandibulare, status:
a. absent; **b.** present.
Note.—"Caput intramandibulare" is synonymous with "m. intramandibularis" of Elzanowski (1987). Musculus prone to variation, wherein "presence" includes vestigia and rare bilateral variation within individuals. See: Hofer (1950); Dullemeijer (1951a: 255); Lubosch (1967: 1036); Elzanowski (1987: 87), who considered avian trait homologous to that of Crocodylia.

2475. M. pseudotemporalis superficialis, pars lateralis, caput quadrati, status:
a. absent or rudimentary; **b.** present.
Note.—"Caput quadrati" is synonymous with "quadrate head of m. pseudotemporalis superficialis" of Barnikol (1953). See: D. Starck and Barnikol (1954) and Elzanowski (1987: 83, 85).

2476. M. pseudotemporalis superficialis, pars medialis, status et forma (**ordered**):
a. absent or minute lobus;
b. present, restricted to ventral half of paries orbitalis;
c. present, extending to dorsal half of paries orbitalis.
Note.—"Pars medialis" is synonymous with "ventral orbital portion" of Elzanowski (1987).

2477. M. pseudotemporalis superficialis, pars medialis, insertio, situs (**unordered**):
a. tendo majoris partis lateralis;
b. adjacent to insertio tendinis majoris;
c. rostral to tendo majoris;
x. noncomparable by absence of pars medialis.

2478. M. pseudotemporalis profundus, status et forma (**unordered**):
a. present, moderately to well developed;
b. present, substantially reduced; **c.** absent.
Note.—This muscle is synonymous with "m. quadratomandibularis" of Hofer (1950), Elzanowski (1987), and Weber (1996).

M. Pterygoideus

Note.—See: Zusi (1962); Morioka (1974); Zusi and Bentz (1984: 42); Prum (1988: character 10); G. Mayr (2002a: legend fig. 9, node 3, character 5).

2479. M. pterygoideus, pars lateralis, caput rostrale, forma:
a. moderate to large; **b.** diminutive.
Note.—This muscle is synonymous with: "m. pterygoideus dorsalis lateralis" and "m. pterygoideus ventralis lateralis" of L. P. Richards and Bock (1973) and Burton (1984); "m. pterygoideus pars lateralis" (in part) of Elzanowski (1987); and "m. pterygoideus ventralis lateralis" of Weber (1996).

2480. M. pterygoideus, pars lateralis, caput rostrale, bipennation, status:
a. absent or rudimentary; **b.** present.

2481. M. pterygoideus, pars lateralis, caput rostrale, situs insertii including facies lateralis rami mandibulae, status et forma (**ordered**):
a. absent; **b.** present;
c. present, in addition to tuberculum m. pterygoidei (processus dorsolateralis) quadrati.
Note.—See: Hofer (1950) and Burton (1974b), regarding insertiones processi zygomaticus of selected Psittaciformes and *Colius*.

2482. M. pterygoideus, pars lateralis, caput rostrale, situs origii including facies dorsalis ossis palatini, status:
a. present; **b.** absent.

2483. M. pterygoideus, pars lateralis, caput rostrale, origo, inclusion of processus palatus maxillaris, status:
a. excludes; **b.** includes.
Note.—See: Burton (1984: 381); Prum (1988: character 10); G. Mayr (2002a: legend fig. 9, node 3, character 5).

2484. M. pterygoideus, pars lateralis, caput caudale, status:
a. absent; **b.** present.

Note.—This muscle is synonymous with: "m. pterygoideus dorsalis medialis, anterior" and "m. pterygoideus dorsalis medialis posterior" of L. P. Richards and Bock (1973); "m. pterygoideus dorsalis medialis" of Burton (1984); "m. pterygoideus pars lateralis" (in part) of Elzanowski (1987); and "m. pterygoideus dorsalis" of Weber (1996).

2485. M. pterygoideus, pars lateralis, caput caudale, situs origii including septum interorbitalis, status:
a. absent; **b.** present.

2486. M. pterygoideus, pars lateralis, caput caudale, origo, rostral extent on arcus pterygopalatina (**ordered**):
a. extremitas distalis ossis pterygoidei;
b. junctura pterygopalatina;
c. os palatinum;
x. noncomparable by absence of caput craniale (palaeognathous taxa).

2487. M. pterygoideus, pars lateralis, capita rostrale et caudale, divisio corporis (**ordered**):
a. absent;
b. limited, narrow furrow or overlap between capita;
c. complete, hiatus between capita;
x. noncomparable (palaeognathous taxa).

2488. M. pterygoideus, pars medialis, caput rostrale, origo including tendo accessoria from os maxillare, status:
a. absent; **b.** present.
Note.—This muscle is synonymous with: "m. pterygoideus ventralis medialis" of L. P. Richards and Bock (1973), Burton (1984), and Weber (1996); and "m. pterygoideus medialis ventralis rostralis" of Elzanowski (1987).

2489. M. pterygoideus, pars medialis, caput caudale, situs insertii (**ordered**):
a. processus medialis mandibulae;
b. processus medialis mandibulae et basis cranii externa;
c. principally or entirely confined to basis cranii externa.
Note.—This muscle is probably synonymous with: "m. pterygoideus retractor" and "m. pterygoideus dorsalis medialis" (in part) of L. P. Richards and Bock (1973); "[m. pterygoideus dorsalis medialis] retractor palatine slip" of Burton (1984); "m. pterygoideus pars medialis dorsalis" and "m. pterygoideus pars medialis ventralis caudalis" of Elzanowski (1987); and "m. pterygoideus ventralis caudalis" of Weber (1996).

M. Ethmomandibularis

2490. M. ethmomandibularis, status:
a. absent; **b.** present.

Note.—See: Hofer (1950); Burton (1974); Homberger (1980, 1986); Vanden Berge and Zweers (1993: annotation 22).

M. Protractor Pterygoidei et Quadrati

Note.—See: Zusi (1962); Bock (1966); Bühler (1981); Vanden Berge and Zweers (1993: annotation 23).

2491. M. protractor pterygoidei et quadrati, corpora, status:
a. present, variably complete; **b.** absent.

2492. M. protractor pterygoidei et quadrati, origo, situs rostralis:
a. ventral or moderately rostral to foramen opticum;
b. rostrad et dorsad on septum interorbitalis.

M. Depressor Mandibulae

Note.—See: Berger (1960a, 1966); Zusi (1962, 1967, 1985); Fujioka (1963); Bock (1966); Bühler (1970); Zweers (1974); Vanden Berge and Zweers (1993: annotation 24).

2493. M. depressor mandibulae, pars superficialis, origo, extensive supraposition with respect to fossa musculorum temporalium, status:
a. absent; **b.** present.
Note.—"Pars superficialis" follows nomenclature of Elzanowski (1987) and Weber (1996).

2494. M. depressor mandibulae, pars profunda, extent of exposure (lateral perspective) rostral to pars superficialis, magnitudo:
a. little or none;
b. moderate to great.
Note.—"Pars profunda" follows Elzanowski (1987) and Weber (1996).

Musculi Apparatus Hyobranchialis (Hyolingualis)

Note.—Myological complexity of apparatus hyobranchialis is reflected in the number of musculi involved for which no characters have been defined, including: mm. intermandibularis (partes ventralis et dorsalis), hyomandibularis (partes lateralis et medialis), cricohyoideus, ceratocricoideus, basiarytaenoideus, ceratohyoideus, ceratoglossus, hyoglossus (partes rostralis et transversus), mesoglossus, supraglossus, genioglossus, cricohyoideus (partes dorsalis et ventralis), hyovalvularis, et tracheovalvularis. See: L. P. Richards and Bock (1973); Bhattacharyya (1982); Zweers (1982); Homberger (1986); Homberger and Meyers (1989); W. Müller and Weber (1998); Tomlinson (2000).

2495. M. branchiomandibularis, pars caudalis, forma corporis:

a. short to moderately truncate, linear or moderately recurved, corpus in parallel with and inserting upon os epibranchiale;

b. elongate, strongly curved to spiral dorsad, corpus strongly recurved or spiraled dorsad, paralleling and inserting upon elongate, variably spiraled (dextrus aut sinistris) os epibranchiale of cornu branchiale, latter terminating on paries medialis orbitae or (extreme variants) cavitas nasalis.

Note.—See: Goodge (1972: fig. 9).

2496. M. hyoglossus obliquus, status et forma (**unordered**):

a. present, massive, occupying entirety of spatium subparaglossorum (**new term**) and encompassing by vagina m. hypoglossorum (**new term**) on terminus rostralis of os basihyale;

b. present, rudimentary; **c.** absent.

Note.—See: Bock and Bühler (1988).

Musculi Laryngeales, Tracheales, et Syringeales

Note.—See: Forbes (1881a); Wunderlich (1886 [1884]); Fürbringer (1888); E. Newton and Gadow (1893); Beddard (1898a); Setterwall (1901); Köditz (1925); Teresa (1933); J. Steinbacher (1937: figs. 23–25); Palmgren (1949); Ames (1971); Warner (1972a–b); Zweers et al. (1981); Zweers (1982); Zweers and Berkhoudt (1987); King (1989); McLelland (1989); Vanden Berge and Zweers (1993: annotation 37).

2497. M. cleidotrachealis, status:

a. present; **b.** absent.

Note.—Reports of this musculus (or superficially similar slips between trachea et clavicula) in single confamilials of *Crax*, Spheniscidae, and *Tokus* are treated as inadequately confirmed or provisionally nonhomologous (McLelland 1989: 98). See: Livezey (1997a: appendix 1, character 117; *corrigenda*, Livezey 1998a).

2498. Musculi interna (intrinsic), *in addition* to mm. tracheolaterales (extrinsic), numerus modalis et musculi inclusiva (**unordered**):

a. zero, musculi absent;

b. one—mm. vocales only present;

c. two—mm. obliquus ventralis et dorsalis present;

d. three—mm. tracheobronchialis dorsalis et ventralis, et syringealis dorsalis present;

e. four—mm. tracheobronchialis dorsalis et ventralis, tracheobronchialis brevis, et tracheobronchialis dorsalis present.

Note.—Separate characters descriptive of status of individual musculi tracheosyringeales considered largely redundant. See: J. Steinbacher (1937: figs. 23–25); King (1989).

Musculi Cranii et Columnae Vertebralis

Note.—Minimally explored for purposes of this analysis, elements of the cervical musculature—e.g., m. biventer cervicis, m. complexus (natal), et m. longus colli—have figured in the phylogenetic assessments of more-limited taxonomic surveys. See: Boas (1929); Fisher (1958, 1961, 1966); Zusi (1962); Bock and Hikida (1968, 1969); Zusi and Storer (1969); Brooks and Garrett (1970); V. E. Hayes and Hikida (1976); Strauch (1978: characters 24–30), reanalyzed by Björklund (1994) and Chu (1995); Gross (1985); Landolt and Zweers (1985); Zweers et al. (1987); Cracraft (1988: series XV, character 13); Vanden Berge and Zweers (1993: annotation 42); Rotthowe and Starck (1998: character 33); G. Mayr (2002b: appendix 1, character 25); G. Mayr et al. (2003: appendix 1, character 73); G. Mayr and Ericson (2004: appendix I, character 82).

2499. M. biventer cervicis, partes cranialis et/aut caudalis, status:

a. present; **b.** absent.

Note.—See: Boas (1929); Vanden Berge and Zweers (1993: annotation 41).

2500. Mm. craniocervicales, m. splenius capitis, origo vertebrae cervicalis, forma:

a. acruciform;

b. cruciform, origiones arising from sides of spinae dorsales opposite to those as insertiones.

Note.—See: Burton (1971a–b); Strauch (1978: characters 24–30), reanalyzed by Björklund (1994) and Chu (1995); Zusi and Bentz (1984: 42); Landolt and Zweers (1985); Zweers et al. (1987); Cracraft (1988: series XV, character 13); Fritsch and Schuchmann (1988); Vanden Berge and Zweers (1993: annotation 43); Rotthowe and Starck (1998: character 33); G. Mayr (2002b: appendix 1, character 25); G. Mayr et al. (2003: appendix 1, character 73); G. Mayr (2004d: appendix 1, character 25); G. Mayr (2005b: appendix A, character 48).

2501. M. longus colli dorsalis, pars caudalis, intertransversarii (vertebrae thoracicae), et ascendentes thoracici, aponeuroses ossificantes (**unordered**), status et forma:

a. absent throughout vertebrae cervicales et thoracicae;

b. present, aponeuroses ossificantes (mm. longus colli dorsalis, partes caudales) restricted to vertebrae thoracicae, arcus vertebrae, lamina dorsalis arcus, processus spinosus;

c. present, aponeuroses ossificantes (mm. intertransversarii, sectio thoracica) restricted to vertebrae thoracicae, arcus vertebrae, processus transversus vertebrae, margo lateralis;

d. present, aponeuroses ossificantes (mm. longus colli dorsalis, partes caudales; and mm. intertransversarii, sectio thoracica, respectively) including both (*i*) vertebrae thoracicae, arcus vertebrae, lamina dorsalis arcus, processus spinosus, and (*ii*) vertebrae thoracicae, arcus vertebrae, processus transversus vertebrae, margo lateralis;

e. present, aponeuroses ossificantes (mm. longus colli dorsalis, partes caudales; mm. intertransversarii, sectio thoracica; and mm. ascendentes thoracici, respectively) involving (*i*) vertebrae thoracicae, arcus vertebrae, lamina dorsalis arcus, processus spinosus; (*ii*) vertebrae thoracicae, arcus vertebrae, processus transversus vertebrae, margo lateralis; and (*iii*) arcus vertebrae, zygopophysis caudalis, margo lateralis;

x. noncomparable where presence of densely ossified notarium precluded examination of included aponeuroses ossificantes.

Note.—See: Zusi (1962); Vanden Berge and Storer (1995). Perhaps optimal to constrain using a step-matrix in which two alternative apomorphic states (states “b” and “c”), each one step from state “a” but two steps apart from each other (reflecting loss of one condition and acquisition of the other), are followed by two, ordered, one-step extensions of aponeurotic ossification (states “d” and “e,” respectively). The corresonding upper-diagonal step-matrix would be:

$$\begin{array}{cc} & \begin{array}{ccccc}\mathbf{a}&\mathbf{b}&\mathbf{c}&\mathbf{d}&\mathbf{e}\end{array} \\ \begin{array}{c}\mathbf{a}\\ \mathbf{b}\\ \mathbf{c}\\ \mathbf{d}\\ \mathrm{e}\end{array} & \left[\begin{array}{ccccc}0&1&2&2&3\\ &0&\mathbf{2}&2&2\\ &&0&1&2\\ &&&0&1\\ &&&&0\end{array}\right]\end{array}$$

Treatment as several simpler characters likely would obviate a step-matrix.

Musculi Trunci, Caudae, et Cloacae

Note.—A number of musculi pertaining to the complexus costosternalis and the abdomen are comparatively uniformly distributed among Neornithes, including: mm. scalenus, levatores costarum, intercostales externi et interni, costosternalis (partes majoris et minoris), costoseptalis, rectus abdominis, obliquus externus abdominis, obliquus internus abdominis, et transversus abdominis.

The uropygium and included pair of bulbi rectricii (integumentary and muscular components supportive of rectrices) are comparatively poorly known, and corresponding myological characters were treated only preliminarily (Baumel 1988). Included musculi are: mm. bulbi rectricium, adductor rectricium, levator caudae (partes vertebralis et rectricalis), depressor caudae (partes proximalis, distalis, et profundus), lateralis caudae, caudofemoralis (pars caudalis), et pubocaudalis (partes externus, internus, pelvicus, et caudalis).

Mm. Cloacales

2502. Apparatus copulationis—mm. retractores phalli caudalis et cranialis (organa masculina) aut mm. levator cloacae et dilator cloacae (organa feminina)—status:

a. present; **b.** absent.

Note.—Musculi organum genitalis are nonstriati. Rautenfeld et al. (1974) suggested that at least Galliformes may manifest condition intermediate to those shown above. Cloaca, an invaginatio multimeatus within the ventus cloacae, eminentia venti of the ventrum trunci—in turn within the crissum—ventus cloacae, manifests indications of phylogenetic signal in selected features. See: King (1981, 1993).

M. Cucullaris

Note.—M. cucullaris cervicis partes nuchalis et interscapularis, minimally involved with alar function and little-studied, were not assessed. The m. cucullaris complex is plesiomorphic for most Reptilia, including Archosauromorpha (Dilkes 1999).

2503. M. cucullaris capitis, pars propatagialis, status:

a. absent or rudimentary;

b. present, distinctly developed.

Note.—A mediodorsal co-component, m. cucullaris capitis interscapularis, extends variably caudad, showing diverse relationships with mm. latissimi dorsi (Vanden Berge and Zweers 1993: annotations 7–9). See: Stejneger (1887, 1888, 1889); Fürbringer (1888); Mitchell (1915); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, 1960a); Fisher and Goodman (1955); Hudson and Lanzillotti (1964); Hoff (1966); Hudson et al. (1969); Vanden Berge (1970); McGowan (1982); Livezey (1992b); Vanden Berge and Zweers (1993: annotation 9).

2504. M. cucullaris capitis, pars clavicularis (**unordered**):

a. absent;

b. present, simple, comprising only deep layer inserting along margo cranialis sterni or extremitas omalis claviculae;

c. present, complex, comprising both (variably developed) superficial layer supportive of the ingluvies (crop)—part of tunica adventia—and deeper counterpart inserting along much of scapus claviculae.

Note.—See: Fürbringer (1888); Mitchell (1915); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–d, 1960a–b); Fisher and Goodman (1955); Hudson et al. (1969); Zweers (1982); Livezey (1989, 1992b, 2003); Vanden Berge and Zweers (1993: annotation 10).

Musculi Alae

Note.—General reviews provided by: Fürbringer (1888, 1902); Howell (1937); George and Berger (1966); Raikow (1985a); Dilkes (1999).

M. Pectoralis

Note.—The most massive muscle in the entire body of neognathous birds, variation aside from simple differences in size of partes sternobrachialis et costobrachialis (Buri 1900; Fürbringer 1902; Simic and Andrejevic 1963, 1964) is primarily limited to pars propatagialis. M. pectoralis of Aves considered homologous with m. pectoralis minor of Mammalia (Howell 1937), apomorphic shift in position, relative size, and function shared by Aves and closely related Archosauria. The latter varies in size, distinctness of division from pars sternobrachialis, and relative development and site of attachment of tendo insertii (Hudson and Lanzillotti 1955). An additional source of variation attends the dermal components, notably partes subcutaneae thoracica et abdominalis (Gadow and Selenka 1891). Reports of divisions within the primary corpus—notably "deep" and "superficial" layers (Fisher 1946; Fisher and Goodman 1955; Kuroda 1961a)—have not proven to be either phylogenetically informative or reliably scored.

2505. M. pectoralis, pars propatagialis, status (**unordered**):

a. absent or vestigial;

b. present, only moderately developed, limited to corpus at articulatio acrocoracoclavicularis *sensu stricto*;

c. present, robust, comprising tendo clavicularis (**new term**) at articulatio acrocoracoclavicularis *sensu stricto*.

Note.—See: Fürbringer (1888); Beddard (1898a); Mitchell (1905); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–d, 1960a–b); Yudin (1964); Hoff (1966); Hudson et al. (1969, 1972); Vanden Berge (1970); Maurer (1977); Maurer and Raikow (1981: table 2, character 6), regarding microstructure; McGowan (1982: 202); Zusi and Bentz (1984: 44); McKitrick (1985b); Livezey (1992b); G. Mayr (2002a: legend fig. 9, node 3, character 7); G. Mayr (2003b: appendices I–II, character 21).

2506. M. pectoralis, pars propatagialis, insertio comprising distinct tendines insertiorum (typically served by variably distinct, distal capitulae) attached to tendines longus et brevis origii m. deltoideus propatagialis, status:

a. absent; **b.** present.

Note.—Apomorphic features termed m. pectoralis propatagialis capita et tendines insertiorum tendo longus et tendo brevis m. deltoideus propatagialis (partes cranialis et caudalis, respectively). See: Fürbringer (1888); George and Berger (1966).

2507. M. pectoralis, partes subcutaneae—i.e., partes thoracica et/aut abdominalis—status:

a. present, distictly developed;

b. vestigial or absent.

Note.—Nomenclatural confusion persists in the literature for partes subcutanea thoracica et abdominalis m. pectoralis; present characterization subsumes both dermal components. See: Fürbringer (1888); Beddard (1898a); Buri (1900); Mitchell (1913a–b, 1915); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1960a–b); Hudson et al. (1969); Vanden Berge (1970); Goodge (1972: 69–70); McGowan (1982); Schreiweis (1982); Strauch (1985: table 3, character H1); Livezey (1992a–b, 2003).

M. Supracoracoideus

2508. M. supracoracoideus, status aut situs:

a. absent, serving as depressor brachii, superficial to m. pectoralis;

b. present, serving as levator brachii, deep to m. pectoralis.

Note.—Howell (1937) inferred homology and internal shift of plesiomorphic m. pectoralis within "Reptilia" (presumptive homologue of m. pectoralis major of Mammalia) prior to or among basalmost Archosauria (Meers 2003: 896) to position of m. supracoracoideus characteristic of Aves, *contra* A. Newton (1893–1896: 606), the mammalian homologue of which proposed to be m. supraspinatus.

2509. Mm pectoralis (partes sternobrachialis et costobrachialis) et supracoracoideus, forma (**ordered**):

a. hypertrophied—approximating one-half the volume of m. pectoralis sternobrachialis, evidently a refinement for levation alae in hovering and enhanced aerial maneuverability or wing-propelled diving;

b. moderately developed—typically having concave facies ventralis and entirely dorsal to margo carinae;

c. distinctly reduced—dorsal to margo carinae and well cranial to margo caudalis corporis sterni, facies ventralis concave, often accompanied by increased proportion of m. pectoralis, typically indicative of limited or secondarily lost capacity for flight, notably power for elevation of wing;

d. vestigial, variably diminutive.

Note.—Excluded confamilials of some exemplary taxa, in which typical familial state is "b," show state "c." Taxa characterized by state "a" for submarine locomotion typically possess osteological corollaries (Raikow 1985a; Raikow et al. 1988). Dorsolateral expansion of m. pectoralis, pars costobrachialis presented a continuous morphocline and therefore was not coded formally.

See: Fürbringer (1888); Beddard (1898a); J. Steinbacher (1937); Lowe (1939b); Fisher (1946); Berger (1954, 1960a–b); Kuroda (1960, 1961a–b, 1967); Simic and Andrejevic (1963, 1964); Hudson and Lanzillotti (1964: 14–15); Cohn (1968); Hudson et al. (1969); Vanden Berge (1970); Maurer (1977); McGowan (1982); Schreiweis (1982); Zusi and Bentz (1984: 26, 43); Raikow (1985b: table 1, characters 1–3; table 3, character 2); Rosser and George (1986); Kaplan and Goslow (1989); Sokoloff et al. (1989); Dial et al. (1991); McKitrick (1991b: characters 4–6), regarding fascia tendinea; Dial (1992); Livezey (1992b); Vanden Berge and Zweers (1993: annotation 75).

2510. M. supracoracoideus (caput ventrale), tendo insertii, orientation relative to caput humeri et situs insertii, forma:

a. caudodorsad, insertio between those of m. deltoideus partes major et minus;

b. dorsad, insertio on margo proximalis of tuberculum dorsalis humeri.

Note.—See: Hudson and Lanzillotti (1964: 14–15).

Mm. Rhomboidea

2511. M. rhomboideus superficialis, status (**ordered**):

a. present; **b.** rudimentary or vestigial;

c. absent.

Note.—In many taxa, m. rhomboideus superficialis, cranial to margo cranialis m. latissimus dorsi cranialis, is distinctly thickened or tumidous ("pars clavicularis," defined by situs insertii, cf. "pars scapularis").

See: Fürbringer (1888); Beddard (1899); Mitchell (1915); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, d, 1960a); Hudson et al. (1969); Goodge (1972); McGowan (1982); Bannasch (1986b: figs. 39–40).

2512. M. rhomboideus superficialis, situs origii:

a. vertebrae thoracicae, spinae dorsales, uncommonly augmented caudad by aponeuroses from ilium;

b. costae vertebrales, facies laterales;

x. noncomparable (Struthionidae, Rheidae).

Note.—See: Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, 1960a–b); George and Berger (1966: 295); Hudson et al. (1969); Vanden Berge (1970).

2513. M. rhomboideus superficialis, ambitus cranialis origii:

a. comparatively elongate craniad, extending at least to acromion scapulae and (typically) including insertio claviculae;

b. comparatively truncate, extending craniad so as to permit only insertio scapulae;

x. noncomparable (ratites).

Note.—See: Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1960a–b); George and Berger (1966: 295); Hudson et al. (1969); Vanden Berge (1970); Goodge (1972: 67).

2514. Mm. rhomboideus superficialis et profundus, corpus, relative craniocaudal positions, forma (**unordered**):

a. significant overlap—"semisyntopy";

b. adjacent—"paratopy";

c. spatium aut hiatus interpartorum—"allotopy."

Note.—"Adjacent" signifies that m. rhomboideus superficialis, margo caudalis is cranial to m. rhomboideus profundus, margo cranialis, with virtually no overlap between musculi. See: George and Berger (1966: 295); Hudson et al. (1969); Vanden Berge (1970).

2515. M. rhomboideus profundus, corpus, status:

a. well developed; **b.** vestigial or absent.

Note.—Typically, mm. rhomboidea superficialis et profundus are positioned relatively craniad and caudad, respectively, together extending the length of scapus scapulae, with insertio marginis cranialis m. rhomboideus profundus coinciding with variably marked angulus dorsalis marginis scapulae. Variants are not uncommon, e.g., Hemiprocnidae are characterized by mm. rhomboidea superficialis et profundus virtually without overlap. In many taxa, relative craniocaudal shift between mm. rhomboidea results in dorsal exposure of profundus caudad et superficialis craniad, e.g., *Campephilus* (Fürbringer 1888: taf. XXV, fig. 7). See: Beddard (1898a: 81), regarding origo; Mitchell (1915); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, 1957, 1960a–b); Hudson et al. (1969); McGowan (1982); Bannasch (1986b: figs. 39–40).

2516. M. rhomboideus profundus, corpora, numerus modalis:

a. one, musculus comprising single, undivided corpus;

b. two, musculus comprising two or three discernable divisiones.

Note.—Weak partitions or afibrous interfasciculi partis profundus may occur in secondarily flightless members of diverse families (Livezey 1990, 1992a–b). See: Vanden Berge (1970); Maurer (1977); Maurer and Raikow (1981: table 2, character 5), regarding subdivision of "bellies."

Mm. Latissimi Dorsi

Note.—See: Vanden Berge and Zweers (1993: annotation 77). Dermal slips limited to pterylae (e.g., partes interscapularis et humeroscapularis) were not evaluated because of inconsistent nomenclature and published descriptions.

2517. M. latissimus dorsi, pars metapatagialis, status:
a. present, laminar, variably wide;
b. vestigial or absent.
Note.—Where coincident with m. serratus superficialis metapatagialis, m. latissimus dorsi metapatagialis of many taxa shares common insertio (axillaris) metapatagialis, in some unified caudal to insertio.
See: Fürbringer (1888); Mitchell (1895); Buri (1900); Pycraft (1907b); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, d, 1960a); Fisher and Goodman (1955); Vanden Berge (1970); Jollie (1977a–c); Livezey (1992a–b).

2518. M. latissimus dorsi, pars metapatagialis, situs origii relative to that of pars caudalis m. latissimus dorsi:
a. dorsal, coincidence complete or partial overlap;
b. dorsocranial or ventrocaudal, completely separate;
x. noncomparable in absence of m. latissimus dorsi pars metapatagialis.
Note.—See: Fürbringer (1888); Beddard (1898a); Buri (1900); Burt (1930); Fisher (1946); Berger (1954, 1960a); Hudson et al. (1969); Jollie (1977a–c); Livezey (1992b).

2519. M. latissimus dorsi, pars metapatagialis, comparatively great breadth and virtual perpendicularity of fibers relative to those of m. latissimus dorsi, pars caudalis, status:
a. absent; **b.** present;
x. noncomparable in absence of m. latissimus dorsi pars metapatagialis.
Note.—See: Fürbringer (1888); Berger (1954, 1960a); Hudson et al. (1969); Schreiweis (1982); Bannasch (1986b: figs. 39–40).

2520. M. latissimus dorsi, pars dorsocutaneous, status:
a. absent or rudimentary;
b. present and substantial.
Note.—Pars dorsocutaneous of *Atrichornis* was illustrated by Raikow (1985b: fig. 2), but this dermal slip, possibly confused with pars "dermo-iliacus" of Shufeldt (1890), is known for few taxa and simply may be diagnostically problematic (Hudson et al. 1969; Vanden Berge and Zweers 1993), in part related to involvement with m. latissimus dorsi metapatagialis et m. cucullaris capitis dorsocutaneous (Fürbringer 1902). See: Beddard (1898a: 80); Fürbringer (1902: 501–502); George and Berger (1966: 294).

2521. M. latissimus dorsi, pars cranialis, status:
a. present; **b.** absent.
Note.—See: Fürbringer (1888); Beddard (1898a, 1899), in which a single, unidentified pars was reported in *Apteryx*; Buri (1900); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1960a); Hudson et al. (1969); Goodge (1972: 67); Jollie (1977a–c); Maurer (1977); McGowan (1982); Schreiweis (1982).

2522. M. latissimus dorsi, pars cranialis, caput accessorium scapulae (**resurrected term**), status:
a. absent; **b.** present.
Note.—See: Fürbringer (1888: taf. XXV; 1902: 484), George and Berger (1966: 289), and Schreiweis (1982: 2–3) regarding "*caput accessorium scapulae*" of latissimus dorsi; Buri (1900); Burt (1930); Berger (1954, 1960a); Hudson et al. (1969); Goodge (1972: 67); Bannasch (1986b: figs. 39–40), concerning "*M. latissimus dorsi accessorischer Teil*" in Spheniscidae.

2523. M. latissimus dorsi, pars caudalis, status (**ordered**):
a. present, including corpus;
b. vestigial, comprising aponeurosis or fascia tendinosa;
c. absent entirely.
Note.—In *Cacatua*, m. latissimus dorsi pars caudalis is bounded dorso*caudad* by mm. rhomboidea. See: Fürbringer (1888); Beddard (1898a–b, 1899); Buri (1900); Mitchell (1905); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, 1957, 1960a, 1968); Hudson et al. (1969); Goodge (1972: 67); Jollie (1977a–c); Raikow (1978: tables 1–2); Bentz (1979: table 1); Maurer and Raikow (1981: table 2, character 1); McKitrick (1985b).

2524. M. latissimus dorsi, pars caudalis, origo et corpus, longitudines:
a. small to moderately long, at most two times that of pars cranialis;
b. markedly elongate, length at least three times that of pars cranialis;
x. noncomparable by absence of at least one pars (Otididae, Trochilidae, Meropidae).
Note.—See: Fürbringer (1888); Beddard (1899); Buri (1900); Mitchell (1905); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, 1957, 1960a, 1968); Hudson et al. (1969); Hudson et al. (1972: 248); Jollie (1977a–c); Raikow (1978: tables 1–2); Bentz (1979: table 1); Schreiweis (1982); McKitrick (1985b); Raikow (1985a: table 1, character 1); McKitrick (1991b: character 1).

2525. Mm. latissimus dorsi, partes cranialis et caudalis, hiatus partorum m. latissimus dorsi (**new term**), status et forma (**ordered**):

a. present, hiatus between partes significant;

b. absent, partes essentially continuous ("paratopy") with margines attached, the conjoined pair termed by some "*m. latissimus dorsi communis*";

c. absent, partes distinctly overlapping significantly proximal to insertiones;

x. noncomparable by absence of at least one pars (Otididae, Trochilidae, Meropidae).

Note.—See: Fürbringer (1888); Beddard (1898a); Buri (1900); Mitchell (1905); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a, 1960a); George and Berger (1966); Hudson et al. (1969); Goodge (1972: 67); McKitrick (1991b: character 2); Livezey (1992b).

2526. M. latissimus dorsi, pars caudalis, situs origii (**ordered**):

a. dorsocranial, from vertebrae thoracicae or (uncommonly) costae immediately ventral;

b. (*i*) (dorso)caudal, from vertebrae synsacrales et (*ii*) ventrad to margo cranialis m. iliotibialis cranialis or ala preacetabularis ilii;

c. ventrocaudal, exclusively from ala preacetabularis ilii, often entirely deep to margo cranialis m. iliotibialis cranialis;

d. ventral, largely from costae thoracicae, facies laterales;

x. noncomparable by absence of pars (Trochilidae, Meropidae).

Note.—See: Fürbringer (1888); Beddard (1898a); Buri (1900); Mitchell (1905); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–d, 1957, 1960a); George and Berger (1966); Hoff (1966); Hudson et al. (1969); Vanden Berge (1970); Goodge (1972: 67); Maurer and Raikow (1981: table 2, character 3); Schreiweis (1982); Raikow (1985a: table 1, character 1); McKitrick (1991b: character 1); Livezey (1992b).

2527. M. latissimus dorsi, pars caudalis, tendo insertii, union with rami tendinorum capita mm. scapulotriceps et deltoideus major, status:

a. absent; **b.** present;

x. noncomparable by absence of pars (Meropidae).

Note.—See: Maurer (1977: 17); Maurer and Raikow (1981: table 2, character 9).

2528. M. latissimus dorsi, partes cranialis et caudalis, tendines insertii, passage through retinaculum m. scapulotricipitis proximate to insertiones humeri, status:

a. absent; **b.** present.

Note.—Distinct from the "humeral anchor," to which tendo insertii m. latissimus dorsi is conjoined variably with that of m. scapulotriceps (McKitrick 1991b: character 3). Another variable of m. latissimus dorsi caudalis, not characterized herein, is the variably marked intrusion by insertio capitis humerale m. humerotricipitis. See: Fisher (1946); Hudson et al. (1969); Schreiweis (1982: fig. 8); Bannasch (1986a–b).

Mm. Serratia

Note.—Musculi pterylarum (subcutanei) or "dermal slips" strictly limited to pterylae (e.g., pars scapulohumeralis) were neither documented adequately in the literature nor reliably characterized by single dissections so as to permit inclusion in this analysis.

2529. M. serratus superficialis, pars cranialis, axis majoris:

a. dorsoventral; **b.** craniocaudal.

Note.—See: Berger (1954, 1956a–d, 1957, 1960a); Goodge (1972: 68); Maurer (1977).

2530. M. serratus superficialis, pars caudalis, fasciculi, numerus modalis:

a. one or two; **b.** three or four.

Note.—Numbers of fasciculi of mm. serratia closely associated with origiones costales. See: Fürbringer (1888); Beddard (1899); Buri (1900); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–d, 1957, 1960a); Hudson et al. (1969); Goodge (1972: 68); Bannasch (1986b: figs. 39–40); Livezey (1990, 1992a–b, 2003); McKitrick (1991b: 122); Vanden Berge and Zweers (1993: annotation 70).

2531. M. serratus superficialis, partes cranialis et caudalis, continuity of corpora without distinct divisio proximalis, status:

a. absent; **b.** present.

Note.—See: Berger (1954, 1956a–d, 1960a); Hoff (1966); Hudson et al. (1969); Vanden Berge (1970); Goodge (1972: 68); Maurer (1977).

2532. M. serratus superficialis, pars metapatagialis, status:

a. present; **b.** absent.

Note.—See: Fürbringer (1888); Buri (1900); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–d, 1960a); Fisher and Goodman (1955); Hudson et al. (1969); Goodge (1972: 68); S. L. Olson and Feduccia (1980a); McGowan (1982); Schreiweis (1982); Zusi and Bentz (1984); Bannasch (1986b: figs. 39–40); Livezey (1990, 1992a–b); Vanden Berge and Zweers (1993: annotation 70).

2533. M. serratus profundus, fasciculi, numerus modalis (**ordered**):

a. one or two; **b.** three or more;

x. noncomparable (Struthionidae, Rheidae, Cracidae, Hemiprocnidae, Apodidae, Trochilidae).

Note.—Numbers of fasciculi of mm. serratia are closely associated with those of underlying costae insertiorum. See: Fürbringer (1888); Beddard

(1898a, 1899); Buri (1900); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1957, 1960a); Hoff (1966); Hudson et al. (1969); Vanden Berge (1970); Goodge (1972: 68); Maurer (1977); Livezey (1990, 1992a–b, 2003).

2534. M. serratus profundus, fasciculi suprascapulares (**new term**), status:
a. absent, orientation of fasciculae typically subparallel and deep to scapus scapulae;
b. present, origiones equal to or significantly dorsal to extremitas cranialis scapulae.
Note.—Numbers of fasciculi of mm. serratia correspond with origiones costales (ancorae origii typically on processes uncinates). McKitrick (1991b: 124) noted two "mystery muscles," one of which is inferred here to comprise fasciculi craniales m. serratus profundus exposed dorsal to corpus (scapus) scapulae (lateral perspective). See: Fürbringer (1888: taf. XXV, figs. 1–3); Burt (1930); Fisher (1946); Berger (1954, 1960a); Hudson et al. (1969); Goodge (1972: 68); Maurer (1977).

Mm. Scapulohumerales

Note.—The diminutive and cryptic m. scapulohumeralis cranialis has a confusing history of nomenclature (George and Berger 1966: 300). Evidently, m. scapulohumeralis caudalis (synonymous with m. dorsalis scapulae, m. scapulohumeralis posterior) is invariably present among Neornithes, hence status *per se* was not coded here. A detailed hypothesis of homologies of the muscles of the pectoral girdle was proposed by Jenkins (1993).

2535. M. scapulohumeralis cranialis, status:
a. present, small but distinct;
b. vestigial or absent.
Note.—Synonymous with m. proscapulohumeralis (brevis). See: Fürbringer (1888); Beddard (1898a); Buri (1900); Pycraft (1900); Mitchell (1905, 1915); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, d, 1960a); George and Berger (1966: 301); Vanden Berge (1970); Jollie (1977a–c), in which two partes were found in *Sagittarius*; Maurer (1977); McGowan (1982); Schreiweis (1982); Raikow (1985a); Raikow et al. (1988: table 3).

2536. M. scapulohumeralis caudalis, ambitus distalis (**ordered**):
a. extremitas caudalis (apex) scapulae;
b. proximal (cranial) two-thirds to three-fourths of scapus scapulae;
c. proximal (cranial) one-half or less of scapus scapulae.
Note.—See: Fürbringer (1888); Mitchell (1905); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, 1960a); Vanden Berge (1970); Jollie (1977a–c); Maurer (1977); McGowan (1982).

Mm. Subcoracoscapulares

Note.—With the possible exception of some ratites (cf. Beddard 1898a), m. subscapularis comprises two capita—capita laterale (externa) et mediale (interna)—in Neornithes (George and Berger 1966: 303). M. subscapularis caput mediale (interna) evidently is invariably present in all Neornithes, and therefore is not characterized here.

2537. M. subscapularis, caput laterale (externa), status:
a. present; **b.** absent.
Note.—See: Fürbringer (1888); Beddard (1899); J. Steinbacher (1937); Fisher (1946); Berger (1956a–b, 1960a); Vanden Berge (1970); Maurer (1977); McGowan (1982: 197), who transposed capita in *Apteryx*.

2538. M. subcoracoideus, caput dorsale, status:
a. present; **b.** absent.
Note.—See: Fürbringer (1888); Buri (1900); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, 1957, 1960a); Hoff (1966); Hudson et al. (1969); Vanden Berge (1970); Goodge (1972: 69); Maurer (1977); Schreiweis (1982); Strauch (1985: table 3, character H2); Bannasch (1986b: fig. 39); Rotthowe and Starck (1998: character 37).

2539. M. subcoracoideus, caput ventrale, status:
a. present; **b.** absent.
Note.—See: Fürbringer (1888); Buri (1900); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, d, 1960a); Hoff (1966); Hudson et al. (1969); Vanden Berge (1970); Goodge (1972: 69); Maurer (1977); Schreiweis (1982); Strauch (1985: table 3, character H2); Bannasch (1986b: fig. 39); Livezey (1992b); Rotthowe and Starck (1998: character 37).

2540. M. subcoracoideus, caput ventrale, forma:
a. subspheroidal or ellipsoidal;
b. dorsoventrally elongate, craniocaudally narrow;
x. noncomparable (Apterygidae, Spheniscidae, Sagittaridae, *Steatornis*).
Note.—See: Vanden Berge (1970: table 3); Maurer (1977).

2541. M. subcoracoideus, caput ventrale, origo exclusively from membrana coracoclavicularis and significant extension to clavicula, status:
a. absent or rudimentary; **b.** present.
Note.—See: Berger (1960a).

M. Sternocoracoideus

2542. M. sternocoracoideus, status et forma (**unordered**):

a. present, including corpus;

b. present, reduced to fascia tendinosa;

c. absent.

Note.—See: Fürbringer (1888); Beddard (1898a); Buri (1900); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, 1957, 1960a); George and Berger (1966: 316); Owre (1967); Hudson et al. (1969); Vanden Berge (1970); Maurer (1977); Zusi and Bentz (1984: 44); Livezey (1992b).

Mm. Coracobrachiales

Note.—M. coracobrachialis caudalis evidently is invariably present in Neornithes, minor variation in details of relative size, tendo insertii, and situs—not amenable to robust, discrete coding—notwithstanding.

2543. M. coracobrachialis cranialis, status:

a. present; **b.** vestigial or absent.

Note.—See: Buri (1900); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, 1957, 1960a, 1968); Hudson and Lanzillotti (1955, 1964); Vanden Berge (1970); Maurer (1977); Raikow (1978: table 2); S. L. Olson and Feduccia 1980b: 20); Schreiweis (1982); Zusi and Bentz (1984: 43); Raikow et al. (1988: table 3).

2544. M. coracobrachialis cranialis, corpus, distal extent:

a. elongate, extending distad to at least one-third of corpus humeri et m. biceps brachii, in extreme cases closely approaching origo m. brachialis;

b. truncate, extending distad less than one-third of corpus humeri, typically limited to facies dorsocranialis cristae deltopectoralis.

Note.—Distal extension of corpus in Tinamiformes parenthetically termed pars distalis by Hudson et al. (1972: fig. 6). See: Buri (1900); Fürbringer (1902: 455); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, d, 1957, 1960a); George and Berger (1966: 315); Hudson et al. (1969); Vanden Berge (1970); Hudson et al. (1972: 220, 249); Maurer (1977); Zusi and Bentz (1984).

Mm. Deltoidea

Note.—M. deltoideus propatagialis currently is considered to comprise caput craniale (comprising variably distinct caput, tendo longa et sectio elasticum) et caput caudale (including variably distinct caput, tendo brevis aut tendines breves) the latter variously confounded by ligamenta aut aponeuroses limitates. Capita giving rise to these typically are moderately well developed (origiones of which may include faciae medialis et caudalis claviculae, extremitas cranialis coracoidei, et acromion scapulae), variably differentiated, and positioned relatively cranial and caudal, respectively. Variation in capita m. deltoideus propatagialis principally involves: (*i*) size or breadth of capita, (*ii*) differentiation between capita partorum craniale et caudale, and (*iii*) differentiation between subparts of caput partis caudale serving tendines longus et brevis. Differentiation of heads associated with tendines longa et brevis appears to begin distally and proceed continuously to proximal apices or origiones, and hence defied meaningful characterization.

Variation of systematic importance of the complexus tendinosus propatagii principally involves tendines comprising “tendo brevis” and variable involvement of m. biceps pars propatagialis. The propatagial complex in Laridae, Alcidae, and Rynchopidae—comprising both typical tendines and ligamenta cubiti limitates, includes variation among tendines insertiorum m. biceps brachii, geometry of tendines m. deltoideus propatagialis, number and arrangement of ligamenta limitates cubiti, extent of partes elasticae tendinorum, and geometry with insertiones of m. extensor (meta)carpi radialis, aponeuroses antebrachii, and manus (Beddard 1898a: figs. 171–175; Vanden Berge and Zweers 1993: fig. 6.11).

2545. M. deltoideus, pars propatagialis, corpus, status et magnitudo (**ordered**):

a. present, hypertrophic, typically concealing (dorsal perspective) majority or entirety of underlying m. deltoideus major;

b. present, moderately robust; **c.** absent.

Note.—Synonymous with m. tensor propatagialis. See: Fürbringer (1888); Pycraft (1900, 1907b); Mitchell (1913a–b); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, 1957, 1960a); Yudin (1957: fig. 8); George and Berger (1966: 318); Hudson et al. (1969); Vanden Berge (1970); Jollie (1977a–c); Maurer (1977); Raikow (1978: table 2); S. L. Olson and Feduccia (1980b: fig. 5); McGowan (1982); Strauch (1985: table 3, characters H3–H5).

2546. M. deltoideus, pars propatagialis, junctura capitorum cranialis et caudalis (especially tendines longa et brevis), forma:

a. absent or limited to proximal junctura capitis;

b. present, essentially throughout length, and assuming aspect of single, robust tendo passing from omalis to carpus proximate to musculi skeleton.

Note.—See: Fürbringer (1888: taf. XIX, fig. 1); Schreiweis (1982).

2547. M. deltoideus, pars propatagialis, caput craniale, tendo longa, status:

a. present; **b.** vestigial or absent.

Note.—See: Fürbringer (1888); Beddard (1898a); Buri (1900); Mitchell (1913b); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, 1957, 1960a); Yudin (1957: fig. 8); Vanden Berge (1970); Jollie (1977a–c); Maurer (1977); S. L. Olson and Feduccia (1980b: fig. 5); Maurer and Raikow (1981: table 2, character 8).

2548. M. deltoideus, pars propatagialis, capita craniale (pars longa) et caudale (pars brevis), tendo longus vestigial (including obsolescence of pars elastica and profound truncation of tendo brevis), latter drawing tendo longus and margo cranialis propatagii caudad into juxtaposition with aponeurosis antebrachii dorsale, rendering propatagium obsolete, status:

a. absent; **b.** present.

Note.—*Balaeniceps* is intermediate in this respect. See: Owre (1967: figs. 2–3) for Phalacrocoracidae and Anhingidae.

2549. M. deltoideus, pars propatagialis, caput caudale (pars brevis), corpus (sectio distalis), et tendo insertii m. extensor (meta)carpi radialis, respectively, status et forma (**ordered**):

a. corpus absent, caput caudale omni-tendinous;

b. corpus present, but caput caudale including variable but significant tendo insertii;

c. corpus present, but caput caudale inserting by truncated tendo;

d. corpus present, comprising entire caput caudale, latter inserting sine tendo.

Note.—See: S. L. Olson and Feduccia (1980b: fig. 5), in which it is proposed that m. deltoideus propatagialis of *Phoenicopterus* comprises three capita origii, pars brevis thereof subtending two tendines insertii (latter shared with *Cladorhynchus*); Zusi and Bentz (1982); Bleiweiss (2002: fig. 1).

M. Deltoideus Propatagalis, Pars (Caput) Caudalis, Tendo Brevis

Note.—Survey of available published diagrams and direct study of most families of Neornithes led to the definition of five primary geometric variants of tendines comprising the homologue of the traditional "tendo brevis," which in combination with the subtending, comparatively caudal (proximal) caput comprises **pars caudalis** m. deltoideus propatagialis. The cranial (distal) caput m. deltoideus propatagialis (**pars cranialis**) gives rise to the prominent tendo longus of the leading margin of the wing. In some taxa, a single caput subtends both tendines longus et brevis, and in many taxa variably elongate segmenta elastica occur in one or both tendines.

States of the "tendo brevis" complex were devised exclusive of variation in ligamenta limitates or aponeuroses propatagii. A general transition series of apomorphic tendinal fissions (especially caudally) of tendinal elements within the "tendo brevis" complex is reflected in the sequence of states given below, a scheme analyzed as unordered to preclude favoring any transition. The presumptively plesiomorphic component of "tendo brevis"—origo of which typically derives from the comparatively proximal or caudal caput m. deltoideus propatagialis (**pars caudalis**, part) as well as caput m. pectoralis propatagialis—is the comparatively distal (tendo distalis), which in many taxa is characterized by dorsoventral bifurcation and resultant dorsal and ventral tendinal counterparts, and in some taxa also manifests variably extensive, distal bifurcation (i.e., immediately proximal to insertiones retinaculum m. extensor (meta)carpi radialis). The paired subtendines resulting from this bifurcation are termed rami proximalis et distalis tendinis distalis brevis (**new terms**), and provisionally considered to represent initial stages in the complete division of tendo brevis. Together with ramus accessoria of ramus distalis tendinis distalis may result in three rami tendinis brevis—"tendines propatagiales breves" of Yudin (1964)—in some taxa.

This complexity of tendines within the "brevis complex" and associated structures, together with the ease with which the propatagium can be damaged unknowingly during dissection, prompted a comparatively robust treatment of states for purposes of the present higher-level reconstruction.

2550. M. deltoideus, pars propatagialis, pars caudale, tendo brevis, primary configuration, forma (**unordered**):

a. tendo single, width variable, united throughout or partially divided distad into rami proximalis et distalis tendinis brevis, the latter bifucation often largely on retinaculum or facies craniodorsalis m. extensor (meta)carpi radialis;

b. tendines (distalis et proximalis) doubled and subparallel throughout common length, tendo distalis partially divided distad (rami proximalis et distalis), but latter typically united proximad (craniad) for majority of length;

c. tendines (distalis et proximalis) doubled, tendo proximalis partially divided distad (rami proximalis et distalis), but typically united proximad (craniad) for majority of length;

x. noncomparable by absence of propatagium (ratites) or strongly apomorphic m. deltoideus propatagialis (Spheniscidae, Apodiformes).

Note.—Ardeidae typically augment the tendo brevis complex with ligamentum from sectio elasticum. See: Fürbringer (1888); Beddard (1898a); Buri (1900); Mitchell (1913b: fig. 126); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, 1960a, 1966); Yudin (1957: fig. 8); Yudin

(1964); George and Berger (1966: 319–322); Berger (1969), regarding Passeriformes; Hudson et al. (1969); Vanden Berge (1970: 308–310); Jollie (1977a–c); Maurer (1977); Bentz (1979: table 1); S. L. Olson and Feduccia (1980b: fig. 5), regarding *Phoenicopterus* and *Cladorhynchus*; Maurer and Raikow (1981: table 2, character 7); McGowan (1982); Raikow (1982: character 9); Zusi and Bentz (1984: 43); Raikow (1985b: table 1, character 4; table 3, character 3); Cracraft (1988: series XX, character 2); Livezey (1992b); Vanden Berge and Zweers (1993: annotation 79); Brown et al. (1994).

2551. M. deltoideus, pars propatagialis, pars caudale, tendo brevis, ramus distalis tendinis proximalis brevis, ramus accessorius, status:

a. absent; **b.** present.

Note.—See: Fürbringer (1888).

2552. M. deltoideus, pars propatagialis, capita craniale et caudale (especially tendines longa et brevis), complexus triangularis tendinorum patagialis (**new term**) comprising—(*i*) caudal triangular triad of juncturae cranial to junctura insertiorum immediately cranial to retinaculum m. extensor carpi radialis; (*ii*) triad between tendines longa et brevis, with ligamentum accessoria between caudalmost tendo brevis to distal tendo longa; and (*iii*) ligamentum between elongate processus supracondylaris dorsalis humeri to junctura tendinorum and typically enclosing one or two large sesamoidea—status:

a. absent; **b.** present.

Note.—See: Fürbringer (1888: taf. XIX); Beddard (1898a: fig. 161); Berger (1956a–b: fig. 1); Yudin (1957: figs. 1, 8); Yudin (1964).

2553. M. deltoideus, pars major, tendo insertii partis caudalis m. latissimus dorsi, status:

a. absent; **b.** present.

Note.—See: Maurer (1977: 31; 133, table 1); Maurer and Raikow (1981: table 2, character 9).

2554. M. deltoideus, pars major, capita craniale et caudale (if distinct), insertio(nes) humeri, ambitus proximodistalis (**ordered**):

a. distinctly elongate, virtually entire length of humerus, typically including processus flexorius humeri;

b. moderately elongate, occupying one-third to two-thirds length of humerus;

c. reduced, between one-third and one-fourth length of humerus;

d. vestigial, less than one-fourth length of humerus;

e. absent.

Note.—Extreme truncation of caput caudale (tendo brevis) in Pteroclidae is associated with absence of ligamenta limitates cubiti and oblique intersection of m. biceps propatagialis with m. extensor (meta)carpi radialis (Yudin 1957).

See: Fürbringer (1888); Buri (1900); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, d, 1960a); Yudin (1957: fig. 8); Vanden Berge (1970); Maurer (1977: 32); Schreiweis (1982); Zusi and Bentz (1984: 43); Raikow et al. (1988: table 3); McKitrick (1991b: character 7); Livezey (1992b).

2555. M. deltoideus, pars major, caput craniale, status (**ordered**):

a. absent, undifferentiated, musculus evidently unicapitate;

b. present, partially partitioned, typically progressing proximodistad;

c. present, complete;

x. noncomparable (Apterygidae).

Note.—See: Mitchell (1895); Beddard (1898a: fig. 180); Burt (1930); Fisher (1946); Berger (1954, 1956a–b, d, 1960a); Vanden Berge (1970); Maurer (1977), capita distinct only proximally; Raikow (1985b: table 3, character 4); Livezey (1992b); Vanden Berge and Zweers (1993).

2556. M. deltoideus, pars major, disproportionate bulk, craniocaudal width concealing m. scapulotriceps (dorsal perspective), status:

a. absent; **b.** present.

2557. M. deltoideus, pars major (capita craniale et caudale), pronounced caudal displacement of corpus relative to tuberculum dorsale et corpus humeri, status:

a. absent; **b.** present.

2558. M. deltoideus, pars major, caput craniale (where differentiated), situs origii:

a. extremitas omalis claviculae et/aut extremitas omalis aut corpus scapulae;

b. os humeroscapulare et extremitas omalis scapulae;

x. noncomparable (Turnicidae).

Note.—Synonymous with “os humeroscapulare” (G. Jäger 1857; Fürbringer 1888), this variably ossified fibrocartilago occurs in the dorsal part of the capsula articularis omalis in a minority of Neornithes (Baumel and Raikow 1993: annotation 100), although a comprehensive survey of taxonomic distribution of this element is not available. Origo capitis craniale m. deltoideus major in Trochilidae is confined to os humeroscapulare.

See: Pycraft (1907b); J. Steinbacher (1937); Berger (1954, 1956a–b, 1957, 1960a); Hoff (1966: 29); Cohn (1968); Maurer (1977); Zusi and Bentz (1984); Vanden Berge and Zweers (1993: annotation 79).

2559. M. deltoideus, pars major, caput profundus (**new term**), status:

a. absent; **b.** present.

Note.—See: Maurer (1977: 30), regarding “pars profundus,” origo ligamentae coracoscapulare dorsale et insertio tendinis partis caudalis m. latissimus dorsi.

2560. M. deltoideus, pars major, caput accessoriale (**new term**), status:
a. absent; **b.** present.
Note.—Variation in ossa origiorum occurs, including ossa clavicula (plesiomorphic), scapula, et coracoideum (Maurer 1977). See: Raikow (1978: fig. 4), uniting *Atrichornis* with *Menura*; origo of this cranialmost pars includes os humeroscapulare; Raikow (1985b: table 1, character 5), in reference to m. deltoideus major, caput proximale.

2561. M. deltoideus, pars minor, status:
a. present, moderately developed;
b. vestigial or absent.
Note.—See: Fürbringer (1888); Beddard (1898a); Pycraft (1900); Burt (1930); J. Steinbacher (1937); Berger (1954, 1956a–b, 1960a–b); Hudson et al. (1972: 249); Maurer (1977); Bentz (1979: table 1); McGowan (1982); Schreiweis (1982); Zusi and Bentz (1984: 43).

2562. M. deltoideus, pars minor, capita dorsale (externa) et ventrale (interna), status (**unordered**):
a. both capita dorsale et ventrale present;
b. caput dorsale alone present or (rarely) with caput ventrale vestigialis;
c. caput ventrale alone present or with caput dorsale vestigialis;
x. noncomparable (Rheidae, Apterygidae).
Note.—Describes differentiation of capita within musculus. See: Watson (1883), in reference to "accessory slip" here provisionally considered elongate caput of m. deltoideus minor; Fürbringer (1888); Beddard (1898a); Buri (1900); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, 1957, 1960a); Hudson et al. (1969); Vanden Berge (1970); Maurer (1977); Raikow (1978: table 2); Bentz (1979); Raikow (1985b: table 1, character 6); Strauch (1985: table 3, character H6); Livezey (1992b).

Mm. Triceps Brachii

2563. M. scapulotriceps, status:
a. present;
b. markedly reduced or vestigial.
Note.—See: Fürbringer (1888); Buri (1900); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, d, 1960a); Yudin (1957: fig. 8); Vanden Berge (1970); Vanden Berge and Zweers (1993: annotation 81).

2564. M. scapulotriceps, capita origii, numerus modalis:
a. one; **b.** two.
Note.—See: George and Berger (1966: 334); Maurer (1977: 36); Maurer and Raikow (1981: table 2, character 14).

2565. M. scapulotriceps, origo(iones), typus:
a. fibrous, at least in part; **b.** tendinous.
Note.—Additional characteristic of *Opisthocomus* that contrasts with states of Cuculiformes is restriction of origo m. scapulotriceps to facies lateralis scapulae (Hudson and Lanzillotti 1964).
See: Buri (1900); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, d, 1960a); Owre (1967); Vanden Berge (1970: 314); Maurer (1977).

2566. M. scapulotriceps, ligamentum tricipitale, status:
a. present; **b.** absent.
Note.—In reference to "humeral anchor" or *Ankerung* (George and Berger 1966: 293), between margo dorsalis m. scapulotriceps et insertio m. latissimi humeri, presence of which tends to coincide in taxonomic distribution with that of m. ambiens.
See: Buri (1900); Burt (1930); Fisher (1946); Berger (1954, 1956a, 1960a); Hoff (1966); Goodge (1972: 67); Hudson et al. (1972); Maurer (1977: 36); Maurer and Raikow (1981: table 2, character 15); Zusi and Bentz (1984); McKitrick (1991b: character 3);. G. Mayr (2002a: legend fig. 9, node 4, character 4); G. Mayr (2003b: appendices I–II, character 22).

2567. M. scapulotriceps, tendo insertii, os sesamoideum m. scapulotricipitis, status:
a. absent; **b.** present.
Note.—Tendo insertii of m. scapulotriceps passes over retinaculum m. scapulotriceps. Sesamoideum in question traditionally termed "*patella ulnaris*" (George and Berger 1966: 333), evidently a concession to a proposal asserting skeletal symmetry between pectoral and pelvic appendages in Tetrapoda. See: Fürbringer (1888: taf. XIX); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a, 1960a); Yudin (1957); Hudson et al. (1969); Vanden Berge (1970); Strauch (1985: table 3, character H7).

2568. M. humerotriceps, forma:
a. robust; **b.** attenuate, reduced.
Note.—Subdivision of origiones mm. humerotriceps et scapulotriceps into variably discernable internal (dorsal) and external (ventral) heads typical among Neornithes (George and Berger 1966). See: Fürbringer (1888); Buri (1900); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a, 1960a); Yudin (1957: fig. 8); Owre (1967); Maurer (1977); Livezey (1992b).

2569. M. coracotriceps, status:
a. present; **b.** absent;
x. noncomparable (ratites, Spheniscidae).

Note.—Synonymous with m. anconaeus coracoideus (George and Berger 1966: 336), vestigial condition and basal distribution suggestive of plesiomorphic retention followed by reductive parallelism (Vanden Berge and Zweers 1993: annotation 82). See: Beddard (1884, 1898a); Fürbringer (1888: taf. XXVI, figs. 24–26); Mitchell (1913b); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, 1960a–b); Yudin (1957: fig. 8); George and Berger (1966: 336–337); Vanden Berge (1970); Maurer (1977); Raikow (1985a: fig. 2.13).

M. Biceps Brachii

Note.—Capita origii partis propatagialis m. biceps brachii manifest a diversity of subtle configurations (Fürbringer 1888: taf. XXVI; Yudin 1964: figs. 59–73) that are poorly documented; consequently, this dimension of propatagial variation was not treated herein.

2570. M. biceps brachii, (especially) corpus et tendo insertii, relative lengths (**ordered**):

a. corpus distinctly greater than tendo (or fibers) insertii;

b. corpus approximately equal to tendo insertii;

c. corpus distinctly shorter than tendo insertii.

Note.—In few Sphenisciformes retaining vestigium m. biceps brachii, tendo insertii elongate (Schreiweis 1982). See: Fürbringer (1888); Beddard (1898a); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1960a–b, 1966); Yudin (1957: fig. 8); Hoff (1966); Vanden Berge (1970); Hudson et al. (1972); Maurer (1977); Schreiweis (1982); Raikow et al. (1979); Raikow et al. (1988: table 3); McKitrick (1991b: character 8); Livezey (1992b); Vanden Berge and Zweers (1993: annotation 83).

2571. M. biceps brachii, origo—capita humerale et/aut coracoideum—status:

a. both capita coracoideum et humerale present;

b. only caput coracoideum and single tendo insertii retained;

x. noncomparable by status of musculus (Spheniscidae).

Note.—Caput scapulare m. biceps brachii, uniformly absent in Aves (Vanden Berge and Zweers 1993: annotation 83), evidently is homologous with caput coracoideum m. biceps brachii of Theropoda, having undergone a positional shift with the incorporation of a vestigium of os coracoideum as a processus of a bi-elemental "composite" os scapulae in Mammalia.

See: Pycraft (1900); Mitchell (1905); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, 1960a); Yudin (1957: fig. 8); Yudin (1964: fig. 41); George and Berger (1966: 329); Hudson et al. (1969); Vanden Berge (1970); Jollie (1977a–c); Maurer (1977); McGowan (1982); Zusi and Bentz (1984); Livezey (1992b); Vanden Berge and Zweers (1993: annotation 83).

2572. M. biceps brachii, capita coracoideum et/aut humerale et tendines insertiorum, divisio(nes), status et forma (**ordered**):

a. capita variably united, tendines insertii variably united by vinculum from corpus to variable extent proximal to bifurcatio (if present) insertiorum ulnare et radiale—tendo capitis coracoideum more frequently undergoing bifurcatio tendinis than that of caput humerale;

b. capita variably united, tendines insertii distinct throughout but enclosed within loose common vagina fasciata;

c. capita et tendines fully separate;

x. noncomparable by absence of musculus or caput (Spheniscidae, *Balaeniceps*, Mesitornithidae, Heliornithidae, Apodidae).

Note.—See: Fürbringer (1888); Beddard (1897b: 289, fig. 1); Beddard (1898a: 405, fig. 190); Mitchell (1905, 1913b); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, 1960a); Yudin (1957, 1964); George and Berger (1966: 329); Hoff (1966); Owre (1967); Vanden Berge (1970); Maurer (1977); Maurer and Raikow (1981: table 2, character 13); Livezey (1992a).

2573. M. biceps brachii, tendo origii capitis coracoideum, ramus tendinis humeri, status:

a. absent; **b.** present;

x. noncomparable by absence of musculus or caput (Spheniscidae, Apodidae).

Note.—See: Fürbringer (1888: taf. XXVI, figs. 6–8); Beddard (1897b: fig. 1).

2574. M. biceps brachii, insertio(nes), numerus et situs (**unordered**):

a. three, both rami ulnaris et radialis tendinis insertii present, latter including bifurcatio distalis to produce ramus accessoria tendinis insertii ulnaris (**new term**) to comprise one insertio radii et two insertiones ulnae;

b. two, both rami ulnaris et radialis tendinis insertii present;

c. one, insertio ulnaris only;

d. one, insertio radialis only;

x. noncomparable by absence of musculus or caput (Spheniscidae, Apodidae).

Note.—Single tendo insertii m. biceps brachii in *Balaeniceps* has bifurcatio terminalis to permit both insertiones ulnae et radii. Variation in tendines insertii m. biceps brachii was described for Alcidae by Hudson et al. (1969: 465). See: Beddard (1884, 1886c–d, 1898a); Fürbringer (1888); Mitchell (1905, 1913b); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, 1960a); Owre (1967);

Sanders (1967); Hudson et al. (1969); Vanden Berge (1970); Maurer (1977); Maurer and Raikow (1981: table 2, character 13); Zusi and Bentz (1984: 42); Strauch (1985: table 3, character H9); McKitrick (1991b: 134–135); Livezey (1992b); Vanden Berge and Zweers (1993).

2575. M. biceps brachii, pars propatagialis, status:
a. absent; **b.** present, variably robust;
x. noncomparable by status of musculus (Spheniscidae, Apodidae).

Note.—The "biceps slip" is necessarily absent in taxa lacking propatagium, notably ratites. See: Beddard (1884, 1886c–d, 1888b, 1898a); Shufeldt (1886d); Fürbringer (1888); Gadow and Selenka (1891); Buri (1900); Mitchell (1905, 1913b); Pycraft (1907b); Burt (1930); J. Steinbacher (1937); Fisher (1946); Lowe (1948); Berger (1954, 1956a–b, 1957, 1960a); Fisher and Goodman (1955); Yudin (1957, 1964); Hudson and Lanzillotti (1964); Yudin (1965); George and Berger (1966: 330–331); Hudson et al. (1969, 1972); Vanden Berge (1970); Jollie (1977a–c); Maurer (1977); McGowan (1982); Raikow (1982: character 8); Zusi and Bentz (1984); McKitrick (1991b: character 9); Livezey (1992b); G. Mayr (2002b: 91).

2576. M. biceps, pars propatagialis, caput distale (**new term**)—corpus within cranial pars elastica tendinis longa with midpropatagial tendo insertii on m. extensor (meta)carpi radialis at angulus propatagii—status:
a. absent; **b.** present;
x. noncomparable by status of musculus (Spheniscidae, Apodidae).

Note.—First noted and illustrated by Fürbringer (1888: taf. XXII, fig. 1). Caput illustrated but not individually labelled by George and Berger (1966: fig. IX.38) for *Columba livia*. In text, George and Berger (1966: 317) expanded the diagnosis: "The anterior edge of the fleshy belly of the biceps slip fuses with the proximal portion of the elastic band [tendo longa, sectio elasticum]." A weakly bicapitate condition of m. biceps pars propatagialis was described for some Alcidae by Hudson et al. (1969: 465).

M. Expansor Secundariorum

Note.—A muscle of widespread taxonomic distribution, composed of smooth muscle and (infrequently) variable combinations of corpora et tendines proximales (scapulae, rarely coracoidei) et distales (humeri et remiges secundarii), the primary function of which pertains to relative positioning of remiges secundarii. Tendo proximalis is related intimately with m. coracotriceps (where latter present), tendines of latter passing in parallel with former (Berger 1956a; George and Berger 1966).

2577. M. expansor secundariorum, status modalis (**ordered**):
a. present; **b.** vestigial or rudimentary;
c. absent.

Note.—See: Garrod (1876e: 193); Beddard (1884, 1886b, d, 1898a); Fürbringer (1888: 124); Buri (1900); Burt (1930); J. Steinbacher (1937); Berger (1954, 1956a–b, 1960a); George and Berger (1966); Hoff (1966); Owre (1967); Cohn (1968); Vanden Berge (1970); Jollie (1977a–c); Maurer (1977); Raikow (1982: character 7); Schreiweis (1982); Zusi and Bentz (1984); G. Mayr (2003a: appendix I, character 41).

2578. M. expansor secundariorum, pars (corpus) cubiti (**new term**), status:
a. present; **b.** vestigial or absent;
x. noncomparable by absence of musculus (ratites, Spheniscidae, *Scopus*, *Chionis*).

Note.—New term synonymous with "ulnar belly," which typically gives rise to tendo insertii remigialium (**new term**). See: Buri (1900); Burt (1930); J. Steinbacher (1937); Owre (1967); Maurer and Raikow (1981: table 2, character 16), using name "humeral belly." Berger (1954, 1956a–b, 1960a) concluded that taxonomic variation in histology—smooth and striated tissues—indicates that this muscle represents a complexus of m. expansor secundariorum (smooth) and m. anconeus (striated).

2579. M. expansor secundariorum, tendo origii (cum rami scapulae et/aut coracoidei) proximalis (**new term**), status:
a. present;
b. vestigial (fine) or absent, et/aut attached by m. anconeus to m. serratus metapatagialis;
x. noncomparable by absence of musculus (ratites, Spheniscidae, *Scopus*, *Chionis*).

Note.—The newly named tendo is intended to distinguish this variable ancora from a more-distal attachment (tendo distalis) to os humerus or trochlea humeroulnaris ("humero-ulnar pulley"). See: Burt (1930); J. Steinbacher (1937); Berger (1954, 1956a–b, 1960a); Owre (1967); Hudson et al. (1969); Vanden Berge (1970); Jollie (1977a–c); Maurer (1977); Zusi and Bentz (1982, 1984).

2580. M. expansor secundariorum, tendo origii (coracoidei) proximalis (**new term**), ancorae coracoidei, numerus modalis:
a. one;
b. two to three, by bi- or tri-furcatio distalis tendinis origii;
x. noncomparable by absence of musculus (ratites, Spheniscidae, *Scopus*, *Chionis*).

Note.—See: Livezey (2003).

Mm. Flexores (Cubiti) Antebrachii

2581. Mm. cubiti—notably mm. flexor digitorum profundus, ulnometacarpalis ventralis, pronatores superficialis et profundus, supinator, extensor (meta)carpi ulnaris, extensor longus digiti majoris (caput proximalis), et ectypicondylo-ulnaris—proximodistal lengths of corpora relative to that of antebrachium, forma:

a. proportionate, i.e., relative lengths typical of majority of Aves;

b. distinctly truncate, mm. cubiti characterized by markedly truncate corpora and elongate tendines insertii;

x. noncomparable (ratites).

Note.—Direct examination suggested that apomorphic condition exceeded that explanable strictly on grounds of elongation of ossa antebrachii.

See: Fisher and Goodman (1955); Owre (1967); Vanden Berge (1970).

2582. M. brachialis, origo, situs (**unordered**):

a. extremitas proximalis humeri;

b. corpus humeri, facies ventralis;

c. extremitas distalis humeri.

Note.—See: Dilkes (1999: 102); Meers (2003: 904).

2583. M. brachialis, impressio insertii, situs (**unordered**):

a. extremitas proximalis ulnae, facies ventrocranialis;

b. extremitates proximales ulnae et radii, facies ventrocranialis et cranioventralis, respectively;

c. extremitas proximalis radii, facies cranioventralis.

Note.—The "*accessory brachialis anticus*" noted by Beddard (1898a: 504) in *Apteryx*, remains unconfirmed. See: J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, d, 1960a–b); Hoff (1966); Hudson et al. (1969); Vanden Berge (1970); Maurer (1977); Schreiweis (1982); Meyers (1996).

2584. M. ectepicondylo-ulnaris, status:

a. present, including significant corpus;

b. vestigial (largely or completely tendinous) or absent.

Note.—Synonymous with m. anconeus (George and Berger 1966). See: Beddard (1898a); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, 1957, 1960a); Vanden Berge (1970); Schreiweis (1982); Raikow et al. (1988: table 3); Meyers (1996).

2585. M. ectepicondylo-ulnaris, corpus, union with that of m. flexor (meta)carpi ulnaris, status:

a. absent; **b.** present.

Note.—See: Pycraft (1900). Distinct from partial union of origiones described by Maurer and Raikow (1981: table 2, character 20).

2586. M. entepicondylo-ulnaris, status:

a. present; **b.** absent.

Note.—Purported presence of musculus in Bucerotidae erroneous, likely based on proximal vestigium of pars caudalis (remigialis) m. flexor (meta)carpi ulnaris. Report of musculus in *Scopus* by Beddard (1884), under synonym "anconeus internus," uncorroborated. See: Burt (1930); Sy (1936); Fisher (1946); Berger (1954, 1956a–b, 1960a); Fujioka (1959); Hudson and Lanzillotti (1964); George and Berger (1966); Hoff (1966); Hudson et al. (1972); Zusi and Bentz (1978); McGowan (1982); Schreiweis (1982); Raikow et al. (1988: table 3); Livezey (1990); Vanden Berge and Zweers (1993: annotation 92); Livezey (1997a: appendix 1, character 118; *corrigenda*, Livezey 1998a); Rotthowe and Starck (1998: character 15), who deemed musculus apomorphic.

Mm. Pronatores et Supinator Antebrachii

2587. M. pronator superficialis (sublimus), status et forma (**ordered**):

a. well developed;

b. distinctly reduced; **c.** absent.

Note.—Beddard (1898a) inferred that mm. pronatores "merged" in most ratites, excepting Rheidae in which m. pronator profundus was judged to be lacking entirely (George and Berger 1966). See: Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, 1957, 1960a); Maurer (1977); Rosser (1980); Schreiweis (1982); Zusi and Bentz (1984); Raikow et al. (1988: table 3); McKitrick (1991b: character 10); Meyers (1996); Livezey (2003).

2588. M. pronator profundus, status:

a. present; **b.** absent.

Note.—See: Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, d, 1960a); Vanden Berge (1970); Maurer (1977); Raikow (1978: table 2); Bentz (1979: table 1); Rosser (1980); McGowan (1982); Schreiweis (1982); Zusi and Bentz (1984); Raikow et al. (1988: table 3); Meyers (1996); Livezey (2003).

2589. M. pronator superficialis, numerus capitorum origii et forma corporis (**unordered**):

a. one, ellipsoidal;

b. one, but corpus bilobate;

c. two, augmented by caput accessoria proximalis (**new term**) uniting proximoventrad with basis corporis m. pronator superficialis proprius;

x. noncomparable (Spheniscidae).

Note.—See: Hudson et al. (1969: fig. 2); Maurer (1977); Livezey (1990).

2590. Mm. pronatores superficialis et profundus, tendines origii, elongation proximad to adjacent, parallel, but separate ancorae, status:

a. absent; **b.** present.

Note.—See: Maurer (1977).

2591. M. pronator superficialis, insertio, forma:

a. fibrous or semitendinous;

b. tendinous;

x. noncomparable (Apterygidae, Spheniscidae).

Note.—See: Buri (1900); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, 1960a); Hoff (1966); Vanden Berge (1970); Maurer (1977); Maurer and Raikow (1981: table 2, character 17); Zusi and Bentz (1984); Meyers (1996).

2592. Mm. pronatores superficialis et profundus, corpora, relative proximodistal lengths, status (**ordered**):

a. profundus distinctly longer than superficialis;

b. profundus approximately equal in length to superficialis;

c. profundus shorter than superficialis;

x. noncomparable (Apterygidae, Spheniscidae).

Note.—Polarity consistent with majority condition as well as former names “longus” (profundus) et “brevis” (superficialis). See: Berger (1956a, d); Maurer (1977).

2593. Mm. pronatores superficialis et profundus, corpora, distal union as single functional unit including tendo insertii, status et forma (**unordered**):

a. absent; **b.** present, proximal;

c. present, distal;

x. noncomparable (Apterygidae, Spheniscidae).

Note.—See: Pycraft (1900); Burt (1930); Maurer (1977).

2594. M. pronator profundus, capita origii, caput accessoria (**new term**), status:

a. absent, one caput;

b. present, two capita, including plicate caput accessoria proximalis;

x. noncomparable (Spheniscidae).

Note.—Where polymorphic, typically characterized by one or two capita, latter augmented distoventrad by caput accessoria distalis (**new term**), uniting distad with m. pronator profundus proprius. See: Berger (1968), reporting apomorphy in some *Dendroica*; Maurer (1977); Raikow (1978: table 2); Bentz (1979), regarding apomorphy in some Estrildidae and Ploceidae.

2595. M. supinator, status et forma:

a. substantial, length at least one-half of that of m. pronator profundus;

b. markedly reduced, vestigial, or absent, length less than one-half of that of m. pronator profundus.

Note.—See: Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, 1960a); Cohn (1968); Vanden Berge (1970); Maurer (1977); Schreiweis (1982); Zusi and Bentz (1984); Raikow et al. (1988: table 3); McKitrick (1991b: character 11); Meyers (1996).

Mm. Flexores Digitorum Antebrachii

2596. M. flexor digitorum superficialis (sublimus), corpus and (to lesser extent) associated ligamentum humerocarpale, status (**ordered**):

a. well developed;

b. vestigial, tendo or fascia only;

c. absent.

Note.—See: Burt (1930); Fisher (1946); Cohn (1968); Hudson et al. (1969); Vanden Berge (1970); Maurer (1977); Stegmann (1981); McGowan (1982); Schreiweis (1982); Zusi and Bentz (1984); Raikow et al. (1988: table 3); Meyers (1996).

2597. M. flexor digitorum superficialis, tendo insertii, phalanges insertii digiti majoris manus, forma:

a. phalanx distalis digiti majoris, typically in combination with insertio phalangis proximalis digiti majoris;

b. phalanx proximalis digiti majoris;

x. noncomparable by extreme reduction of manus (ratites, Spheniscidae).

Note.—Mechanism by which insertiones tendinorum occur were considered by Dorfl (1980a–b). Virtually throughout Neornithes, m. flexor digitorum superficialis separates from the ligamentum humerocarpale at or proximal to the ancora ligamenti on os carpi ulnare; the minor tendo insertii passes distad, typically in variably close association with tendo insertii m. flexor digitorum profundus to insertio digiti majoris m. flexor digitorum superficialis. See: Burt (1930); Fisher (1946); Berger (1954, 1956a–b, 1960a); Tipton (1962: 177); Hoff (1966); Hudson et al. (1969); Vanden Berge (1970); Maurer (1977: 41–44); Meyers (1996).

2598. M. flexor digitorum profundus, forma:

a. corpus et/aut tendo insertii;

b. tendo only.

Note.—See: Burt (1930); Berger (1954, 1960a); Hudson et al. (1969); Vanden Berge (1970); Maurer (1977); Stegmann (1981); Schreiweis (1982); Zusi and Bentz (1984); Raikow et al. (1988: table 3).

2599. M. flexor digitorum profundus, corpus, length relative to that of ulna:

a. greater than one-half length of ulna;

b. no longer than one-half length of ulna.

Note.—See: Pycraft (1900); Fisher (1946); George and Berger (1966); Hudson et al. (1972).

2600. M. flexor digitorum profundus, numerus capitorum origii:

a. one, single caput origii proximally positioned distal or ventral (commonly) or dorsal (rarely) to insertio m. brachialis ulnae;

b. two, dual capita origii divided by insertio m. brachialis ulnae;

x. noncomparable (Spheniscidae).

Note.—See: Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1960a–b); Hoff (1966); Hudson et al. (1969); Vanden Berge (1970: 317, 319); Maurer (1977); Raikow (1978: fig. 4); S. L. Olson and Feduccia (1980b: 23); Maurer and Raikow (1981: table 2, character 18); Zusi and Bentz (1984); Cracraft (1988: series XII, character 2); Livezey (1990, 1992a–b); Meyers (1996).

2601. M. flexor digitorum profundus, origo, caput accessoria superficiale (**new term**), status et forma origii (**ordered**):

a. absent, single caput origii distoventral to insertio m. brachialis;

b. present, primary caput augmented ventrad by caput accessoria superficiale (**new term**), arising by fibers (interposed between origiones mm. pronatores, and merging with corpora mm. flexores digitorum superficialis et profundus;

c. present, primary caput augmented ventrad by caput accessoria superficiale (**new term**), arising by tendo humeralis (interposed between origiones mm. pronatores, and merging with corpora mm. flexores digitorum superficialis et profundus;

x. noncomparable (Spheniscidae).

Note.—See: Cohn (1968: 102–103); Zusi and Bentz (1984: 28–29).

2602. Mm. flexores digitorum superficialis et profundus, capita et tendines origii, union, status:

a. present, tendines and proximal parts of capita origii joined;

b. absent, arising separately by distinct capita, former often with origo on facies interosseus ulnae.

Note.—Where origio communis occurs, it (together with characteristic union ligamentum humerocarpale) reflects a common primordium shared by this pair of mm. flexores manus (Sullivan 1962: annotation 85). See: Pycraft (1900: 240) for condition in palaeognathous Neornithes; George and Berger (1966: 351–352); Hudson et al. (1972); Vanden Berge and Zweers (1993: annotation 86).

2603. M. flexor digitorum profundus, phalanx insertii digiti majoris:

a. phalanx proximalis; **b.** phalanx distalis;

x. noncomparable (Spheniscidae).

Note.—Mechanism by which insertiones tendinorum are elaborated were considered by Dorfl (1980a–b). See: Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, 1957, 1960a); Tipton (1962: 177); Hudson et al. (1969); Vanden Berge (1970); Maurer (1977); Livezey (1992b); Meyers (1996).

2604. M. flexor digitorum profundus, tendo insertii phalangis digiti alulae (**new term**), status natalis et definitivum (**unordered**):

a. present, (presumptively) all ages;

b. present, natalis only;

c. absent, throughout ontogeny and adulthood;

x. noncomparable (ratites, Spheniscidae).

Note.—Tendo commonly ephemeral in nestlings of taxa in which unguis alulae is functional (e.g., Galliformes, *Opisthocomus*, *Otus*), therefore retention into adulthood represents paedomorphic atavism in Neornithes. Paucity of natal spirit specimens rendered under-representation of state "b" likely. Uncertainty whether juvenile manifestation represents rudimentum (plesiomorphy) or vestigium (apomorphy) necessitated unordered treatment.

See: Gadow and Selenka (1891: 280–281); Schestakova (1927); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, 1960a); George and Berger (1966); Hoff (1966); Vanden Berge (1970: 319); Hudson et al. (1972: 226); Maurer (1977); Stegmann (1978).

Mm. Extensores Carpi Ulnaris aut Radialis

2605. M. extensor (meta)carpi ulnaris, corpus, forma:

a. unipennate; **b.** bipennate.

Note.—See: Maurer (1977: 49).

2606. M. extensor (meta)carpi ulnaris, tendo insertii, situs (**unordered**):

a. os metacarpale (majus) II, typically on margo spatii intermetacarpalis, often on processus intermetacarpalis;

b. os carpi ulnare, synostosis intermetacarpalis proximalis, including processus pisiformis aut extensorius;

c. os metacarpale (minus) III, facies dorsalis, proximal to spatium intermetacarpale;

x. noncomparable (Spheniscidae).

Note.—Situs insertii tendinis digiti majoris is synonymous with "flexor tubercle" of Woolfenden (1961). See: Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, d, 1960a); Fisher and Goodman (1955); Stegmann (1965), in positional shift of insertio involving processus intermetacarpale was proposed; George and Berger (1966: 361); Hudson et al. (1969); Vanden Berge (1970); Maurer (1977); Rosser (1980); Zusi and Bentz (1984); Livezey (1990: fig. 15); Livezey and Humphrey (1992: fig. 20), illustrating homologous feature as impressio in *Tachyeres* (Anatidae); Meyers (1996); G. Mayr (2002a: legend fig. 9, node 3, character 6); G. Mayr et al. (2003: appendix 1, character 44); G. Mayr (2004d: appendix I, characters 42 and 49); G. Mayr (2005a: appendix 1, character 50).

2607. M. extensor (meta)carpi ulnaris, tendo insertii, os sesamoideum, status:
a. absent; **b.** present;
x. noncomparable (Spheniscidae).
Note.—See: Cohn (1968); Maurer (1977); Zusi and Bentz (1984).

2608. M. extensor (meta)carpi radialis, tendo(iones) insertii, numerus modalis:
a. two, emerging separate but united variably distad to distinct capita;
b. one, emerging united from variably joined capita ventrale et dorsale;
x. noncomparable (Spheniscidae).
Note.—In addition to variation in distinctness of tendines insertii, partially covarying degrees in union of capita ventrale et dorsale also occur. George and Berger (1966: 358) referred to two heads as "*partes anconalis et palmaris*"; we follow Rosser (1980) in designation of capita. These capita arise respectively from: (*i*) tuberculum supracondylare dorsale humeri and (*ii*) between latter and origo m. extensor digitorum communis; second origo involves m. ectepicondylo-ulnaris in some taxa.
See: Pycraft (1900: 240); Fisher (1946); Tipton (1962); Hudson and Lanzillotti (1964); Vanden Berge (1970: 320); Hudson et al. (1972); Maurer (1977); Zusi and Bentz (1978); Maurer and Raikow (1981: table 2, character 19); Cracraft (1988: series XV, character 2); Raikow et al. (1988: table 3).

2609. M. extensor (meta)carpi radialis, tendo origii, os sesamoideum, status:
a. absent or indiscernable;
b. present, prominent;
x. noncomparable (Spheniscidae).
Note.—Prominence of os sesamoideum enhanced by location at terminus of elongate processus supracondylare dorsale humeri. See: Yudin (1957).

Mm. Flexores Carpi Ulnaris aut Radialis

2610. M. flexor (meta)carpi ulnaris, status et situs (**ordered**):
a. hypertrophied, including extension of corpus to os metacarpale, sine retinaculum;
b. well developed, comprising corpus et tendo, cum retinaculum;
c. vestigial, comprising tendo only.
Note.—Typically origo is firmly united by aponeurosis with that of m. flexor digiti profundus. See: Pycraft (1900: fig. 5A); Lowe (1942); Fisher (1946); Hudson et al. (1969); Vanden Berge (1970); Maurer (1977); Schreiweis (1982); Raikow et al. (1988: table 3).

2611. M. flexor (meta)carpi ulnaris, pars (caudalis) remigialis, status:
a. present; **b.** vestigial or absent.
Note.—Pars remigialis (formerly pars caudalis) comprises variably extensive muscle fibers along margines caudales musculi et ligamentum humerocarpale and fasciae tendinosa with calami remigii secundariae.
See: Buri (1900); Pycraft (1900: fig. 6A); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, 1960a–b); Hudson et al. (1969); Vanden Berge (1970); Maurer (1977); Meyers (1996); Livezey (2003).

Mm. Extensores Digitorum Antebrachii

Note.—Homologies of extensores et flexores digitorum between Crocodylia and Aves are problematic given the complexity of musculi serving independent ossa (meta)carpalia et digiti I–V of Crocodylia (Meers 2003).

2612. M. extensor digitorum communis, status:
a. present; **b.** vestigial or absent.
Note.—See: Beddard (1884); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, 1960a); Hudson et al. (1969); Vanden Berge (1970); Maurer (1977); Stegmann (1981); McGowan (1982); Schreiweis (1982); Raikow et al. (1988: table 3); Meyers (1996).

2613. M. extensor digitorum communis, os(sa) origii:
a. humerus; **b.** humerus and radius.
Note.—See: Maurer and Raikow (1981: table 2, character 21).

2614. M. extensor digitorum communis, tendo insertii phalangis digiti alulae (**new term**), status modalis definitivum:
a. present; **b.** absent;
x. noncomparable by absence, or profound modification, of digitus alularis (*Casuarius*, *Dromaius*, *Apteryx*, Spheniscidae).
Note.—See: Beddard (1884); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, d, 1960a); Hudson and Lanzillotti (1964); Cohn (1968: 107); Hudson et al. (1969); Vanden Berge (1970); Stegmann (1974); Maurer (1977); Maurer and Raikow (1981: table 2, character 22); Zusi and Bentz (1984: 43); Meyers (1996).

2615. M. extensor digitorum communis, tendines insertiorum phalangis proximalis digiti (II) majoris mm. extensor digitorum communis et abductor digiti majoris on extremitas distalis carpometacarpi, forma:
a. former deviates craniad et/aut latter deviates caudad (i.e., converge distally) distal to sulcus

tendineus to insert: (*i*) immediately caudal or (*ii*) coincident and deep to tendo insertii m. abductor digiti majoris on facies ventralis phalangis proximalis digiti majoris;

b. both continue distad through sulcus et vagina tendinorum to insert on cranioproximal vertex of phalanx, oriented approximately parallel, mutually and with axis majoris ossis;

x. noncomparable (Spheniscidae).

Note.—See: Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, 1960a); George and Berger (1966: 362–363); Hudson et al. (1969); Vanden Berge (1970); Stegmann (1974: fig. 6); Maurer (1977); Livezey (1990: fig. 15); Meyers (1996).

2616. M. extensor longus alulae, capita, numerus et situs (**unordered**):

a. two, comprising both capita radiale et ulnare present;

b. one, caput radiale only;

c. one, caput ulnare only;

x. noncomparable by absence of digitus alularis (Dromaiidae, Casuariidae, Spheniscidae).

Note.—In some taxa, partes distalis et proximalis capitis radiale—are apparent, defining an irregular margo ventralis of caput radiale. See: Beddard (1884); Mitchell (1895); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, 1960a); George and Berger (1966: 370); Hudson et al. (1969); Vanden Berge (1970); Maurer (1977); Maurer and Raikow (1981: table 2, characters 25–26); Stegmann (1981); McGowan (1982: 212); Schreiweis (1982); Zusi and Bentz (1984: 43); Meyers (1996).

2617. M. extensor longus alulae, capita radiale et ulnare, tendines insertii, proximal (antebrachial) separation, status:

a. absent, single tendo insertii;

b. present, capita having separate tendines insertii proximally;

x. noncomparable by absence of caput radiale aut ulnare (Struthionidae, Rheidae, Apterygidae, Pelecanidae, Sagittaridae, Musophagidae, Trochilidae, Todidae, Motmotidae, Upupidae, Phoeniculidae, Bucerotidae, Galbulidae, Indicatoridae).

Note.—Apomorphic condition apparently reflection of evolutionary derivation of two capita of m. extensor longus alulae from separate extensores ulnaris et radii alulae. See: Fisher (1946); Berger (1956a–b, d); Maurer (1977).

2618. M. extensor longus digiti (indicus) majoris, pars distalis (caput distale), status modalis (**ordered**):

a. present; **b.** vestigial; **c.** absent;

x. noncomparable (ratites, Spheniscidae).

Note.—Synonymous with "m. flexor metacarpi brevis" of Berger (1960a) and Owre (1967), and "m. extensor medius brevis" of Sullivan (1962), this small corpus is situated on facies dorsalis ossis carpi radiale, capsula articularis radiocarpo-metacarpale dorsale, et/aut extremitas proximalis carpometacarpi, the tendo insertii of which typically uniting distad with tendo insertii partis proximalis (George and Berger 1966: 367). Evidently the avian musculus is the vestigium of a separate flexor of the manus—"m. flexor digitorum longus pars carpalis" in Crocodylia (Meers 2003)—and plesiomorphic for Archosauria (Haines 1950; Meers 2003). The larger caput proximale is provisionally homologous to m. flexor digitorum longus pars ulnaris.

See: Beddard (1884: 548); Burt (1930); J. Steinbacher (1937); Lowe (1943); Fisher (1946); Berger (1954, 1956a–b, d, 1957, 1960a); Fisher and Goodman (1955); Hudson et al. (1955, 1966, 1969, 1972); Sullivan (1962); Hudson and Lanzillotti (1964); Hoff (1966); Sanders (1967); Vanden Berge (1970); Maurer (1977); Zusi and Bentz (1978; 1984); Maurer and Raikow (1981: table 2, character 24); Stegmann (1981); McGowan (1982: 212), regarding *Apteryx*; Schreiweis (1982); Livezey (1990: fig. 15; 1992a–b; 2003); McKitrick (1991b: character 12); Meyers (1996); G. Mayr (2003b: appendices I–II, character 23).

Mm. Flexores Carpi

2619. M. ulnometacarpalis dorsalis, status (**unordered**):

a. present, bicapitate, comprising both capita dorsale et ventrale;

b. present, unicapitate, provisionally representing caput dorsale;

c. absent.

Note.—Synonymous with "m. flexor carpi ulnaris, pars posterior" or "m. flexor metacarpi posterior." Caput dorsale inserts on margo dorsocaudalis ossis metacarpale minus, and caput ventrale on os ulnare. See: Buri (1900); Burt (1930); J. Steinbacher (1937); Fisher (1946); Berger (1954, 1956a–b, 1957, 1960a); Hudson et al. (1969); Vanden Berge (1970); Stegmann (1974: fig. 5; 1981: 13), contrasting Podicipedidae with Gaviidae; Maurer (1977); Schreiweis (1982); Strauch (1985: table 3, character H11); Raikow et al. (1988: table 3); McKitrick (1991b: character 13); Livezey (1992b); Meyers (1996).

2620. M. ulnometacarpalis ventralis, status et forma (**ordered**):

a. present, substantial, length at least one-half that of ulna;

b. present, moderate, length less one-half that of ulna;

c. vestigial or absent.

Note.—Two capita (caudale et craniale) variably recognized. See: Burt (1930); J. Steinbacher (1937);

Fisher (1946); Berger (1954, 1956a–b, 1957, 1960a); Hudson and Lanzillotti (1955); Hoff (1966); Vanden Berge (1970); Maurer (1977); Schreiweis (1982); Raikow et al. (1988: table 3); Meyers (1996).

2621. M. ulnometacarpalis ventralis, capita origii, terminus proximalis:

a. subacuminate;

b. bifurcate or bicapitate, caput caudale from facies caudoventralis ulnae et caput craniale from facies cranialis ulnae, moderately;

x. noncomparable (Spheniscidae).

Note.—See: George and Berger (1966: 357); Cohn (1968).

Mm. (Meta)carpi et Manus

Note.—For reviews of the musculature of the manus in Aves and other Archosauria, see: Haines (1939, 1950), Dilkes (1999), and Meers (2003). Mm. interossea dorsalis et ventralis of Aves evidently are homologous to m. interosseus dorsalis digiti III et m. interosseus ventralis digiti II of Crocodylia, respectively (Meers 2003: fig. 18).

2622. M. interosseus dorsalis (volaris), corpus, status et magnitudo (**ordered**):

a. present, corpus at least of equal size to m. interosseus ventralis;

b. present, corpus distinctly smaller than that of m. interosseus ventralis;

c. vestigial or absent, typically associated with reduction of spatium intermetacarpale.

Note.—Where m. interosseus dorsalis is significantly reduced or (especially) where absent, ostium dorsalis of spatium intermetacarpale typically is correspondingly restricted compared to ostium ventralis of spatium intermetacarpale, former often effected by intrusions of lamina proximad and distad within spatium. The tendines of mm. interossea serve as raphes between opposing unipennate fibers within the spatium intermetacarpale, and both tendines insertii emerge distally to insert on facies dorsalis digiti majoris (Berger 1960a; George and Berger 1966).

See: Buri (1900); Burt (1930); Fisher (1946); Berger (1954, 1956a–b, 1957); George and Berger (1966: 377); Hudson et al. (1969); Vanden Berge (1970); Stegmann (1974, 1981); Maurer (1977); Maurer and Raikow (1981: table 2, character 28); McGowan (1982); Schreiweis (1982); Raikow et al. (1988: table 3); Meyers (1996).

2623. M. interosseus dorsalis (volaris), forma:

a. bipennate, tendo insertii arising as central raphe;

b. unipennate, corpus typically limited to margo cranialis spatii;

x. noncomparable by absence of musculus aut spatium (Dromaiidae, Casuariidae, Apterygidae, Upupidae, Phoeniculidae, Jyngidae, Picidae).

Note.—See: Buri (1900); Burt (1930); Fisher (1946); Berger (1954, 1956a–b, 1960a); Hudson et al. (1969); Vanden Berge (1970); Maurer (1977); Maurer and Raikow (1981: table 2, character 27); Meyers (1996).

2624. M. interosseus ventralis (palmaris), status:

a. present; **b.** absent.

Note.—"Normal" in penguins, unlike m. interosseus dorsalis (Schreiweis 1982). See: Buri (1900); Burt (1930); Fisher (1946); Berger (1954, 1960a); Hudson et al. (1969); Vanden Berge (1970); Maurer (1977); Stegmann (1981); McGowan (1982); Raikow et al. (1988: table 3); Meyers (1996).

2625. M. interosseus ventralis (palmaris), tendo insertii, bifurcatio at (facies dorsalis) margo proximalis phalangis proximalis digiti majoris resulting in (proximal) ramus tendinis insertii digiti minoris (**new term**) and (distal) ramus tendinis insertii digiti majoris (**new term**), status:

a. absent, tendo insertii single;

b. present, bifurcatio distalis—augmenting tendo insertii digiti majoris (**new term**) with ramus tendinis insertii digiti minoris (**new term**).

Note.—See: Berger (1956a–b, d); Tipton (1962); George and Berger (1966: 377); Maurer (1977); Rosser (1980); Livezey (2003).

2626. M. interosseus ventralis (palmaris), forma:

a. bipennate, tendo insertii arising as midline raphe;

b. unipennate, associated with reduction of spatium intermetacarpale;

x. noncomparable by absence of musculus et/eut spatium (Dromaiidae, Casuariidae, Apterygidae, Spheniscidae).

Note.—See: Buri (1900); Burt (1930); Fisher (1946); Berger (1954, 1956a–b, 1960a); Hudson et al. (1969); Vanden Berge (1970); Maurer (1977); Maurer and Raikow (1981: table 2, character 29); Meyers (1996).

2627. Mm. interosseus dorsalis (volaris) et ventralis (palmaris), both weakly to moderately developed proximally, typically bipennate, but failure of corpora to occlude spatium intermetacarpale distad, tendines insertii alone extending distad, status:

a. absent; **b.** present;

x. noncomparable (Dromaiidae, Casuariidae, Apterygidae, Spheniscidae).

Note.—This form of reduction of mm. interossea occurs in the absence of lamina ossea extending into spatium intermetacarpale. See: Maurer (1977).

2628. M. extensor brevis alulae (pollicus), status modalis:

a. present, variably substantial; **b.** absent.

Note.—Where present, as is typically the case (George and Berger 1966: 371–372), m. extensor brevis alulae comprises one or (rarely) more weakly distinguished fasciculi, its small size and position holding the potential for confusion with caput dorsale m. abductor alulae, itself prone to variation. E.g., see: Fisher and Goodman (1955: fig. 18), Hudson and Lanzillotti (1964: fig. 1), Owre (1967: fig. 2), Vanden Berge (1970: fig. 1), Hudson et al. (1972: fig. 1), Rosser (1980), Livezey (1990, 1992a–b, 2003), McKitrick (1991b: fig. 17). This confusion likely afflicted the misidentification of m. extensor brevis alulae as m. abductor alulae in Trochilidae by Zusi and Bentz (1984: fig. 16). See: Beddard (1884); Mitchell (1895); Buri (1900); Burt (1930); Fisher (1946); Berger (1954, 1956a–b, 1957, 1960a); Owre (1967); Vanden Berge (1970); Maurer (1977); Stegmann (1981); McGowan (1982); Schreiweis (1982); Raikow et al. (1988: table 3); Meyers (1996); Livezey (2003).

2629. M. abductor alulae (pollicus), status:

a. present; **b.** vestigial or absent.

Note.—This small musculus comprises one (Anhimidae, Pelecanidae) or two variably distinct capita origii (capita dorsale et ventrale). Evidently two capita are distinct in Cathartidae, whereas a single caput was reported for Ciconiiformes (Vanden Berge 1970: 325). Potential confusion exists between caput dorsale and adjacent m. extensor brevis alulae.

See: Buri (1900); Burt (1930); Fisher (1946); Hudson et al. (1969); Vanden Berge (1970); Maurer (1977); S. L. Olson and Feduccia (1980b: 24); McGowan (1982); Schreiweis (1982); Raikow et al. (1988: table 3); Livezey (2003).

2630. Aponeurosis carpo-alularis dorsalis (**new term**), status:

a. absent or weakly developed;

b. present, broad and robust.

Note.—In most taxa possessing apomorphic state, provisionally considered an elaboration of ligamentum ulnocarpo-metacarpale dorsale, and typically associated with hypertrophy of ligamentum obliquum alulae, the two structures restricting ventral (palmar) movement of digitus alulae.

2631. M. flexor alulae (pollicus), status:

a. present; **b.** vestigial or absent.

Note.—See: Buri (1900); Burt (1930); Fisher (1946); Hudson et al. (1969); Vanden Berge (1970); Maurer (1977), in which musculus not treated for Trogoniformes and Coraciiformes; Stegmann (1981); McGowan (1982); Schreiweis (1982); Raikow et al. (1988: table 3); Meyers (1996); G. Mayr and Ericson (2004: appendix I, character 83).

2632. M. adductor alulae (pollicus), status:

a. present; **b.** absent.

Note.—Musculus is notable for attachments on calami of remiges alulae, often sine situs ossis (Hoff 1966). See: Burt (1930); Fisher (1946); Berger (1954, 1956a–b, 1960a); Hudson et al. (1969); Vanden Berge (1970); Maurer (1977); Stegmann (1981); Schreiweis (1982); Raikow et al. (1988: table 3); Meyers (1996).

2633. M. abductor digiti majoris (indicus), status (**ordered**):

a. present, including corpus;

b. vestigial, principally or wholly tendinous;

c. absent.

Note.—Typically comprises capita dorsale (subject to confusion with caput dorsale m. extensor digiti majoris) et ventrale, tendines of both uniting with tendo insertii m. flexor alulae. See: Buri (1900); Burt (1930); Fisher (1946); Berger (1954, 1956a–b, 1960a); George and Berger (1966: 376); Hudson et al. (1969); Vanden Berge (1970); Maurer (1977); Stegmann (1981); McGowan (1982); Schreiweis (1982); Zusi and Bentz (1984); Raikow et al. (1988: table 3); Meyers (1996).

2634. M. abductor digiti majoris (indicus), caput accessoriale (**new term**), status (**ordered**):

a. absent;

b. present, weakly differentiated but distinctly augmented;

c. present, strongly developed, especially proximoventrally.

Note.—See: Burt (1930); Fisher (1946); Berger (1954, 1956a–b, 1960a); Hudson and Lanzillotti (1964: 30), in reference to "a small supernumerary belly…lying along the anterodorsal surface of the Abd. ind., opposite the pollex and sending a long, delicate tendon to the distal end of the Car. met."; Hudson et al. (1969); Maurer (1977); Stegmann (1981); Meyers (1996).

2635. M. flexor digiti minoris, status:

a. present; **b.** absent.

Note.—Condition plesiomorphic in Sphenisciformes (Schreiweis 1982). See: Buri (1900); Burt (1930); Fisher (1946); Berger (1954, 1956a–b, d, 1960a–b); Hudson and Lanzillotti (1964); Hudson et al. (1969); Vanden Berge (1970); Maurer (1977); Stegmann (1981); McGowan (1982); Raikow et al. (1988: table 3); Meyers (1996).

Musculi Membri Pelvici

Note.—Basal Theropoda—particularly as exemplified by *Tyrannosaurus* and characterized by Gatesy (1990), Hutchinson and Gatesy (2000), Hutchinson (2001a–b), Carrano and Hutchinson

(2002), and Hutchinson (2002)—provide critical insights into homologies and nomenclature; character states of pelvic musculature are elucidated in part by phylogenetically distant but anatomically complete archosaurian outgroups of Aves, especially Crocodylia (Rowe 1986). A major study of variation of musculi membri pelvici among Aves is Hudson (1937). Other publications of interest include: Hudson et al. (1972) on **Tinamiformes**; Gadow (1880), McGowan (1979), and Vanden Berge (1982) on **ratites**; Howell (1938), Fujioka (1962), Holmes (1963), and Gatesy (1999) on **Galliformes**; Stolpe (1932, 1935a–b), A. H. Miller (1937), Raikow (1970), Weinstein et al. (1984), and Schulin (1987) on **Anseriformes**; Wilcox (1952) on **Gaviiformes**; Schreiweis (1982) on **Sphenisciformes**; Klemm (1969) on **Procellariiformes**; Owre (1967) on **Pelecaniformes**; Vanden Berge (1976) and S. L. Olson and Feduccia (1980b) on **Ciconiiformes**; Beddard (1890b, 1893a), Fisher and Goodman (1955), and Berger (1956a) on **Gruiformes**; T. H. Fleming (1966), Hudson et al. (1969), S. L. Olson and Feduccia (1980b), and M. McKitrick (pers. comm.) on **Charadriiformes**; Fisher (1946), Hudson (1948), Berger (1956b), and Jollie (1977a–c) on **Falconiformes**; Hoff (1966) on **Strigiformes**; Berger (1952, 1953a, 1955b, 1960b), and Sych (1988) on **Cuculiformes** and *Opisthocomus*; Berman (1984) on **Psittaciformes**; Cracraft (1971c) on **Columbiformes**; Hoff (1966) on **Caprimulgiformes**; Zusi and Bentz (1984) on **Apodiformes**; Berman and Raikow (1982) on **Coliiformes**; Maurer and Raikow (1981) on **Coraciiformes**; Burt (1930), Scharnke (1930), Goodge (1972), Swierczewski and Raikow (1981), and Berman et al. (1998) on **Piciformes**; Leach (1914), Berger (1968), Raikow (1976, 1977b, 1978, 1985b), Bentz (1979), Raikow et al. (1979, 1993), McKitrick (1985b, 1986), Berman et al. (1990), Rudge and Raikow (1992), and Verstappen et al. (1998) on **Passeriformes**.

2636. Musculi membri pelvici, ossificatio(nes) tendinorum insertii, status et musculi (**ordered**):

a. absent or limited to sectio distalis tendinis m. flexor digitorum longus;

b. present, throughout tendines mm. flexores digitorum longus et/aut hallucis longus;

c. present, extensive in several or most musculi pelvici.

Note.—Many especially conspicuous in large-bodied taxa, a bias most influential in assessments based on skeletal specimens. See: Fujioka (1962), regarding origiones et insertiones musculorum pelvici; Bledsoe et al. (1993), regarding Passeriformes; Raikow (1994: table 2, character 27); Vanden Berge and Storer (1995: table 7); Livezey (1998b: appendix A, character 362); Patak and Baldwin (1998); Hutchinson (2002).

Mm. Iliotibiales

2637. M. iliotibialis cranialis, divisio (septum) longitudinalis corporis (**new term**)—i.e., divisio musculi proximal to insertio, status:

a. absent; **b.** present.

Note.—Synonymous with m. iliotibialis 1 of Carrano and Hutchinson (2002: table 1). Present also in *Recurvirostra*. S. L. Olson and Feduccia (1980a) confused this longitudinal division of m. iliotibialis cranialis with the coincidence of m. iliotibialis medialis.

2638. M. iliotibialis cranialis, origo, extension onto margo caudoventralis ala preacetabularis ilii, status:

a. absent; **b.** present.

Note.—See: Swierczewski and Raikow (1981: character 1).

2639. M. iliotibialis lateralis, pars preacetabularis, status:

a. present; **b.** vestigial or absent.

Note.—Synonymous with m. iliotibialis 2 et 3 of Carrano and Hutchinson (2002: table 1). See: McKitrick (1991a: appendix 1, character 2); McKitrick (1992: appendix 1, character 2).

2640. M. iliotibialis lateralis, pars acetabularis, status et forma (**ordered**):

a. present, corpus; **b.** present, aponeurosis;
c. absent.

Note.—See: Hoff (1966); Maurer and Raikow (1981: table 2, character 30); Berman and Raikow (1982); Zusi and Bentz (1984: 44); McKitrick (1991a: appendix 1, character 3); McKitrick (1992: appendix 1, character 3); G. Mayr (2003b: appendices I–II, character 24); G. Mayr and Clarke (2003: appendix A, character 115); Dyke and van Tuinen (2004: appendix 1, character 84); G. Mayr (2004a: appendix 1: character 62).

2641. M. iliotibialis lateralis, pars postacetabularis, status et forma (**ordered**):

a. present, robust; **b.** present, reduced;
c. absent.

Note.—See: Hoff (1966); Bentz (1979: table 2); Maurer and Raikow (1981: table 2, character 31, part); Swierczewski and Raikow (1981: character 5); Berman and Raikow (1982); Schreiweis (1982); Raikow (1982: table 1; character 2); Zusi and Bentz (1984: 44); McKitrick (1991a: appendix 1, character 4); McKitrick (1992: appendix 1, character 4); G. Mayr (2003b: appendices I–II, character 25).

2642. M. iliotibialis lateralis, pars postacetabularis, insertio cruris (**new term**), status:

a. absent; **b.** present.

Note.—Accessory insertio extensive and caudal on mm. flexores digitorum cruris, limited to *Podiceps* (and possibly to *Aechmophorus*), hence strictly polymorphic for Podicipedidae. See description for *Podiceps nigricollis* in Hudson (1937: 19) and for *P.*

major in Beddard (1896a) under "m. glutaeus maximus."

2643. M. iliotibialis medialis, status:
a. absent; **b.** present.
Note.—Originally described by Weldon (1883: 648–649) and Gadow (1891a: 150) as caput of "m. sartorius," Vanden Berge (1970: 334) referred to it as "an extra muscle in the thigh associated with the sartorius…occurring certainly in Phoenicopteridae." S. L. Olson and Feduccia (1980b) erroneously reported its presence in *Cladorhynchus*. This subpart is comparatively rare in taxonomic distribution, and shares a tendo insertii with other partes complexus m. iliotibialis (Vanden Berge and Zweers 1993: annotation 101). See: McKitrick (1991a: appendix 1, character 1); McKitrick (1992: appendix 1, character 1); G. Mayr (2004a: appendix 1: character 61).

M. Supinator Cruris

2644. M. supinator cruris (**new term**), status:
a. absent; **b.** present.
Note.—Evidently unique to Gaviiformes. Not mentioned by Wilcox (1952); however, a possible reference to this muscle in *Gavia immer* was given by Coues (1863: 167, 171) in regard to "m. rectus femoris," and it was illustrated but not labelled by Gadow and Selenka (1891: fig. 3, pl. 18A). The muscle originates from the pelvis immediately caudal to m. iliotibialis lateralis and inserts on aponeuroses insertii m. gastrocnemius.

M. Iliofibularis

2645. M. iliofibularis, insertio, forma:
a. entirely or principally by narrow tendo;
b. broad, flat tendo.
Note.—*Heliopais* (R. Zusi, pers. comm.) and possibly *Heliornis* characterized by state "a," whereas *Podica* possesses an insertio comprising a broad, flat tendo distal to the primary narrow tendo, supplemented by a flat, fleshy slip from the corpus m. iliofibularis to that of m. gastrocnemius lateralis (Beddard 1890a–c).

2646. Ansa m. iliofibularis, status et numerus ligamentorum (**unordered**):
a. present, two or three;
b. present, single; **c.** absent.
Note.—See: Schreiweis (1982); McKitrick (1991a: appendix 1, character 10); McKitrick (1992: appendix 1, character 10).

M. Ambiens

2647. M. ambiens, status:
a. present; **b.** absent.
Note.—Polymorphism indicated for *Chlidonias* evident by inclusion of other Sternini. See: George and Berger (1966: 421); Hudson et al. (1969); Cracraft (1981a: 693); Maurer and Raikow (1981: table 2, character 45); Raikow (1982: character 11); Schreiweis (1982); Strauch (1985: table 3, character H12); Cracraft (1988: series XVII, character 1); McKitrick (1991a: appendix 1, character 29); McKitrick (1992: appendix 1, character 29); Vanden Berge and Zweers (1993: 218, annotation 103); G. Mayr (2003a: appendix I, character 42); G. Mayr and Clarke (2003: appendix A, character 125); G. Mayr et al. (2003: appendix 1, character 74); Dyke and van Tuinen (2004: appendix 1, character 94); G. Mayr (2004a: appendix 1: character 65); G. Mayr (2004b: appendix 1, character 51); G. Mayr (2004c: appendix I, character 50); G. Mayr (2005b: appendix A, character 47).

2648. M. ambiens, origiones ossium ilii et/aut pubici, situs:
a. corpus ossis ilii, tuberculum preacetabulare;
b. corpora ossium ilii et pubici, tuberculum preacetabulare.
Note.—See: Schulin (1987: table 1); McKitrick (1991a: appendix 1, character 30); McKitrick (1992: appendix 1, character 30); Livezey (1997a: appendix 1, character 121; *corrigenda*, Livezey 1998a); G. Mayr and Clarke (2003: appendix A, character 126); Dyke and van Tuinen (2004: appendix 1, character 95); G. Mayr (2004d: appendix I, character 50); G. Mayr (2005a: appendix 1, character 51); G. Mayr (2005b: appendix A, character 47).

Mm. Iliotrochanterici

2649. M. iliotrochantericus caudalis, forma:
a. robust; **b.** reduced.
Note.—M. iliotrochantericus caudalis of Aves is synonymous with m. iliofemoralis of Crocodylia (Hutchinson 2001b: table 1). See: McKitrick (1991a: appendix 1, character 5); McKitrick (1992: appendix 1, character 5).

2650. M. iliotrochantericus caudalis, origo pelvici, situs:
a. crista dorsolateralis ilii;
b. crista spinosa synsacri.
Note.—M. iliotrochantericus caudalis of Aves is synonymous with m. iliofemoralis of Crocodylia (Hutchinson 2001b: table 1). See: Maurer and Raikow (1981: table 2, character 32).

Mm. Iliofemoralis

Note.—Musculi traditionally included within mm. iliofemoralis complex not conformal with structural homologies, and even those included among iliofemoralis currently are comparatively unrelated. See: McKitrick (1991a).

2651. M. iliofemoralis externus, status et forma (**ordered**):
a. present, well developed;
b. present, diminutive; **c.** absent.
Note.—M. iliofemoralis externus of Aves is synonymous with m. iliofemoralis of Crocodylia (Hutchinson 2001b: table 1). See: Hoff (1966); Hudson et al. (1972); Raikow et al. (1979); concerning "reestablishment" (atavistic reversal) in basal Passeriformes; Maurer and Raikow (1981: table 2, character 46); Raikow (1982: character 10); Raikow (1985b: table 2, character 1); Strauch (1985: table 3, character H13); Cracraft (1988: series XVII, character 2); McKitrick (1991a: appendix 1, character 7); McKitrick (1992: appendix 1, character 7); G. Mayr (2003b: appendices I–II, character 26); G. Mayr and Clarke (2003: appendix A, character 116); G. Mayr et al. (2003: appendix 1, character 75); Dyke and van Tuinen (2004: appendix 1, character 85); G. Mayr (2004d: appendix I, character 51); G. Mayr (2005a: appendix 1, character 52).

2652. M. iliofemoralis internus, status:
a. present; **b.** absent.
Note.—M. iliofemoralis partes internus of Aves is synonymous with m. pubo-ischio-femoralis 1 (part) of Crocodylia (Hutchinson 2001b: table 1). See: Swierczewski and Raikow (1981: character 20); Zusi and Bentz (1984: 44); Cracraft (1988: series XIV, character 1); Prum (1988: character 17); McKitrick (1991a: appendix 1, character 27); McKitrick (1992: appendix 1, character 27); G. Mayr and Clarke (2003: appendix A, character 123); Dyke and van Tuinen (2004: appendix 1, character 92).

2653. M. iliofemoralis internus, status et forma generalis (**ordered**):
a. present, fusiform;
b. present, short and broad; **c.** absent.
Note.—M. iliofemoralis partes internus of Aves is synonymous with m. pubo-ischio-femoralis 1 (part) of Crocodylia (Hutchinson 2001b: table 1). See: McKitrick (1991a: appendix 1, character 28); McKitrick (1992: appendix 1, character 28).

Mm. Femorotibiales

2654. M. femorotibialis medialis (internus), extensive divisio (septum) longitudinalis musculi (**new term**), status et forma (**ordered**):
a. absent, musculus comprises single caput et tendo;
b. present, musculus comprises two capita et one tendo;
c. present, musculus comprises two capita et tendines.
Note.—M. femorotibialis intermedius (medialis) of Aves is synonymous with m. femorotibialis internus (part) of Crocodylia (Hutchinson 2001a: table 1). See: Swierczewski and Raikow (1981: character 9), with respect to "two bellies"; Raikow (1985b: table 2, character 3), with respect to one or two capita et tendines of this muscle in basal passeriforms; McKitrick (1991a: appendix 1, character 9), under name m. femorotibialis internus; McKitrick (1992: appendix 1, character 9); Schreiweis (1982).

Mm. Flexores Cruris

Note.—Phylogeny of mm. flexores cruris (mm. semitendinosus et semimembranosus) was attempted by McMurrich (1905). Homologies with non-avialan musculi inferred by Hutchinson (2001a–b, 2002).

2655. M. flexor cruris lateralis (semitendinosus), pars pelvica, status:
a. present; **b.** absent.
Note.—Synonymous with m. flexor tibialis externus. See: Prum (1988: character 119); McKitrick (1991a: appendix 1, character 13); McKitrick (1992: appendix 1, character 13); G. Mayr and Clarke (2003: appendix A, character 119); G. Mayr and Clarke (2003: appendix A, character 118); G. Mayr et al. (2003: appendix 1, character 76); Dyke and van Tuinen (2004: appendix 1, character 87).

2656. M. flexor cruris lateralis (semitendinosus), pars pelvica, insertio, situs (**unordered**):
a. m. gastrocnemius (pars intermedia aut medialis) et os tibia;
b. os tibia only;
c. m. gastrocnemius (pars intermedia aut medialis) only.
Note.—Synonymous with m. flexor tibialis externus. Variation evident within Picidae. See: Prum (1988: character 119); McKitrick (1991a: appendix 1, character 13); McKitrick (1992: appendix 1, character 13); G. Mayr and Clarke (2003: appendix A, characters 118–119); G. Mayr et al. (2003: appendix 1, character 76); Dyke and van Tuinen (2004: appendix 1, character 87).

2657. M. flexor cruris lateralis (semitendinosus), pars accessoria femoris (**new term**), status:
a. present and wide;
b. vestigial or absent.
Note.—Variation evident within Larini and Galbulidae. See: Goodge (1972: 71); Maurer and Raikow (1981: table 2, character 33); Swierczewski and Raikow (1981: character 11); Schreiweis (1982); Zusi and Bentz (1984: 44); Schulin (1987: table 1); McKitrick (1991a: appendix 1, characters 12 and 14);

McKitrick (1992: appendix 1, characters 12 and 14); Raikow (1994: table 2, character 25); Livezey (1997a: appendix 1, character 120; *corrigenda*, Livezey 1998a); G. Mayr (2003a: appendix I, character 44); G. Mayr and Clarke (2003: appendix A, character 118); G. Mayr et al. (2003: appendix 1, character 77); Dyke and van Tuinen (2004: appendix 1, character 88); G. Mayr (2004b: appendix 1, character 52).

2658. M. flexor cruris medialis (semimembranosus), status:
a. present; **b.** absent.
Note.—Synonymous with m. flexor tibialis externus 3 (Carrano and Hutchinson 2002: table 1). See: Schulin (1987: table 1); Livezey (1997a: table 4).

2659. Mm. flexores crurales lateralis (semitendinosus) et medialis (semimembranosus), tendines insertiorum, forma:
a. fused or coincident; **b.** disjunct;
x. noncomparable by absence of musculus (Podicipedidae).
Note.—See: Goodge (1972: 71); Swierczewski and Raikow (1981: character 12); Raikow (1987: table 1; character 8), regarding conjoinment of tendines insertiorum; McKitrick (1991a: appendix 1, character 18); McKitrick (1992: appendix 1, character 18); Raikow (1994: table 2, character 9).

2660. M. flexor cruris medialis (semimembranosus), divisio corporis (**new term**), status:
a. absent, unipartite; **b.** present, bipartite.
Note.—See: McKitrick (1991a: appendix 1, character 17); McKitrick (1992: appendix 1, character 17).

M. Caudofemoralis

2661. M. caudofemoralis, pars caudalis, status et forma (**ordered**):
a. present, well developed;
b. present, poorly developed;
c. absent.
Note.—Corresponds to factor "A" in formula of George and Berger (1966: table IX.1). Synonymous with m. caudofemoralis longus of Crocodylia (Carrano and Hutchinson 2002: table 1). See: Gadow (1893); Beddard (1898a); Mitchell (1915); Tipton (1962); Hudson et al. (1969); McKitrick (1991a: appendix 1, character 15); McKitrick (1992: appendix 1, character 15); G. Mayr and Clarke (2003: appendix A, character 120); Dyke and van Tuinen (2004: appendix 1, character 89); G. Mayr (2004a: appendix 1: character 63); G. Mayr and Ericson (2004: appendix I, character 84).

2662. M. caudofemoralis, pars pelvica, status et forma (**ordered**):
a. present, extremely large;
b. present, small to moderately large;
c. absent.
Note.—Synonymous with factor "B" in formula of George and Berger (1966: table IX.1), m. caudofemoralis brevis, and m. iliofemoralis, pars pelvica (McKitrick 1991a: 15). Character essentially refers to condition in which origo partis pelvica is discernable from origo partis caudalis. M. caudofemoralis pars pelvica of Aves is synonymous with m. caudofemoralis brevis of Crocodylia (Hutchinson 2001b: table 1).
See: Gadow (1893); Beddard (1898a); Mitchell (1915); Hudson et al. (1969); Hudson et al. (1972: 248), under m. piriformis; Raikow (1982: character 12); Schreiweis (1982); McKitrick (1991a: appendix 1, character 16); McKitrick (1992: appendix 1, character 16); Vanden Berge and Zweers (1993: 220, annotation 110); G. Mayr (2003a: appendix I, character 45); G. Mayr and Clarke (2003: appendix A, character 121); G. Mayr et al. (2003: appendix 1, character 78); Dyke and van Tuinen (2004: appendix 1, character 90); G. Mayr (2004a: appendix 1: character 64); G. Mayr (2004b: appendix 1, character 53); G. Mayr (2004d: appendix I, character 52); G. Mayr and Ericson (2004: appendix I, character 85); G. Mayr (2005a: appendix 1, character 53).

2663. M. caudofemoralis, pars pelvica, corporis centralis, forma:
a. fibrous; **b.** extensively aponeurotic;
x. noncomparable by absence of musculus or pars thereof (see status).
Note.—See: McKitrick (pers. comm.).

2664. M. caudofemoralis, pars pelvica, caput craniale (**new term**), status:
a. absent; **b.** present;
x. noncomparable by absence of musculus or pars thereof (see status).
Note.—Caput partitioned from corpus proprius by nervus sciaticus et arteria. See: Garrod (1873b), Gadow (1880), Hudson et al. (1972), and McGowan (1979).

M. Obturatorius

2665. M. obturatorius medialis, corpus, forma:
a. small, oval; **b.** large, triangular.
Note.—M. obturatorius medialis of Aves is synonymous with m. pubo-ischio-femoralis externus pars 2 of Crocodylia (Hutchinson 2001b: table 1). See: McKitrick (1991a: appendix 1, character 25); McKitrick (1992: appendix 1, character 25).

2666. M. obturatorius medialis, capitorum origii et tendines insertii femoris, numerus:
a. one; **b.** two.
Note.—M. obturatorius medialis of Aves is synonymous with m. pubo-ischio-femoralis externus

pars 2 of Crocodylia (Hutchinson 2001b: table 1) and with "obturator, pars postica of Holmes (1963). See: McKitrick (1991a: appendix 1, characters 23–24); McKitrick (1992: appendix 1, characters 23–24).

2667. M. obturatorius medialis, origo, caput fossae renalis pelvici (**new term**), status:
a. absent; **b.** present, typically prominent.
Note.—M. obturatorius medialis of Aves is synonymous with m. pubo-ischio-femoralis externus pars 2 of Crocodylia (Hutchinson 2001b: table 1).

M. Pubo-ischio-femoralis

2668. M. pubo-ischio-femoralis, divisio partorum corporis, status:
a. present, partes cranialis (lateralis) et caudalis (medialis) delimited thereby;
b. absent, united as single corpus.
Note.—Mm. pubo-ischio-femorales cranialis (lateralis) et caudalis (medialis) are synonymous with mm. adductores femoris (partes 1 et 2) of Crocodylia, respectively (Hutchinson 2001b: table 1). See: Goodge (1972: 72, under "Adductor longus et brevis"; Cracraft (1981a: 702); Swierczewski and Raikow (1981: characters 15–16); Schreiweis (1982); Zusi and Bentz (1984: 43); Cracraft (1988: series XII, character 2; series XX, character 6); McKitrick (1991a: appendix 1, character 19), in which names used were partes cranialis et caudalis; McKitrick (1992: appendix 1, character 19).

2669. M. pubo-ischio-femoralis, capita origii, axis majoris delimitans:
a. lateromedial; **b.** craniocaudal;
x. noncomparable by absence of divisio capitis (see status).

M. Tibialis Cranialis

2670. M. tibialis cranialis, tendines insertii, numerus modalis:
a. one;
b. two, cum bifurcatio tendinis et capita femorale et tibiale.
Note.—Synonymous with m. tibialis anterior (Hutchinson and Carrano 2002: table 1). See: Schreiweis (1982: 30) in reference to "very weak branch laterally to metatarsus II"; McKitrick (1991a: appendix 1, character 37); McKitrick (1992: appendix 1, character 37). Does not include small ramus tendinis from tendo majoris that inserts variously as described by Hudson (1937: 30).

2671. M. tibialis cranialis, divisio capitorum femorale et tibiale, status:
a. present; **b.** absent.
Note.—See: Hoff (1966); Vanden Berge and Zweers (1993).

Mm. Extensores Digitorum

2672. M. extensor digitorum longus, capita origiorum, numerus:
a. one, caput tibiale;
b. two, caput tibiale et caput fibulare.
Note.—Synonymous with m. extensor digitorum longus (Hutchinson and Carrano 2002: table 1). See: Hudson (1937); Zusi and Bentz (1984: 43); McKitrick (1991a: appendix 1, character 38); McKitrick (1992: appendix 1, character 38).

2673. M. extensor digitorum longus, tendo hallucis (**new term**), status:
a. absent; **b.** present.
Note.—See: Berman and Raikow (1982); Berman (1984); McKitrick (1991a: appendix 1, character 39); McKitrick (1992: appendix 1, character 39); G. Mayr and Clarke (2003: appendix A, character 128); G. Mayr et al. (2003: appendix 1, character 85); Dyke and van Tuinen (2004: appendix 1, character 96).

2674. M. extensor digitorum brevis (**new term**), status:
a. absent; **b.** present.
Note.—In *Hemiprocne,* this muscle originates from facies dorsalis tarsometatarsi adjacent to insertio m. tibialis cranialis and (proximad) deep to tendo m. extensor digitorum longus. Insertion is on the plantar surfaces of rami tendinis m. extensor digitorum longus to digiti II, III, and IV, immediately distal to the trifurcation. The two "extra extensors" on the tarsometatarsus of *Nyctibius* described by Hoff (1966) may not be homologous with this muscle, as details reported by Hoff (1966: 87–88, figs. 12–14) of their tendines insertii are somewhat conflicting and incomplete. In retrospect, they could have been coded as muscles unique to *Nyctibius*, but further study of the "extra extensors" is required.

Mm. Fibulares (Peronei)

2675. M. fibularis longus, status et forma (**ordered**):
a. present, well developed;
b. present, poorly developed;
c. absent.
Note.—See: Beddard (1886a); Mitchell (1913a); Goodge (1972: 72); Maurer and Raikow (1981: table 2, character 42); Swierczewski and Raikow (1981: character 23); Zusi and Bentz (1984: 44); McKitrick (1991a: appendix 1, character 40); McKitrick (1992: appendix 1, character 40); G. Mayr (2002b: 91–92); G. Mayr et al. (2003: appendix 1, character 79).

2676. M. fibularis longus, origo, forma capitorum (**unordered**):
a. both capita tibiale et fibulare;
b. caput fibulare only;
c. caput tibiale and underlying musculi;
x. noncomparable by absence of m. fibularis longus (see status).
Note.—See: McKitrick (1991a: appendix 1, character 41); McKitrick (1992: appendix 1, character 41).

2677. M. fibularis longus, tendo insertii, ramus m. flexor perforatus tendinis digiti III (**new term**), status:
a. present; **b.** absent;
x. noncomparable by absence of m. fibularis longus (see status).
Note.—See: Maurer and Raikow (1981: table 2, character 41); McKitrick (1991a: appendix 1, character 42); McKitrick (1992: appendix 1, character 42); G. Mayr and Clarke (2003: appendix A, character 130); Dyke and van Tuinen (2004: appendix 1, character 97).

2678. M. fibularis brevis, status et forma (**ordered**):
a. present, well developed;
b. present, weakly developed;
c. absent.
Note.—See: Mitchell (1913a); Cracraft (1981a: 693); Schreiweis (1982); Cracraft (1988: series XIII, character 1); McKitrick (1991a: appendix 1, character 43); McKitrick (1992: appendix 1, character 43).

M. Gastrocnemius

2679. M. gastrocnemius, pars lateralis, origo, numerus capitorum:
a. one; **b.** two.
Note.—M. gastrocnemius partes lateralis et intermedia collectively synonymous with m. gastrocnemius externus (Carrano and Hutchinson 2002: table 1). Includes the "fourth head of origin" of Vanden Berge (1970: 344). See: Hudson et al. (1969); Raikow (1970, 1978, 1987); Bentz (1979: table 2); Maurer and Raikow (1981: table 2, character 39); Strauch (1985: table 3, character H15) regarding "extra head from tibia"; Cracraft (1988: series XII, character 1); McKitrick (1991a: appendix 1, character 32); McKitrick (1992: appendix 1, character 32); G. Mayr (2003a: appendix I, character 43); G. Mayr (2004a: appendix 1: character 66), with respect to "fourth head."

2680. M. gastrocnemius, origo tendinis m. femorotibialis intermedius (**new term**), status et forma (**ordered**):
a. present, extensive;
b. present, moderate; **c.** absent.
Note.—M. gastrocnemius pars medialis synonymous with m. gastrocnemius internus (Hutchinson and Carrano 2002: table 1). See: Raikow (1985b: table 3, character 7); McKitrick (1991a: appendix 1, character 33); McKitrick (1992: appendix 1, character 33).

2681. M. gastrocnemius, pars medialis, origo, numerus capitorum:
a. one; **b.** two.
Note.—See: McKitrick (1991a: appendix 1, character 34); McKitrick (1992: appendix 1, character 33); G. Mayr and Clarke (2003: appendix A, character 127).

2682. M. gastrocnemius, pars intermedia, status et forma (**ordered**):
a. present, well developed;
b. present, weakly developed; **c.** absent.
Note.—Pars intermedia is conjoined with m. flexor cruris lateralis, pars accessoria femoris in some Procellariiformes (Klemm 1969) and Sterninae. See: McKitrick (1991a: appendix 1, character 34); McKitrick (1992: appendix 1, character 33); G. Mayr and Clarke (2003: appendix A, character 127).

2683. M. gastrocnemius, pars intermedia, origo, numerus capitorum:
a. one; **b.** two.
Note.—Polymorphism indicated within *Grus*. Includes the "fourth head" described for *Tyto* by Hoff (1966: 74). See: Fisher and Goodman (1955); McKitrick (1991a: appendix 1, character 34); McKitrick (1992: appendix 1, character 33); G. Mayr and Clarke (2003: appendix A, character 127).

M. Plantaris

2684. M. plantaris, status et forma (**ordered**):
a. absent; **b.** present, abbreviate;
c. present, elongate.
Note.—See: Hudson et al. (1969); Bentz (1979: table 2); Maurer and Raikow (1981: table 2, character 44); Swierczewski and Raikow (1981: character 32); Zusi and Bentz (1984: 44); Strauch (1985: table 3, character H17); McKitrick (1991a: appendix 1, characters 49–50); McKitrick (1992: appendix 1, characters 49–50); G. Mayr and Clarke (2003: appendix A, character 133); Dyke and van Tuinen (2004: appendix 1, character 100).

M. Popliteus

2685. M. popliteus, status:
a. present; **b.** absent.
Note.—See: Hoff (1966); Hudson et al. (1972); Maurer and Raikow (1981: table 2, character 43); Swierczewski and Raikow (1981: character 33); McKitrick (1991a: appendix 1, character 57); McKitrick

(1992: appendix 1, character 57); G. Mayr (2003b: appendices I–II, character 27); G. Mayr and Clarke (2003: appendix A, character 137); G. Mayr et al. (2003: appendix 1, character 80); Dyke and van Tuinen (2004: appendix 1, character 103).

Musculi Tarsometatarsi et Digitorum Pedis

Note.—Myological elements pertaining to various proposals of "types" of *Sehnenhalteren* (J. Steinbacher 1935): (*i*) m. flexor perforans et perforatus digiti II, (*ii*) m. flexor perforans et perforatus digiti III, (*iii*) m. flexor perforans et perforatus digiti IV, (*iv*) m. flexor perforatus digiti II, (*v*) m. flexor perforatus digiti III, (*vi*) m. flexor perforatus digiti IV, (*vii*) m. flexor hallucis longus, (*viii*) m. flexor digitorum longus, (*ix*) m. extensor hallucis longus (partes proximalis et distalis), (*x*) m. flexor hallucis brevis, (*xi*) m. abductor digiti II, (*xii*) m. adductor digiti II, (*xiii*) m. extensor proporius digiti III, (*xv*) m. extensor brevis digiti IV, (*xvi*) m. abductor digiti IV, (*xvii*) m. adductor digiti IV, et (*xviii*) vinculum tendinum flexorum.

Mm. Flexores (Perforantes et) Perforati Digitorum

Note.—See: Vanden Berge and Zweers (1993: annotation 121).

2686. M. flexor perforatus digiti II, status (**ordered**):
a. well developed; **b.** vestigial;
c. absent.
Note.—See: Storer (1960b, 2000); Swierczewski and Raikow (1981: character 27); Zusi and Bentz (1984: 44); Prum (1988: characters 6–7).

2687. M. flexor perforatus digiti II, situs superficio-profundus:
a. deep; **b.** superficial.
Note.—See: McKitrick (1991a: appendix 1, character 48); McKitrick (1992: appendix 1, character 48).

2688. M. flexor perforans et perforatus digiti II, situs relative to m. flexor perforans et perforatus digiti III:
a. does not overlap or conceal;
b. overlaps and conceals;
x. noncomparable by absence of musculus (*Struthio*).
Note.—See: McKitrick (1991a: appendix 1, character 45); McKitrick (1992: appendix 1, character 45).

2689. M. flexor perforans et perforatus digiti III, vinculum tendinis flexoris to m. flexor perforans digiti III, status:
a. present; **b.** absent.
Note.—See: Hudson (1937); Maurer and Raikow (1981: table 2, character 52); Schreiweis (1982: 30); Raikow (1985a–b, 1987); McKitrick (1991a: appendix 1, character 44); McKitrick (1992: appendix 1, character 44); Vanden Berge and Zweers (1993: 222, annotation 122); G. Mayr and Clarke (2003: appendix A, character 131); G. Mayr et al. (2003: appendix 1, character 81); Dyke and van Tuinen (2004: appendix 1, character 98).

M. Flexor Hallucis Longus

2690. M. flexor hallucis longus, tendo hallucis (**new term**), forma (**ordered**):
a. absent; **b.** rudimentary;
c. well developed.
Note.—See: Schreiweis (1982); McKitrick (1985a: fig. 16); McKitrick (1991a: appendix 1, character 51); McKitrick (1992: appendix 1, character 51); G. Mayr (2002a: legend fig. 9, node 5, character 7); G. Mayr and Clarke (2003: appendix A, character 134); G. Mayr et al. (2003: appendix 1, character 83); G. Mayr (2004c: appendix I, character 54).

2691. M. flexor hallucis longus, numerus capitorum (**ordered**):
a. one; **b.** two; **c.** three;
x. noncomparable by absence of musculus (ratites).
Note.—See: Swierczewski and Raikow (1981: character 36); Cracraft (1988: series XIV, character 4; series XIX, character 2); McKitrick (1991a: appendix 1, character 53); McKitrick (1992: appendix 1, character 53); G. Mayr and Clarke (2003: appendix A, character 136); G. Mayr et al. (2003: appendix 1, character 82); Dyke and van Tuinen (2004: appendix 1, character 102); G. Mayr (2004c: appendix I, character 53).

M. Flexor Digitorum Longus

2692. M. flexor digitorum longus, numerus capitorum:
a. two, caput femoris lacking;
b. three, caput femoris present.
Note.—See: McKitrick (1991a: appendix 1, character 54); McKitrick (1992: appendix 1, character 54).

2693. M. flexor digitorum longus, capita tibiale et fibulare, interposition by tendo insertii m. iliofibularis, status:
a. absent; **b.** present.
Note.—See: Schulin (1987: table 1), potentially confusing in reference to "additional external head lateral to biceps tendon" in "m. flex. dig. long."

2694. M. flexor digitorum longus, corpus, forma (**unordered**):

a. moderately developed, long;
b. distinctly enlarged, elongate;
c. extremely thick, truncate.

Note.—See: McKitrick (1991a: appendix 1, character 55); McKitrick (1992: appendix 1, character 55).

2695. M. flexor digitorum longus, corpus, situs superficio-profundus:

a. deep; **b.** superficial.

Note.—See: McKitrick (1991a: appendix 1, character 56); McKitrick (1992: appendix 1, character 56).

Tendines Plantares Digitorum Pedis

Note.—Status, forma, et situs of m. flexor digitorum longus, vinculum tendinorum flexores et tendines insertii—tendines plantares or "plantar tendons"—have been subjected to significant study, most summarized within the context of multifactorial, essentially phenetic "types":

- **typus I**—tendo m. flexor hallucis longus joining tendo m. flexor digitorum longus well proximad to trifurcatio, vinculum absent;
- **typus II–IV**—tendines mm. flexor hallucis longus (if hallux present) et m. flexor digitorum longus united variably extensively to form single tendo, with trifurcatio distad corresponding to insertiones digitorum II–IV pedis, vinculum absent;
- **typus V**—tendo of m. flexor hallucis longus (*i*) united distally either to ramus of tendo m. flexor digitorum longus to digitus III by vinculum, or (*ii*) united throughout lengths without vinculum;
- **typus VI**—tendo m. flexor hallucis longus bifurcates proximad to extremitas distalis tarsometatarsi, forming ramus digiti IV pedis and (by subsequent bifurcatio) rami tendinis digitorum I et II pedis, vinculum present;
- **typus VII**—tendo m. flexor hallucis longus inserts only on digitus I pedis, with tendo m. flexor digitorum longus having trifurcatio forming insertiones digitorum II–IV pedis, vinculum absent;
- **typus VIII**—tendo m. flexor hallucis longus (with bifurcatio distad) forming tendines insertii digitorum I et II (hallux), uniting proximal to bifurcatio m. flexor digitorum longus to digiti III et IV.

"Types" presented above are based on summaries by Raikow (1985a: fig. 2.33) and Vanden Berge and Storer (1995: table 7), and exclude minor, positional variants of the digiti pedis listed by some authors ("types" IX and X). Typological groups of this kind explicitly combine several (at least partly) independent characters manifesting contradictory phylogenetic patterns. These traditional "types" typically present difficulties in phylogenetic analysis, especially conflicting scoring and semiredundancy. Accordingly, we distilled the minimal, phylogenetically informative characters subsumed within the traditional "types" into four largely independent characters that collectively capture most of the phylogenetic signal included within the traditional multifactorial types while permitting informative signals of each included feature to be encoded separately.

Deep plantar tendons of birds were treated by comparatively traditional protocols by: Garrod (1875a); Sundevall (1886); Gadow and Selenka (1891); Gadow (1892); F. A. Lucas (1895); Mitchell (1901a: fig. 85); Hudson (1937, 1948); Compton (1938); George and Berger (1966); Hoff (1966); Owre (1967); Hudson et al. (1969); Vanden Berge (1970); Vanden Berge and Zweers (1993: annotation 121; fig. 6.19). See: Cracraft (1971d: fig. 2), depicting hypothetical transition from (plesiomorphic) Coraciiformes to (apomorphic) Trogoniformes; Sibley and Ahlquist (1972: table 2); Jollie (1977a–c); Maurer (1977: table 13, figs. 53–55, 72), detailing arrangements of tendines plantares digitorum pedis for Coraciiformes and allies, and indicating that "typus V" may comprise a four-state grade within this assemblage; Swierczewski (1977); Bentz (1979: table 2); Maurer and Raikow (1981: table 2, characters 53–55, and 57); S. F. Simpson and Cracraft (1981: character 1); Swierczewski and Raikow (1981: character 35); Raikow (1982: character 18); Schreiweis (1982); Berman (1984); Zusi and Bentz (1984: 43–44); Raikow (1987: table 1; character 18); Cracraft (1988: series XVII, character 3); Cracraft (1988: series XIX, character 1 for typus 1; series XX, character 5 for typus VII); McKitrick (1991a: appendix 1, character 52); McKitrick (1992: appendix 1, character 52); Vanden Berge and Zweers (1993: annotation 123); Livezey (1997a: appendix 1, character 122; *corrigenda*, Livezey 1998a); G. Mayr (2003b: appendix I, character 28); G. Mayr and Clarke (2003: appendix A, character 135); G. Mayr et al. (2003: appendix 1, character 84); Dyke and van Tuinen (2004: appendix 1, character 101); G. Mayr (2004b: appendix 1, character 54); G. Mayr (2004d: appendix I, characters 54–55); G. Mayr (2005a: appendix 1, characters 55–56).

2696. Mm. flexores hallucis longus et digitorum longus, tendines insertiorum, status syntendinosis et vinculum et situs proximodistalis (**ordered**):

a. tendons directly united;

b. tendons moderately united, broad vinculum present;

c. tendons weakly united, narrow vinculum present;

d. tendons separate, vinculum absent.

Note.—See: Gadow (1892); George and Berger (1966); Hoff (1966); Zusi and Bentz (1984); Raikow (1985b: table V, fig. 2.33).

2697. Mm. flexores hallucis longus et digitorum longus, vinculum, situs proximodistalis relative to bifurcatio tendinis insertii:

a. proximal; **b.** adjacent or distal;

x. noncomparable in absence or extreme apomorphy in form of vinculum or tendines.

Note.—See: Hoff (1966); Raikow (1985b: table V, fig. 2.33).

2698. M. flexor hallucis longus, rami tendinis insertii, digiti insertiorum (**unordered**):

a. digiti I–IV; **b.** digiti II–IV;

c. digiti I–II, et IV;

d. digiti I–II; **e.** digitus I;

x. noncomparable in absence or vestigial condition of digitus I et/aut II.

Note.—An alternative to unordered treatment is a step-matrix, of which two (conditional on presumed plesiomorphic state) present themselves. Under the hypothesis that the basal polarity is the presence insertiones on all digiti pedis retained (typically I–IV) and steps are equated to numbers of digiti to which insertiones were lost, the following is considered optimal:

$$\begin{array}{c|ccccc|} & \mathbf{a} & \mathbf{b} & \mathbf{c} & \mathbf{d} & \mathbf{e} \\ \mathbf{a} & 0 & 1 & 1 & 2 & 3 \\ \mathbf{b} & & 0 & 2 & 3 & 4 \\ \mathbf{c} & & & 0 & 1 & 2 \\ \mathbf{d} & & & & 0 & 1 \\ \mathbf{e} & & & & & 0 \end{array}$$

The transpose of this matrix corresponds to the hypothesis of basal polarity of tendines insertiorum limited to digitus I.

2699. M. flexor digitorum longus, rami tendinis insertii, digiti insertiorum (**unordered**):

a. digiti I–IV; **b.** digiti II–IV;

c. digitus III;

x. noncomparable in absence or vestigial condition of digitus I et/aut II.

Note.—Digits not listed for m. flexor hallucis longus, where retained, invariably are served by m. flexor digitorum longus. See: Hoff (1966); Raikow (1985b: table V, fig. 2.33).

M. Flexor Hallucis Brevis

2700. M. flexor hallucis brevis, status (**ordered**):

a. present; **b.** vestigial;

c. absent;

x. noncomparable in absence or vestigial condition of digitus I.

Note.—See: Swierczewski and Raikow (1981: character 37); Schreiweis (1982); Raikow (1985b: table 2, character 15); Raikow (1987: table 1; character 21); McKitrick (1991a: appendix 1, character 58); McKitrick (1992: appendix 1, character 58).

Mm. Extensores Digiti IV

2701. M. extensor brevis digiti IV, status (**ordered**):

a. present, well developed;

b. present, vestigial; **c.** absent.

Note.—See: Maurer and Raikow (1981: table 2, character 50); Swierczewski and Raikow (1981: character 41); Berman and Raikow (1982); McKitrick (1991a: appendix 1, character 65); McKitrick (1992: appendix 1, character 65); Vanden Berge and Zweers (1993: annotation 129).

2702. M. extensor proprius digiti IV, status:

a. absent; **b.** present.

Note.—See: Berman and Raikow (1982); Vanden Berge and Zweers (1993).

M. Extensor Hallucis Longus

2703. M. extensor hallucis longus, status:

a. present; **b.** vestigial or absent;

x. noncomparable in absence or vestigial status of digitus I.

Note.—Polymorphism in Tinamiformes related to variation in retention of hallux. See: Swierczewski and Raikow (1981: character 43); McKitrick (1991a: appendix 1, character 60); McKitrick (1992: appendix 1, character 60); G. Mayr and Clarke (2003: appendix A, character 138); Dyke and van Tuinen (2004: appendix 1, character 104).

Mm. Abductores Digitorum

2704. M. abductor digiti II, status et forma (**ordered**):

a. present, hyptertrophic;

b. present, moderately developed;

c. present, vestigial; **d.** absent;

x. noncomparable by absence of digitus II et musculus (*Struthio*).

Note.—See: Hudson (1948); George and Berger (1966); Hudson et al. (1972); Cracraft (1981a: 702); Maurer and Raikow (1981: table 2, character 47); Raikow (1982); McKitrick (1991a: appendix 1, character 63); McKitrick (1992: appendix 1, character 63); G. Mayr (2002a: legend fig. 9, node 4, character 8); G. Mayr et al. (2003: appendix 1, character 86).

2705. M. abductor digiti IV, status:

a. present, typically vestigial; **b.** absent.

Note.—See: Berger (1960a, 1966); Maurer and Raikow (1981: table 2, character 51); Raikow (1987: table 1; character 23); Vanden Berge and Zweers (1993: 224, annotation 130), noting widespread but vestigial status.

Mm. Adductores Digitorum

2706. M. adductor digiti II, status et forma (**ordered**):

a. well developed; **b.** vestigial;

c. absent;

x. noncomparable by absence of digitus II (*Struthio*).

Note.—See: Maurer and Raikow (1981: table 2, character 48); Swierczewski and Raikow (1981: character 39); Schreiweis (1982); Zusi and Bentz (1984: 43); McKitrick (1991a: appendix 1, character 64); McKitrick (1992: appendix 1, character 64).

M. Lumbricalis

2707. M. lumbricalis, status:

a. present, distinct;

b. vestigial or absent.

Note.—See: Schreiweis (1982); Zusi and Bentz (1984: 44); Schulin (1987: table 1); McKitrick (1991a: appendix 1, character 66); McKitrick (1992: appendix 1, character 66).

Miscellanea Anatomica

INTEGUMENTUM COMMUNE

Note.—Characters of the integumentum are those pertaining entirely or principally to features of keratinized structures (Rawles 1960; Romanoff 1960; Spearman and Hardy 1985), i.e., those of pennae, rhamphotheca, crista carnosa, paleae, scutellae, pulvinae, calcarae, and ungues. Characters concerning color patterns or pigmentation (Auber 1957) largely were not amenable to coding across avian orders. Unavoidable confoundment between these aspects of the externum and the underlying skeleton exists, but where logically consistent, were listed as characters under OSTEOLOGIA.

Caput

Note.—Some characters evident in entire specimens are treated under OSTEOLOGIA, especially some general aspects of caput (e.g., angulus craniofacialis) and rostrum.

Regiones Capitis

2708. Areae pennarum, status et forma (**unordered**):

a. present throughout;

b. present, but sparse and heterogeneous throughout much of caput et collum, some apennate in limited regiones;

c. present, exclusive of regiones facialis, lorum, et circumorbitalis only;

d. present, exclusive of restricted regio postrostralis and narrow lorum only;

e. present, exclusive of regio circumorbitalis only;

f. absent throughout entire regio capitis, or present only on corona et nucha.

Note.—See: Livezey (1998b: appendix A, characters 410, 425, 454, and 456), regarding regiones sine pennarum capitis; Dyke et al. (2003: appendix 1, character 101).

2709. Paleares frontales et/aut malares, rictalis (**emended term**), status:

a. absent; **b.** present.

Note.—See: Raikow (1987: table 1, characters 1 and 26), regarding paleares orbitales (**emended term**), excluded here.

2710. Cera, status, situs, et forma (**unordered**):

a. absent;

b. present, including apertura nasi, sine pennarum;

c. present, including apertura nasi, cum pennarum;

d. present, caudal to apertura nasi, sine pennarum.

Note.—Lacinia integumenta (**new term**)—"fleshy flaps"—over the regio nasalis of the anserine *Cereopsis* is considered distinct from a cera vera. See: Livezey (1998b: appendix A, character 405); G. Mayr and Clarke (2003: appendix A, character 143); G. Mayr et al. (2003: appendix 1, character 4); Dyke and Van Tuinen (2004: appendix 1, character 106).

2711. Lorum, status pennarum:

a. present, pennate; **b.** absent, apennate.

Note.—In some taxa, apennation extends to regio circumorbitalis, or apennate condition limited to circumorbital strip (*Tockus*, Ramphastidae).

See: Livezey (1997a: appendix 1, character 102; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, characters 427 and 429); Dyke et al. (2003: appendix 1, character 98).

2712. Sulcus infraorbitalis (sinus antorbitalis), status:
a. absent; **b.** present.
Note.—See: Bellairs and Jenkin (1960).

2713. Pileum, cassis, status:
a. absent; **b.** present.
Note.—Most prominent cassis (cf. *Casuarius*) principally is composed of a core of os spongiosum, evidently derived from or related to ossa frontale et mesethmoidale, enclosed by (typically multiple) laminae of integumentum cornificium.

2714. Pileum, occiput, punctus occipitalis, pennarum occultus (**new term**), status:
a. absent; **b.** present;
x. noncomparable, occiput definitivum sine pennae (*Gyps*, Cathartidae).
Note.—See: Hafner and Hafner (1977), regarding presence among Accipitridae of punctus occipitalis albus formed by distinctly pale basiorum pennarum regionis, and revealed upon voluntary elevation of pennae by musculi (nonstriati dermates) pennarum.

2715. Projectio (crista) pennarum, status et forma (**unordered**):
a. absent;
b. present, as crista of frons, corona et/aut occiput;
c. present, as floccus (**new term**) frontalis.
Note.—Minority of state "b" extending to collum, especially dorsum collumaris. See: Livezey (1997a: appendix 1, character 101; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, character 466).

2716. Crista (lobus aut cornu) carnosa frontalis, status:
a. absent;
b. present, variably prominent, sexually selected crista, lobus, aut cornu.
Note.—See: Livezey (1998b: appendix A, characters 393–401).

2717. Apertura auris externae, forma:
a. exposed, i.e., regio auricularis at least locally apennate;
b. concealed, i.e., at least locally concealed by pennae.

2718. Lobus auricularis, status:
a. absent; **b.** present.

Integumentum Rostri Maxillae et Mandibulae: Rhamphotheca

Note.—Each of the primary functional units of the skeletal rostrum—rostrum maxillae et rostrum mandibulae—is enclosed by distinct subparts of the rhamphotheca—rhinotheca et gnathotheca, respectively.

2719. Rhinotheca et gnathotheca, status generalis:
a. absent, lacking integumental derivations pertaining to "bill-like" differentiation;
b. present, including notably lateral and anterior expansions of keratinized externum of rostum maxillae et mandibulae.
Note.—Rhamphotheca constitutes the cornified epithelium (A. M. Lucas and Stettenheim 1972) that ensheaths the maxilla (to or including apertura nasi) and mandibula (typically to rictus at least on rami mandibulae). Condition in fossil Avialae inferred from form of underlying rostri maxillare et mandibulare.

2720. Rhinotheca et gnathotheca, sulci longitudinales basilares (**new term**), status:
a. absent; **b.** present.
Note.—See: Giannini and Bertelli (2004: appendix 2, characters 2–3).

2721. Rhinotheca et gnathotheca, sulci longitudinales symphysiales (**new term**), status:
a. absent;
b. present, by lamina mediana on both rostri maxillare et mandibulare.
Note.—See: Parkes and Clark (1966); Cracraft (1974: series 2, character 2); Raikow (1987: table 1, character 25); Houde (1988: table 27, character 12); Rotthowe and Starck (1998: appendix, character 8); G. Mayr and Clarke (2003: appendix A, character 40).

2722. Rhinotheca et gnathotheca, tomia maxillare et mandibulare, lacinia oro-ocularis (**new term**), status et forma (**ordered**):
a. absent;
b. present, abbreviate, typically extending approximately one-half of the distance between rictus et oculus;
c. present, extensive, typically extending virtually or wholly the distance between rictus et oculus.
Note.—Similar to lorum apennatus, this feature refers to a narrow, elongate divisio pennarum at bases maxillare et mandibulare, of which terminus rostralis initiates at angulus oris and extends caudad to the angulus rostralis of palpebrae dorsalis et ventralis oculus. Extreme apomorphy appears as furrow or plica between extensiones maxillares et mandibulares to vertex rostralis ocularis, which (if underlying epidermis exposed) typically is apennate.

2723. Rhinotheca et gnathotheca, tomia maxillare et mandibulare, angulus oris, rictus, extension caudal to oculus, status:
a. absent; **b.** present.
Note.—Apomorphy represents comparatively extensive gape relative to oculus. Minor variation within apomorphic state includes truncation of caudal extension to vertex ventrorostralis oculus, or in-

creased contribution by enlarged orbitus ocularis (e.g., Bucerotidae).

2724. Rhinotheca et gnathotheca, tomia maxillare et mandibulare, ungues maxillaris et mandibularis, lamellae rostri verae—typus anseriformis—status et forma (**ordered**):

a. absent; **b.** present, rudimentary;

c. present, well developed.

Note.—"Typus anseriformis (α)" is characterized by a single row of lamellae maxillae opposing two rows of lamellae mandibulae, neither of which are dorsoventrally elongate, enclosed within variably broad but essentially straight rostrum that is passed through medium with caput typically subhorizontal with water surface. Primary structures associated with the rostrum maxillae; although fundamentally integumentous, also include osteological substructures in larger taxa. "Lamellae" of Phoenicopterygiformes are neither homologous nor functionally comparable to those of Anseriformes (Jenkin 1957), and therefore the former condition is treated separately, as an ordinal autapomorphy, herein. See: Goodman and Fisher (1962); S. L. Olson and Feduccia (1980a–b: table 1, character 23); Livezey (1986: appendix 1, character 13); Zweers et al. (1995); Livezey (1997a: appendix 1, character 103; *corrigenda*, Livezey 1998a); Rotthowe and Starck (1998: appendix, character 20); G. Mayr and Clarke (2003: appendix A, character 3); G. Mayr (2004a: appendix 1, character 2).

2725. Rhinotheca et gnathotheca, lamellae rostri "typus ϕ," status:

a. absent; **b.** present, exceptionally refined.

Note.—This distinctly different lamellar complex is characterized by opposing, largely laterally positioned lamellae on the rhinotheca and parallel structures on distinctly angular rostri maxillae et mandibulae (Jenkin 1957). A weakly convergent condition (not treated herein) occurs in *Pachyptila* (Procellariiformes, Procellariidae). Lamellar morphology of typus "ϕ" is characterized by elongate jugae maxillae interposed with comparably structured sulci mandibulae, enclosed within a strongly angular rostrum that is passed through the foraging medium with caput vertical to surface. *Anastomis* (Ciconiidae) possesses rudimentary state of these lamellae, limited to pars proximalis maxillae, i.e., that basal to sectiones arcuales maxillae et mandibulae (Beddard 1898a).

2726. Rhinotheca et gnathotheca, aspectus externum, ungues maxillaris et mandibularis, tumidity relative to more-basal portions of rostrum, forma:

a. similar;

b. significantly greater, manifesting apical tumidity.

Note.—See: Pycraft (1910); McLelland (1979: fig. 3.5); Livezey (1996b: appendix 1, characters 1–3); Livezey (1997b: appendix 1, characters 1–3). Prum (1988: character 12) distinguished Ramphastidae by their uniquely large, voluminous, low-density bills.

2727. Rhinotheca, caudal (basal) extent relative to apertura nasalis, forma (**unordered**):

a. limited to area within ovate or fissuriform spatium integumentum;

b. moderately extensive basally, but apertura nasalis enclosed within incisura of integument (cum pennarum) extending rostrad from regio facialis;

c. very extensive basally, apertura nasalis enclosed within rhamphotheca propria, i.e., rhinotheca extends caudad to form comparatively expansive lamina postnasalis rhinothecae (**new term**) between apertura nasalis and basis rhinothecae;

x. noncomparable through obfuscation by cera (Falconiformes *sensu lato*, Columbiformes *sensu lato*, Strigiformes).

Note.—Rhamphotheca comprises rhinotheca (pars maxillae) et gnathotheca (pars mandibulae).

2728. Rhinotheca, caudal extent through lorum to oculus or lorotheca (**new term**) distinctly caudal to margo caudalis generalis rhinothecae, status:

a. absent; **b.** present.

2729. Rhinotheca, lamina rostri, numerus partorum et forma (**unordered**):

a. one, simple and undifferentiated;

b. two, including bilateral lamina tomiales;

c. two, including lamina (rictales) basolaterales;

d. three or four, paries laminae.

Note.—See: Lönnberg (1904); Boetticher (1928); Chu (1998: character 120).

2730. Rhinotheca, lamina rostri, ecdysis annularis (**new term**), status:

a. absent, single state throughout annual cycle;

b. present, two or more structural states within annual cycle.

Note.—See: Ridgway (1880); Chu (1998: character 121).

2731. Rhinotheca, crista cornea internasalis, status:

a. absent;

b. present, manifesting significant intraspecific variation.

2732. Rhinotheca, serratia maxillaro-tomiales rhinothecae (**new term**), status et forma (**unordered**):

a. absent, tomia essentially linear or subtly, monotonically curved;

b. present, subserratia (**new term**), typically subtle, subtubercular;

c. present, serratia, typically extending majority of tomium.

Note.—Traditionally described (e.g., Van Tyne and Berger 1976) as having terminal, medial "hooks" and bilateral, subterminal "teeth" (latter pertaining here). See: G. A. Clark (1961); Holman (1961); Brooks and Garrett (1970); Swierczewski and Raikow (1981: character 50); Prum (1988: character 11), in reference to serratiae and tomium with single quasi-denticulus integumentum; Prum (1988: character 18), in reference to "forcepslike" bill of *Semnornis*; Raikow (1994: table 2, character 26); Dyke et al. (2003: appendix 1: character 2), regarding galliforms.

2733. Rhinotheca, tomium, pars basalis (**new term**), lateromedial extension and ventral planarity, status:

a. absent; **b.** present.

Note.—Apomorphic condition forms narrow lamina tomialis (**new term**) at basis rhinothecae.

2734. Rhinotheca, tomium, unguis maxillaris, status:

a. absent;

b. present, differentiated by chroma, forma externa, et sulci marginales rhamphothecae.

Note.—Typically in apposition to ungues mandibulares; rounded, hemi-elliptical form of Anseriformes alternatively termed dertrum and possessing functional refinements (Berkhoudt 1976).

2735. Gnathotheca, unguis mandibularis, gonys, lamina cuneata symphysialis (**new term**), status:

a. absent; **b.** present.

Note.—Lamina under consideration extends from apex mandibulae to margo caudalis symphysialis, typically reaches maximum of ventral prominence and lateromedial width at midpoint, and is distinct from simple (sometimes prominent) sulcus symphysialis (e.g., *Spheniscus*).

2736. Gnathotheca (rostrum mandibulae), facies lateralis, regio basalis (rictus), invaginatio pennarum basalis (**new term**), status:

a. present; **b.** absent.

Note.—Invaginatio typically relatively broad basally and tapering rostrad to variably acuminate apex.

2737. Gnathotheca, regio interramalis, pars gularis, palear gularis (**emended term**), status:

a. absent; **b.** present, palear sine pennarum.

Note.—See: Livezey (1998b: appendix A, character 464).

2738. Gnathotheca, regio interramalis, pars gularis, saccus gularis, status et forma (**unordered**):

a. absent;

b. present, cum pennarum, homochromatic, nondistensible;

c. present, sine pennarum, heterochromatic, semidistensible;

d. present, sine pennarum, heterochromatic, distensible.

Note.—Sacci gulares in which undulatory ventilation or vascular engorgement are supplied by plexus subcutaneous collaris, vena cutanea cervicalis ascendens/descendens. See: Coe (1960); Bock et al. (1973); Cracraft (1985: character 36); McLelland (1989); Cracraft (1988: series VIII, character 6); King (1989); Livezey (1995c: appendix II, character 42); Siegel-Causey (1997: table I, character 20); G. Mayr (2003a: appendix I, character 47); G. Mayr and Clarke (2003: appendix A, character 142). In cervical examples, typically involves diverticulae cervicocephalicae G. A. Clark (1993: annotation 27); G. Mayr (2004b: appendix 1, character 56).

Regio Nasalis

Note.—Subtly complex as intersections of integumentum (e.g., rhamphotheca), cartilagines, et underlying ossa, characterization of the regio nasalis using conventional specimens is challenging, and the remnants typically encountered in study of skeletal specimens was outlined best by Bang (1971: 5): "Nostrils (hornified epithelium)…may be placed on the beak dorsally, ventrally, laterally, at the very tip, at the feather margin, or the cere; may be tubular, partly or entirely covered by secondary overgrowth of hornified cells, partly or entirely screened by feathers; may have an operculum (overhanging upper margin). The 'tubercles' or 'transverse laminae' sometimes described as nostril structures in dried specimens are actually dessicated cartilages of anterior conchae."

Coding of traditional categories of "rhiny" as defined (Van Tyne and Berger 1976) from the externum (e.g., "holorhiny," "schizorhiny," "pseudoschizorhiny," and "amphirhiny"). Skeleton underlying the integument (Garrod 1873a; Feduccia 1967) is treated by Baumel and Witmer (1993). For cladistic use, see: Livezey (1998b: appendix A, character 384).

2739. Naris internum, status definitivum (**ordered**):

a. apertus or "open";

b. semi-apertus;

c. obstructed or "closed."

Note.—See: Sibley and Ahlquist (1972: table 2); S. L. Olson and Feduccia (1980b: table 1, character 38); G. Mayr (2003a: appendix I, character 2).

2740. Naris externum, septum nasi (nasale), perforatum transeptalis (**new term**), status:

a. aperforate; **b.** perforate.

Note.—Septum composed of ossa mesethmoidale, vomeris, maxillare, ectethmoidale, conchae nasales ossificantes, et/aut integumentum. See: Technau (1936); Bang and Wenzel (1985: table I); G. Mayr

(2003a: appendix I, character 5); G. Mayr et al. (2003: appendix 1, character 1).

2741. Valvula nasalis, status:
a. absent; **b.** present.
Note.—See: Bang (1971); Bang and Wenzel (1985: table II).

2742. Naris externum, operculum nasale corneum (**emended term**), status et situs dorsoventralis (**unordered**):
a. absent;
b. present, ancora proximodorsal to apertura;
c. present, ancora (rostro)ventral to apertura.
Note.—See: Van Tyne and Berger (1976); Bang and Wenzel (1985: 200); Raikow (1994: table 2, character 21); Veron (1999: appendix: character 17).

2743. Naris externum, operculum nasale pennarum (**emended term**), status:
a. absent; **b.** present.
Note.—Refers to well-developed, obscuring plumae dorsal to basis rostri maxillae; not to be confused with setae faciales, which co-occur in some taxa (e.g., Caprimulgiformes). See: Strauch (1985: character 22), for similar but distinct, dense feathering at the basis rostri maxillae of some Alcidae; Veron (1999: appendix: character 17).

2744. Naris externum, ducti tubulares (bilaterally paired ostia externa), comprising ostium efferens glandulae et ostium efferens respiratorium, status et forma (**ordered**):
a. absent throughout ontogeny;
b. present in early ontogeny, absent in juvenile and definitive semaphorants;
c. present throughout ontogeny, retained through adulthood.
Note.—See: C. A. Fleming (1941); Bang (1971); Cracraft (1985: character 21); Bang and Wenzel (1985); Raikow (1994: table 2, character 20); G. Mayr (2003a: appendix I, character 3); Giannini and Bertelli (2004: appendix 2, character 16). In some species of Diomedeidae, two internal tubae are merged into single ostium externum communis.

2745. Naris externum, lamella verticalis naris, status:
a. absent; **b.** present.
Note.—See: Bang (1971); King (1975); Prum (1988: character 32), regarding piciforms.

Truncus et Cauda

2746. Ventrum trunci, area incubationis endocrinae (**emended term**), status et typus genus (**unordered**):
a. absent in both sexes;
b. present, ambigenus;
c. present, gynogenus;
d. present, androgenus;
x. noncomparable by area produced by (nonhomologous) auto-depennation (Anseriformes).
Note.—Character herein limited to endocrinogenic, typically seasonal forms (Columbidae excepted) involving one or three pterylae of ventrum trunci (Strauch 1985). Characterizations of Ardeidae, Balaeniceps, *Pterocles*, Musophagidae, *Opisthocomus*, and Coraciiformes were based on aviary data.

See: B. W. Tucker (1943); D. E. Davis (1945); Bailey (1952, 1955); Selander (1964); Höhn and Cheng (1965); Drent (1975); Strauch (1985: character 25).

2747. Ventrum trunci, area incubationis depennarum autonomosa (**emended term**), status:
a. absent; **b.** present.
Note.—See: Hanson (1959); R. E. Jones (1971).

2748. Bulbus rectricium caudae, status:
a. absent; **b.** present.
Note.—See: Baumel (1988), in reference to uropygium and enclosed (typically) bilaterally by bulbi fibro-adiposi in which calami et musculi rectriciorum are positioned. Rectrices emerge from margo caudalis bulbae, whereas tectrices caudae (if present) adorn dorsum et ventrum caudae.

Rectrices

2749. Rectrices, numerus definitivum parum (**ordered**):
a. ten to 12; **b.** eight or nine;
c. six or seven; **d.** four or five;
e. zero, rectrices absent.
Note.—Apparently numerous rectrices of *Struthio* instead considered to be modified tectrices dorsales et ventrales majores caudae, and related to an enlarged bulbus rectricium in this massive, cursorial genus. Of carinate taxa, Podicipedidae pose greatest difficulties in tallies (Pycraft 1907a, 1909).

See: Cabanis (1847), especially for European Passeriformes; Garrod (1874d), for Columbidae; Short (1976); Sibley and Ahlquist (1972: table 2); Welty (1975), for variation among Neornithes; Van Tyne and Berger (1976) stated rectrices for *Struthio* to be "very numerous"; Strauch (1985: character 27); Livezey (1998b: appendix A, character 519); Dyke et al. (2003: appendix 1, character 91), who partitioned galliforms using breakpoint of eight; Xu et al. (2003) for estimate for fossil *Microraptor*.

2750. Rectrices, ecdysis rectricialis, modus typicalis definitivum (**unordered**):
a. "**centrifugal**"—moda 1–4 of Stresemann and Stresemann (1966)—focus (i.e., initial pair molted) variable;

b. "**centripetal**" or "**alternating**"—moda 5–9 of Stresemann and Stresemann (1966)—foci among intermediate pairs, proceeding divergently (laterad) or convergently (mediad);

c. "**subsynchronous**"—modus 10 of Stresemann and Stresemann (1966)—foci and direction variable and lacking clarity of pattern;

d. "**quasi-random**" of Stresemann and Stresemann (1966: 25), lacking discernable, stable pattern.

Note.—See: Friedmann (1930); Stresemann and Stresemann (1966: 25–27), including taxa studied regarding molt of rectrices, differences between juvenile and adult birds, and intraspecific variation among adults. Classes of molt and taxonomic composition thereof suggest a plesiomorphic state lacking distinct pattern of molt, from which several comparatively stable, distinguishable patterns emerged apparently independently.

2751. Rectrices, forma generalis:

a. variably flexible and elongate (cf. other pennae contornae), relative lengths various;

b. virtually inflexible, elongated, and pennae graduated in length, latter bilaterally increasing lateromediad or (rarely) mediolaterad.

Glandula Uropygium

2752. Glandula uropygialis, status definitivum:

a. absent; **b.** present.

Note.—With respect to basal, nonavialian Theropoda, may consider alternatively assuming status of glandula in taxa known or parsimoniously inferred to have been pennate. See: Paris (1913); Johnston (1988); Livezey (1998b: appendix A, character 375).

2753. Glandula uropygialis, situs *sensu* profunda integumentum:

a. profundus, capsula glandulae largely or completely enclosed;

b. superficialis, capsula glandulae largely superficial to surrounding integument;

x. noncomparable where glandula absent.

Note.—See: Johnston (1988), who quoted Paris (1913: 180) describing condition as "almost standing up [on the skin]."

2754. Lobus glandulae uropygialis, status et numerus modalis (**ordered**):

a. zero, glandula absent;

b. one, unilobate;

c. two, indistinctly bilobate;

d. two, distinctly bilobate.

Note.—See: Johnston (1988). "Distinctness" somewhat subjective, evidently a function of the medial constriction imposed by the septum interlobare on the externum of the capsula glandulae uropygialis.

2755. Papilla uropygialis, status et forma (**ordered**):

a. absent; **b.** small;

c. moderate to large.

Note.—See: Berger (1960b, table 4, character 90); S. L. Olson and Feduccia (1980b: table 1, character 32); Johnston (1988); Prum (1988: character 20); G. Mayr (2003b: appendix I, character 19); G. Mayr and Ericson (2004: appendix I, character 86).

2756. Papilla uropygialis, circulus uropygialis, status et forma pennarum (**ordered**):

a. absent, glandula apennate;

b. present, rudimentary or vestigial, sparsely pennate;

c. present, variably substantial, glandula moderately or densely pennate;

x. noncomparable where glandula absent.

Note.—Circulus refers to ringlet of feathers that encloses terminus of ductus et porus glandulae uropygialis. See: Berger (1960b: table 4, character 9); Raikow (1982: character 4); Johnston (1988) for primary source of data; G. Mayr et al. (2003: appendix 1, character 87); Dyke and van Tuinen (2004: appendix 1, character 107); G. Mayr and Clarke (2003: appendix A, character 144).

Patagia Alae

Note.—Although the patagia possess important implications for aerodynamic function, especially in relation to body mass or other morphometric attributes (Helm 1884; Stolpe and Zimmer 1939; Sundevall 1886; Sy 1936; R. S. Wray 1887a; Fisher 1946; Herzog 1968; Kipp 1959; Meunier 1951), few reliably characterized aspects were found to be applicable in a phylogenetic context.

2757. Patagia alae—patagium cervicale, propatagium, patagium alulae, patagium proprius, metapatagium, postpatagium, status (**ordered**):

a. absent;

b. present, structurally extensive, aerodynamically functional;

c. obsolete, limited to plica vestigialium, nonfunctional.

Note.—A variably developed cervical extension of the propatagium—patagium cervicale (G. A. Clark 1993: annotation 52)—is distinctly developed in some avian orders (e.g., Psittaciformes, Piciformes, and Passeriformes), but a robust assessment of this feature proved elusive.

See: Nachtigall and Kempf (1971); G. Mayr (1996); Chiappe and Lacasa-Ruiz (2002), regarding *Noguerornis*; Livezey (2003).

2758. Patagia alae, metapatagium, marsupium metapatagio-axillarum (**new term**), status:

a. absent; **b.** present.

Note.—See: Alvarez del Toro (1971: figs. 4–6); Livezey (1998b: appendix A, character 530).

Ungues Digitorum Manus

2759. Unguis digiti (I) alularis, status modalis definitivum:

a. present; **b.** absent;

x. noncomparable because of absence of manus (Dinornithiformes) or digitus alularis (Aepyornithdae, Casuariidae, Dromaiidae, Apterygidae) or extreme autapomorphy of digitus alularis (*Aptornis*).

Note.—See: Nitzsch (1811); Jeffries (1881a–b, 1882b); Shufeldt (1881c); Forbes (1882b); Sclater (1886); W. K. Parker (1888c); R. S. Wray (1887a); Pycraft (1903b); Wetmore (1920); Fisher (1940); W. C. O. Hill and Skead (1952); Gauthier (1986: 13); Stephan (1992); Baumel and Witmer (1993: annotation 224); G. Mayr (1996); Livezey (1998b: appendix A, character 559).

2760. Unguis digiti (II) majoris, status modalis definitivum:

a. present; **b.** absent;

x. noncomparable because of absence of manus (Dromornithiformes), incomplete digitus majoris (Aepyornithidae, *Aptornis*).

Note.—See: Jeffries (1881a–b, 1882b); Shufeldt (1881c); Forbes (1882b); Sclater (1886); Pycraft (1903b); Wetmore (1920); Fisher (1940); W. C. O. Hill and Skead (1952); G. Mayr (1996); Gauthier (1986: 13); Stephan (1992); Livezey (1998b: appendix A, character 559).

2761. Unguis digiti (III) minoris, status modalis definitivum:

a. present; **b.** absent;

x. noncomparable because of absence of manus (Dinornithiformes), incomplete or fundamentally apomorphic digitus minoris (other ratites, *Aptornis*).

Note.—See: Fisher (1940); W. C. O. Hill and Skead (1952); Ostrom (1976a–b, 1978); Nicolls and Russell (1985); Gauthier (1986: 13, unindexed synapomorphy of Ornithurae); Sereno (1993); Currie (1995, 1997); G. Mayr (1996); Livezey (1998b: appendix A, character 559); Chiappe et al. (1999).

Calcares Alae

2762. Calcar metacarpale proximalis (alulae, processi extensorius), cornu calcaris, status et forma:

a. present, a blunt, cornified eminentia, lacking cornu verae;

b. present, an elongate cornu calcaris;

x. noncomparable by absence of calcar (other Neornithes).

Note.—Cornu employed in reference to "spur" to distinguish it from unguis or "nail" of termina (apices) digitorum. Underlying structure treated under os carpometacarpus; variation in overlying integumentum characterized here. See: Rand (1954); Livezey (1986: appendix 1, character 42); Livezey (1997a: appendix 1, character 73; *corrigenda*, Livezey 1998a).

2763. Calcar metacarpale distalis, status:

a. absent;

b. present, comprising underlying calcar osseum et unguis metacarpalis distalis.

Note.—Integumentary counterpart (typically) to skeletal structure of carpometacarpus. See: Rand (1954); Livezey (1986: appendix 1, character 40); Livezey (1997a: appendix 1, character 76; *corrigenda*, Livezey 1998a).

Pennae et Calcares Membri Pelvici

Note.—Pennation of the membrum pelvicum among Neornithes universally includes the coxa et femur, with substantial variation characteristic from genu distad to pes.

2764. Pennae generis et cruris, limitus distalis pennarum, situs (**ordered**):

a. proximal to genu; **b.** genu;

c. proximal one-third of crus;

d. proximal two-thirds of crus;

e. at articulatio intertarsalis;

f. distal to articulatio intertarsalis (some Dinornithiformes, Tetraonidae, *Fregata*, *Pterocles*, *Ducula*, Strigiformes, some Apodidae), encoded below.

Note.—Crus synonymous with "tibia" of Van Tyne and Berger (1976). Pennation of pelvic limb among Neornithes obscures position of coxa and femur, with distalmost skeletal landmark being the genu. Xu et al. (2003) tallied at least 14 large pennae attached to pteryla membri pelvici, pars tarsometatarsalis of *Microraptor* (increasingly asymmetrical distad in vexillae), with a few smaller, less apomorphic pennae crurales.

2765. Pennae tarsalis, limitus pennarum distalis, status et situs (**ordered**):

a. absent;

b. present, proximal one-half tarsus;

c. present, terminus distalis tarsi;

d. present, digiti pedis.

Note.—See: Dyke et al. (2003: appendix 1, character 90). Extreme condition wherein pennation extends distad to dorsum digitorum pedis (e.g., some Tetraonidae) not represented among extant exemplars. However, Worthy and Holdaway (2002: 117) reported that of Dinornithiformes, at least *Megalapteryx didinus* possessed pennation distad to digiti pedis.

2766. Calcar metatarsale, cornea externum, furcatio(nes), numerus modalis cornuarum (**unordered**):

a. acalcarate, acornuate;

b. unicalcarate, calar unicornuate;

c. bicalcarate, each calcar unicornuate.

Note.—Calcar metatarsale (underlying structure treated under OSTEOLOGIA; variation in overlying integument to be characterized here. Apices of cornea externum of calcares typically acuminate in adults (especially males), but may remain blunt or covered by dermis in juveniles. See: Rawles (1960); A. M. Lucas and Stettenheim (1972); Stettenheim (1972); A. M. Lucas (1979); Davison (1985); Spearman and Hardy (1985).

Integumentum Tarsalis

Note.—In the four characters that follow, dorsal and plantar aspects of the tarsus and pes are characterized separately, thereby partitioning variation into four, comparatively distinct sources of variation. Integument of the tarsus and pes is traditionally treated by the combined characteristics of both facies dorsalis and facies plantaris. The categories that follow pertain largely to variation among passerine birds and seem to be variants on the "scutellate-reticulate" theme, but several (e.g., "exaspidean" and "endaspidean," pertaining to medial and lateral apomorphy) are of limited utility to taxa exclusive of Passeriformes:

- "*Pycnaspidean*"—facies plantaris reticulate;
- "*Exaspidean*"—scuta on facies dorsalis extending around lateral surfaces of tarsus;
- "*Endaspidean*"—scuta on facies dorsalis extending around medial surfaces of tarsus;
- "*Holaspidean*"—facies plantaris covered by single series of broad, rectangular scuta;
- "*Taxaspidean*"—facies plantaris covered by two or three series of small, rectangular or hexagonal scuta;
- "*Booted*"—scutae fused into a single, smooth sheath (in some taxa does not extend to distalmost section);
- "*Laminiplantar*"—facies dorsalis scutellate, but facies plantaris covered by a smooth, undivided sheath.

An extreme state, in which pennation encompasses the tarsus (treated elsewhere), has been termed "*booted*" or "*ptilopody*," the latter ambiguous in that it implies pennation of the pes as opposed to the tarsus (Van Tyne and Berger 1976: 558). The integumentum dorsalis tarsalis et digitorum pedis often is similarly patterned, with finer subdivision of scut(ell)a(e) et reticulae overlying the junctura metatarsophalangealis and (to a lesser degree) area interphalangeales; tarsi scutellate dorsally et plantad often separated lateromedially by variably narrow strips of reticulae.

2767. Podotheca, facies dorsalis—acrotarsium—typus integumentum (**unordered**):

a. reticulate; **b.** scutellate;

c. ascutellate or "naked";

x. noncomparable where pennation obfuscative.

Note.—See: Blechschmidt (1929); Boetticher (1929); Blaszyk (1935); Oliver (1949: fig. 7); G. A. Clark (1977); Van Tyne and Berger (1976: fig. 12), for summary of classical types of "tarsal scutellation" proposed by Ridgway (1901–1901); Küchler (1936); Rand (1959); G. A. Clark (1977); Brush (1985); Raikow (1985a); Strauch (1985: character 29); K. Lee et al. (1997: character 1); Livezey (1986: appendix 1, character 2); Livezey (1997a: appendix 1, character 113; *corrigenda*, Livezey 1998a); Chu (1998: characters 126–127); Livezey (1998b: appendix A, characters 560–562); Rotthowe and Starck (1998: appendix, character 22); Bertelli et al. (2002: appendix 2, characters 61–66); Worthy and Holdaway (2002: figs. 4.26–4.27, 4.30).

2768. Podotheca, facies plantaris—plantotarsium (**new term**)—typus integumentum (**unordered**):

a. reticulate; **b.** euscutellate;

c. mega-circular scutellate;

d. divided scutellate;

e. ascutellate or "naked";

x. noncomparable where pennation obfuscative.

Note.—See: Oliver (1949: fig. 7); Berger (1957: fig. 3); Worthy and Holdaway (2002: figs. 4.26–4.27, 4.30); G. Mayr and Ericson (2004: appendix I, character 90); references under acrotarsium. Scutellation characterized by proximodistal, median division of scutellae on facies plantares.

2769. Pulvinus hypotarsalis, status et typus (**unordered**):

a. absent or indistinct;

b. present, definitive, typically comprising two distinct substructures—pulvinus medialis et pulvinus accessorius;

c. present, predefinitive, associated with nestlings of cavity-nesting taxa.

Note.—Pulvinus protects articulatio intertarsalis, facies plantaris, in repose. Traditionally referred to as "callosities" in *Struthio* (Lowe 1926b), and indicated as present in *Dinornis* (Oliver 1949: fig. 7), this character includes as separate, unordered state the "heel pads of nestlings." Not to be confused with histologically similar, more-distal "pads" at the base of the digiti pedis (pulvinus metatarsalis)—here coded as present where substantially differentiated from adjacent integumentum tarsalis (Van Tyne and Berger 1976). Present character modelled after Manegold et al. (2004: character 6) for Capitonidae (*sedis incertae*) and Ramphastidae.

2770. Pulvinus metatarsalis, status et forma (**ordered**):

a. absent or obsolete; **b.** present, moderate; **c.** present, prominent, typically spinose.

Note.—This pulvinus is limited to that plantad to extremitas distalis tarsometatarsalis aut facies plantaris articulationis metatarsophalangealis. Where prominent, often accompanied by comparatively well-developed pulvinae (inter)digitales. Indicated as present in *Dinornis* Oliver (1949: fig. 7). Given association with body mass and graviportality, Raphidae probably had moderate to prominent pulvinae.

2771. Plica metatarsalis plantaris, status:

a. absent; **b.** present, distinctly serrate.

Note.—See: Oliver (1949: fig. 7); Van Tyne and Berger (1976).

Integumentum Pedis

2772. Facies dorsalis—acropodium (**new term**)—typus integumentum:

a. scutellate; **b.** reticulate.

Note.—See: Boetticher (1929); Blaszyk (1935); Oliver (1949: fig. 9); G. A. Clark (1977); Brush (1985); König (1982: fig. 1); Livezey (1997a: appendix 1, character 114; *corrigenda*, Livezey 1998a); Bertelli et al. (2002: appendix 2, character 67); Worthy and Holdaway (2002: figs. 4.26–4.27, 4.30). "Scaleless" or **ascutellate** condition (evidently secondary), having aspect of "naked" epidermis, occurs in some coraciiform taxa (e.g., some Alcedinidae).

2773. Facies ventralis—infrapodium (**new term**)—typus integumentum (**unordered**):

a. reticulate; **b.** scutellate; **c.** ascutellate.

Note.—See references under acropodium.

2774. Digitus I pedis (hallux), situs proximodistalis relative to planum interdigitalis II–IV pedis, i.e., "elevation" on tarsus:

a. "**elevated**"—proximal relative to other digiti, distally reaching planum digitorum pedis but only obliquely;

b. "**incumbent**"—topological position and function similar to those of other digiti;

x. noncomparable where digitus I pedis lacking or vestigial.

Note.—See: Oliver (1949: fig. 9); Sibley and Ahlquist (1972: table 2), regarding Gruiformes; König (1982: fig. 1), contrasting Ciconiidae, Accipitridae, with Cathartidae; Raikow (1982: character 16); Raikow (1985a: table V); Worthy and Holdaway (2002: figs. 4.26–4.27, 4.30); Dyke et al. (2003: appendix 1, character 89).

2775. Digiti II–IV pedis, angulae interdigitales (**new term**), i.e., "dactyly" (**unordered**):

a. "**homodactyly**"—os metatarsale I et digitus I essentially in subparallel or flabellate arrangement (i.e., not "opposed") relative to digiti II–IV pedis;

b. "**anisodactyly**"—digiti II–IV craniad, digitus I caudad;

c. "**pamprodactyly**"—as in "anisodactyly," except digitus I is rotated to mediocranial position, placing all digiti craniad;

d. "**heterodactyly**"—as in "anisodactyly," except digitus II rotated (clockwise, viewing digiti from dorsum) to mediocaudal position and all digiti shift toward symmetry;

e. "**semi-zygodactyly**"—as in "anisodactyly," except facultative, bidirectional, rotation craniocaudad of digitus IV on lateral side;

f. "**zygyodactyly**"—as in "anisodactyly," except digitus IV rotated or reversed to laterocaudal position in concert with shift toward symmetry by all digiti ("euzygodactyly"), including facultative laterocranial rotation or reversibility of digitus IV ("ectroprodactyly"), or facultative laterocranial rotation or reversibility ("extreme ectroprodactyly") of *both* digiti I et IV;

x. noncomparable (Struthionidae, Rheidae).

Note.—States based on relaxed positions (e.g., those of recently collected specimens), hypothesized to have arisen independently from the plesiomorphic state of "anisodactyly" essentially by shifts in relative positions of digits (Raikow 1985a: 113); hence this character is unordered and unweighted. The precursor of the presumptively plesiomorphic "anisodactyly" of Aves among nonavian Theropoda—provisionally termed "homodactyly"—is an osteological character deriving from torsion of pars distalis of os metatarsale I et (digitus I) hallux (Middleton 2001), preceded by or associated with loss of digitus V pedis.

See: Zehltner (1890); Bock and Miller (1959); Currie (1981); S. F. Simpson and Cracraft (1981: character 2); Swierczewski and Raikow (1981: character 44); Raikow (1982: character 14); Collins (1983); Thulborn (1984: 126–127, character 24); Raikow (1987: table 1; character 24); G. Mayr (2002a: legend fig. 9, node 2, character 4; node 5, character 6).

2776. Pulvinus digitalis pedis, pulvinus ungualis, status:

a. absent or indistinct;

b. present, typically prominent.

Note.—Apomorphic state typically serves as pad largely accommodated by concavitas palmaris unguis. See: Spearman and Hardy (1985: figs. 1.4–1.5).

2777. Pulvinus digitalis pedis, papillae pulvinae (reticulae spinosae; **new term**), status:

a. absent, reticulae essentially laminate;

b. present, reticulae protrusive and acuminate.

Note.—See: Lennerstedt (1975), regarding specialized papillae pulvinae digitorum pedis in Psittaciformes, Strigiformes, and Passeriformes.

2778. Unguis digiti III pedis, scutum dorsale, margo pectinatus medialis (**emended term**), status (**ordered**):

a. absent;

b. rudimentary, margo medialis variably expanded but lacking incisurae;

c. present, replete with incisurae and denticulae ("tines") defined thereby.

Note.—Biochemical analysis confirms microhomology of ungues integumentum of Mesozoic avialians and modern Aves (Schweitzer et al. 1999a). Presence in Pelecaniformes, Ciconiiformes, and Caprimulgiformes associated, perhaps preconditioned, with elongation of digitus III et/aut unguis digiti III relative to adjacent digiti II et IV pedis. "Rudimentary" margines pectinates distinguished by moderately to prominently ala medialis unguis (causing lateral curvature, in some chromatically delimited) with shallow and/or few incisurae pectinates, distinctness of both varying considerably (Mitchell 1913b: fig. 120). See: Sibley and Ahlquist (1972: table 4); Raikow (1982: character 17); Chu (1998: character 130); G. Mayr (2003a: appendix I, character 53); G. Mayr and Clarke (2003: appendix A, character 114); G. Mayr (2004b: appendix 1, character 60).

2779. Ungues digitorum pedis, scuta dorsale et plantare, dorsoplantar differentiation and resultant definition of margines peripherales et concavitas plantaris, status et forma (**unordered**):

a. absent, scuta dorsale et plantare essentially undifferentiated, unguis approximately conical;

b. present, scutum dorsale with margines variably defined, scutum plantare planar or variably concave;

c. present, extreme, scutum dorsale prominently compressed and broad, nail-like.

Note.—See: Boetticher (1929); Blaszyk (1935); Van Tyne and Berger (1976); Spearman and Hardy (1985: figs. 1.4–1.5); G. A. Clark (1993: annotation 87); Dyke et al. (2003: appendix 1, character 88), regarding sulcus longitudinus ungualis.

2780. Areae (interpulvinares) interphalangeales digitorum pedis, contrastingly dark pigmentation ("knuckle-marks"), status:

a. absent; **b.** present.

Note.—See: Van Tyne and Berger (1976); Spearman and Hardy (1985: figs. 1.4–1.5); Livezey (1998b: appendix A, character 566).

2781. Telae interdigitales, status et typus (**unordered**):

a. "apalmate"—absent, telae lacking or not extending beyond articulatio interphalangealis proximalis or possessing plicae aut lobae;

b. "semipalmate"—present, incomplete telae of variable distal extent and phalangeal involvement, occurring between pairs of digiti II–III, et/aut digiti III–IV;

c. "(eu)palmate"—present, complete telae (i.e., margines distales of telae approximately at bases of ungues digitorum, but margines distales can be variably incised between digiti), occurring between digiti II–III et III–IV;

d. "totipalmate"—present, complete telae (i.e., margines distales of telae approximately at bases of ungues digitorum), occurring between margines of digiti I–II, II–III, et III–IV, precluded by absence of hallux.

Note.—See: S. L. Olson and Feduccia (1980b: table 1, character 22); Cracraft (1985: character 35); Spearman and Hardy (1985: figs. 1.4–1.5); Livezey (1986: appendix 1, character 4); Cracraft (1988: series VIII, character 5); G. A. Clark (1993a: fig. 2.4), illustrating sectiones telae interdigitales pedis, II to III—intermedia, III to IV—lateralis, and I to II—medialis. Livezey (1997a: appendix 1, character 115; *corrigenda*, Livezey 1998a); Siegel-Causey (1997: table I, character 19); Chu (1998: character 129); Livezey (1998b: appendix A, characters 565, 567–568); G. Mayr (2003a: appendix I, characters 48 and 50); G. Mayr and Clarke (2003: appendix A, characters 111–112); G. Mayr and Ericson (2004: appendix I, character 81). Sibley and Ahlquist (1972: table 1); G. Mayr (2004a: appendix 1, character 60); G. Mayr (2004b: appendix 1, characters 57 and 59).

2782. Hemi-tela(e) interphalangeales basales (**new term**) digitorum III–IV pedis, "syndactyly," status (**unordered**):

a. absent, including anisodactyly;

b. present, between digiti III et IV only;

c. present, both minor between digiti II et III and major between digiti III et IV.

Note.—Occurs in minority of Passeriformes, but not represented among conordinal exemplars. See: Bock and Miller (1959); Raikow (1985a: table V), regarding variation in these small integumentary flaps between basalmost phalanges of lateral digits that act to bind the digits during medial rotation of digitus II toward digitus I, and considered herein distinct from tela interdigitalis; Spearman and Hardy (1985: figs. 1.4–1.5); G. Mayr (2003b: appendix I, character 16), perhaps regarding osseous junctures; G. Mayr et al. (2003: appendix 1, character 71); G. Mayr (2004d: appendix 1, character 48); G. Mayr (2005a: appendix 1, character 49).

2783. Tela(e) interphalangeales terminales (**new term**) digitorum II–IV pedis (where present), situs proximodistalis relative to ungues, facies plantares (**unordered**):

a. proximal to or coincident with basis ungualis;

b. extends distad to approximate midpoint of unguis to tuberculum, latter with underlying osseous foundation;

c. extends distad to terminus of unguis, facies plantaris;

x. noncomparable by unique ungues (Phoenicopterygidae) or apalmate and hemipalmate condition (other Neornithes).

Note.—Despite absence of telae verae in Podicipedidae (*Podiceps*), attachment of integument digitorum to ungues approaches state "c."

2784. Plica marginalis digitorum (**new term**), status:

a. absent, including taxa possessing telae interdigitales;

b. present, plica interphalangealis sine incisurae at margines lateralis et medialis.

Note.—See: Blaszyk (1935: fig. 17), illustrating unidigital, bimarginate, nonincised form of plica as opposed to true tela or incisurate loba; margines digitorum II–IV: (*i*) comprise proximodistal series of lateromedially elongate, sublinear scutellae; (*ii*) which partly separated by incisurae interdigitales; and (*iii*) termina of which are protected by uniquely short, dorsoventrally flattened ungues.

2785. Lobae digitorum (**new term**), status:

a. absent;

b. present, loba (plica) cum incisurae at margines laterales et mediales of juncturae interphalangeales.

Note.—See: Blaszyk (1935: fig. 18), with respect to similar, medially conspicuous incisurae of *Fulica*; Livezey (1998b: appendix A, characters 567–568), considered herein distinct from plicae marginales sine incisurum.

Partes Pennae

Note.—Morphological corollaries of function (e.g., hydrodynamics or insulative capacity) were not found to be productive or useful phylogenetic characters (Mascha 1904; Rutschke 1960, 1966; Sick 1937; Steiner 1957).

2786. Scapus pennae, remex distalis (decimus), relative elongation, status:

a. absent; **b.** present.

Note.—See: Gadow (1892); relative elongation apparently related at least in part to function of processus pectinatus.

2787. Scapus pennae, remiges primarii et secundarii, calamus pennae, apex calami et folliculus relative to ossa alae, situs:

a. in articulation with ossa et associated ligamenta;

b. embedded in musculi and not in articulation with ossa.

2788. Hypopenna, status et forma (**unordered**):

a. vestigial or absent;

b. present, diminutive, hypovexillum structurally distinct from associated scapus pennae (barbae umbilicales apparently lacking), hyporhachis slender;

c. present, approximating one-half length of associated scapus pennae, and structurally robust with rhachis;

d. present, elongate (especially hypovexillum), approximating length of associated scapus pennae.

Note.—Refers to traditional descriptive terms "aftershaft" or *Afterschafte* (Steiner 1943; Ziswiler 1962). See: Beddard (1885b, 1898a); Gadow (1892, 1893); Pycraft (1900); A. C. Chandler (1916); Lowe (1924); W. deW. Miller (1924); Stresemann (1934); Oliver (1949: fig. 24); Berger (1960b: table 4, character 10); Ziswiler (1962); Sibley and Ahlquist (1972: tables 2–3); Van Tyne and Berger (1976); S. L. Olson and Feduccia (1980b: table 1, character 5); Livezey (1997a: appendix 1, character 99; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, character 377); Worthy and Holdaway (2002: 117); G. Mayr (2003b: appendix I, character 17); G. Mayr and Ericson (2004: appendix I, character 89).

Microanatomia Pennarum

Note.—Most microanatomical characters employed by Dove (2000: appendix 3, characters 1–38) for Charadriiformes were not extendable to sufficient diversity of higher-order taxa for formal analysis.

2789. Basis plumulae, faciae dorsalis et ventralis, villi, status et forma (**unordered**):

a. absent;

b. present, hamulate, oriented (recurved) toward barba;

c. present, blunt or subglobular, oriented toward pennulum.

Note.—Villi of Ramphastidae uniquely prominent. See: Brom and Visser (1989); Brom (1990); G. Mayr (2004d: appendix I, character 56).

2790. Scapus pennae, rachis pennae contornae, sulcus ventralis, status:

a. present; **b.** absent.

Note.—See: A. C. Chandler (1916); Giannini and Bertelli (2004: appendix 4, character 20).

2791. Scapus pennae, vexillum pennae, truncate quasi-scutelliform shape, status:

a. absent; **b.** present.

Note.—See: Giannini and Bertelli (2004: appendix 4, character 19).

2792. Scapus pennae, vexillum pennae ventralis, barba pennae, ramus, crista ventralis, tegmen, status:
a. absent; **b.** present.
Note.—See: A. C. Chandler (1916); G. Mayr et al. (2003: appendix 1, character 89).

2793. Scapus pennae, vexillum pennae, barba pennae, ramus, crista ventralis, tegmen, villi, status:
a. absent or undetectable; **b.** present.
Note.—See: G. A. Clark (1993: annotation 28); Dove (2000: appendix 3, character 37).

2794. Scapus pennae, vexillum pennae, barba pennae, ramus, rugae (proximales et distales) et hamuli, status definitivum:
a. present; **b.** absent or disfunctional.
Note.—See: A. C. Chandler (1916); Oliver (1949: 47–48); Worthy and Holdaway (2002: fig. 4.31).

2795. Scapus pennae, vexillum pennae, barba pennae, barbula rami, forma generalis definitivum (*sensu* four diagnostic aspects):
a. "eutrophic"—possessing differentiated (*i*) vexillae barbae proximales et distales, (*ii*) basis et stylosa, (*iii*) rugae dorsales et ventrales, and (*iv*) hamuli barbulae;
b. "hypotrophic"—lacking differentiated (*i*) vexillae barbae proximales et distales, (*ii*) basis et stylosa, (*iii*) rugae dorsales et ventrales, and (*iv*) hamuli barbulae.
Note.—See: A. C. Chandler (1916); Oliver (1949: 47–48); Worthy and Holdaway (2002: fig. 4.31).

2796. Scapus pennae, vexillum pennae, barba pennae, barbula rami, basis barbulae, margo dorsalis, flexura, status modalis (**ordered**):
a. absent; **b.** present, series incomplete;
c. present, series complete.
Note.—Flexurae replace stylae dorsales and arise from facies dorsalis of bases barbulorum of pennae contornae in many aquatic taxa. See: A. C. Chandler (1916); Brom and Visser (1989); G. A. Clark (1993: annotation 37).

2797. Scapus pennae, vexillum pennae, barba pennae, barbula rami, basis barbulae, margo dorsalis, flexura, ungulae, status modalis (**ordered**):
a. absent; **b.** present, series incomplete;
c. present, series complete.
Note.—Ungulae occur only in subsets of both taxa lacking and possessing flexurae, but are positively associated with possession of flexurae. See: Brom and Visser (1989).

2798. Scapus pennae, vexillum pennae, barba pennae, barbula rami, pennula, cilia dorsale et/aut ventrale, status:
a. present, variably developed; **b.** absent.
Note.—See: A. C. Chandler (1916); Worthy and Holdaway (2002: fig. 4.31).

Pterylographia (Pterylosis)

Note.—Although a phylogenetic, taxonomically inclusive treatment of pterylographic characters (e.g., status and form of homologous pterylae and apterylae) is lacking, works by Clench (1970, 1985, 1992) and earlier treatises of pterylosis and molt by Nitzsch (1840), D. W. Thompson (1901), W. deW. Miller (1915, 1924), Burt (1929), Compton (1938), Fisher (1939, 1942, 1943), Humphrey and Parkes (1959), Humphrey and Clarke (1961), A. M. Lucas and Stettenheim (1972), and Komárek et al. (1982a–b) indicated several evidently useful candidates for characters. See: Cracraft (1986: character 1); Gauthier (1986: 12); Prum (1988: character 31); Hou et al. (1996: character 1).

2799. Pterylae capitalis et dorsalis (spinalis), interposed apteryla, status:
a. absent; **b.** present.
Note.—See: Clench (1992), detailing this apomorphy of Old World suboscine Passeriformes.

2800. Pteryla dorsalis, pars cervicalis (spinalis), broad separation of paired (post-bifurcation) subpterylae so as to approximate lateral linea cervicales, status:
a. absent; **b.** present.
Note.—See: Nitzsch (1840: figs. 2–10).

2801. Pteryla dorsalis, pars cervicalis (spinalis), comparatively cranial bifurcation, caudal extension of paired subpterylae to re-unite at dorsum of pyga, status:
a. absent; **b.** present.
Note.—See: Nitzsch (1840: figs. 2–10).

2802. Apteria trunci, status et distributiones (**unordered**):
a. absent;
b. present, typically widespread;
c. present, but limited to apterium cervicale laterale et apterium scapulare, otherwise pennation essentially lacking distinct subdivision or pterylae.
Note.—See: Nitzsch (1840: figs. 2–10); Gadow (1892); Spearman and Hardy (1985); Livezey (1997a: appendix 1, character 98; *corrigenda*, Livezey 1998a); Giannini and Bertelli (2004: appendix 2, character 23).

Pennae

Note.—Many possibly informative characters of the integumentum of birds, including those of definitive plumages, were excluded for lack of published foundational works (Goodchild 1886, 1891), e.g., status and patterns of tectrices remigium ventrales "inverteres" (**new term**) or "reversed wing coverts" despite encouraging, early reviews (e.g., Bates 1918). This problem was especially severe where characters cannot be scored readily using traditional study skins (e.g., ventral aspect of wings or concealed feathers).

2803. Penna contorna, pennae contornae generales, status generalis:
a. absent, i.e., **apennate**;
b. present, i.e., **penniform** or **pennate**, structurally variable.
Note.—See: Schweitzer et al. (1999b) and Schweitzer et al. (1999a), for paleobiochemical evidence of featherlike structures in *Shuvuuia*, and Schweitzer et al. (1999b) for *Rahonavis*; Norell et al. (2002); Lingham-Soliar (2003), regarding integumental fibers of some Ichthyosauria bearing resemblances to hypothetical "protofeathers" of Aves; Xu et al. (2004b), for evidence of protopennae in tyrannosauroid *Dilong*.

2804. Penna contorna, scapus pennae, rhachis pennae, status:
a. absent, reminiscent of plumulae;
b. present.

2805. Pluma, plumula, status et pterylographica (**unordered**):
a. absent;
b. present, confined to apterylae;
c. present, uniformly throughout (a)pterylae.
Note.—See: A. C. Chandler (1916: 256).

2806. Penna contorna, pulvipennae, status et distributio (**unordered**):
a. absent, sparse, or rudimentary;
b. present, in one or more, distinctly delimited papillae;
c. present, widespread, comparatively uniformly distributed.
Note.—Known commonly as "powder down." See: A. C. Chandler (1916); Schüz (1927), noting sparse down of *Balaeniceps*; Forbes (1882b); Beddard (1888a, 1898a); Fürbringer (1888), cited by Sibley and Ahlquist (1972: table 2), which differed for a minority of states given for traditional Gruiformes (e.g., Otididae and Gruidae); Mitchell (1913b); König (1982); Livezey (1998b: appendix A, character 376); G. Mayr (2003a: appendix I, character 46); G. Mayr (2004d: appendix 1, character 55); G. Mayr and Ericson (2004: appendix I, character 88).

2807. Penna contorna, seta facialis—recto-nasalis aut loralis (**new terms**)—status:
a. absent; **b.** present.
Note.—Setae are stiff, tapered, typically melanistic, and specialized pennae; barbae (if present) are confined to basis. Setae most conspicuous near rictus and considered sensory (Necker 1985). See: Berger (1960b: table 4, character 11); Stettenheim (1974); Swierczewski and Raikow (1981: character 45); Prum (1988: characters 14 and 23).

2808. Penna contorna, seta limbi palpebrae oculis (**new term**), status:
a. absent or inconspicuous;
b. present and conspicuous.
Note.—Refers to elongate, differentiated "eyelashes," and pertains to setae of both palpebrae dorsalis et ventralis. See: Maurer (1977).

2809. Penna contorna, filopluma, status generalis:
a. present; **b.** absent.
Note.—Filoplumae are slender and hairlike, any barbae of which typically are restricted to termina distales and sensory. See: A. C. Chandler (1916); Spearman and Hardy (1985).

2810. Penna contorna, setae nariales, status:
a. absent; **b.** present.
Note.—See: A. C. Chandler (1916); Spearman and Hardy (1985).

2811. Penna contorna, vexillum pennae, barba pennae, barbula rami et pennula, hamulus:
a. absent, lack of stabilizing microstructure and rigid vexillae;
b. present, presence of stabilizing microstructure and rigid vexillae.
Note.—Absence of barbulae et hamulae in ratites (McGowan 1989) evidently represents reversal(s).

Pennae Volatus

Note.—An extensive literature treats this subject, one substantially expanded with the discovery of fossilized feathers in nonavian Theropoda. An intriguing hypothesis is a biochemical "phylogeny" for derivatives of ϕ-keratin (e.g., reticulae, scutae, ungues, rhamphotheca, plumulae natales, et pennae verae) by Brush (1993: fig. 4); also see Fjeldså (1989).

See: A. C. Chandler (1916); Lowe (1928b), regarding purportedly plesiomorphic pennae of ratites; Lowe (1933), regarding purportedly plesiomorphic pennae of penguins; Maderson (1972), proposing hypothesis of transformation of archosaurian scuta to avian penna; Ostrom (1976a–b); Thulborn (1984: 126–127, character 26); Spearman and Hardy (1985); Cracraft (1986: character 1); Gauthier (1986: 12, unindexed synapomorphy of Avialae, part); Cracraft (1988: set I, character 1); Houde (1988: table 27, character 2); McGowan (1989); Livezey (1990, 1992a–b, 1993, 1994, 1998b, 2003); Brush (1993); Hou et al. (1996: character 1); Chen et al. (1998); Ji et al. (1998); Chiappe et al. (1999); Prum (1999); Chatterjee (1999: character 50, modified); T. D. Jones et al. (2000), regarding *Longisquama* are considered herein to be mistaken; Stokstad (2000); Zhang and Zhou (2000); Zhou and Wang (2000); Chiappe (2001a: appendix 1, characters 168–169), regarding presence of pennae and alulae; Norell et al. (2001: appendix 1: character 1); Xu et al. (2001); Ji et al. (2001) and J. M. Clark et al. (2002a: appendix 2.2, character 1), regarding symmetry of vexillae; Chiappe (2002: appendix 20.2, characters 168–169), regarding presence of pennae and alulae, respectively; J. M. Clark et al. (2002a: appendix 2.2, character 1); Xu (2002: suite II; characters 52–56), with respect to filamentous structures, differentiation symmetry of vexillae; Xu et al. (2002: character 1); Rauhut (2003: character 165); Ji et al. (2003a–b: 24); Xu et al. (2004b).

This evidence suggests a virtually linear evolutionary scheme, summarized provisionally as follows (cf. Zhang and Zhou 2000; Ji et al. 2001):

- **apennatus**—integumentum lacking pennae of any form;
- **protopennatus**—unifibrous, lacking central rhachis and stabilizing microstructure ~ stage I of Prum and Brush (2002: fig. 6)—in some cases substantiated by presence of trace β-keratin; e.g., *Dilong* (Xu et al. 2004b)
- **mesopennatus**—multifibrous, heterogeneously arranged, lacking central rhachis and stabilizing microstructure (e.g., barbulae and hamulae), approximately stage II of Prum and Brush (2002: fig. 6)—reminiscent of plumulae of some Neornithes;
- **semiplumatus**—multifibrous, uniformly structured, including central axis (rhachis), but lacking stabilizing microstructure, asymmetry of vanes, or incisurae, structurally reminiscent of neornithine semiplumae, approximately stage IIIa (rhachis) or stage IIIb (microstructure) of Prum and Brush (2002: fig. 6)—but also differentiation of remiges and tectrices;
- **prevolatus**—pennae contornae generales—multifibrous, structured, possessing a central rhachis and stabilizing microstructure of barbulae et hamulae, approximately stage IV of Prum and Brush (2002: fig. 6);
- **euvolatus**—pennae contornae volatus, including **remiges** and **rectrices**, showing asymmetry of vexillae, incisurae vexillarum, relatively robust calami, and (typically) disproportionate elongation.

2812. Pennae volatus—rectrices (caudae) et/aut remiges (alae)—status et typus (**unordered**):

a. rectrices et remiges both absent, including some taxa possessing other, less-specialized pennae or proto-pennae;

b. rectrices et remiges both present;

c. remiges present but poorly differentiated, rectrices present;

d. remiges absent, rectrices present;

e. rectrices et remiges both obsolete or lost secondarily.

Note.—Assignments to "absence" were conservative, given comparative rarity of preservation of integumentary structures. Rectrices differentiated from other pennae volatae by relative elongation, breadth, rigidity, and bilateral gradation in size in which central pair greatest; as in other pennae volatae, rigidity of vexillae maintained by interrelation of hamuli and barbulae. Where present, remiges typically differentiated into remiges primarii et secundarii. Apparent remiges of Sphenisciformes provisionally considered homologous with tectrices of other Neornithes (A. C. Chandler 1916). See: Chiappe et al. (1999); Currie and Chen (2001); Chiappe and Lacasa-Ruiz (2002), regarding *Noguerornis*; Elzanowski (2002); Witmer (2002) for phylogenetics among Mesozoic taxa; Xu et al. (2003), regarding remiges secundarii; Giannini and Bertelli (2004: appendix 4, character 22).

2813. Remiges primarii—excluding remiculus (**new term**)—numerus modalis definitivum (**ordered**):

a. 12–16; **b.** 11;
c. ten; **d.** nine;
e. seven or eight; **f.** one to six;

x. noncomparable (Dinornithiformes) or where homology problematic (Sphenisciformes).

Note.—The **remiculus**, where present, is diagnosed as the distalmost caudal penna attached to distal part of major digit, typically apex phalangis distalis digiti majoris (Stresemann and Stephan 1968); formerly judged a reduced remex primarii (R. S. Wray 1887a; Stegmann 1962), this penna currently is considered a variably differentiated tectrix primarii (Stephan 2002). The remiculus is elongate in some taxa—e.g., Tinamiformes, Galliformes, Anseriformes, and Pelecaniformes—and can cause confusion in some tallies (R. S. Wray 1887a; Gadow 1888). The **remex carpalis** is a moderately large penna volatus positioned between remiges primariae et secundariae, caudal to carpus (G. A. Clark 1993: annotation 69); this penna may account for an additional remex in state "b" (above).

See: Gadow (1877), regarding *Phoenicopterus*; T. J. Parker (1891), W. K. Parker (1891a–b), and Beddard (1899), in which variation total remiges of *Apteryx* detailed; Pycraft (1900), for data on paleognathous taxa; Verheyen (1958f); Stegmann (1962, 1974); Stresemann (1963); Sibley and Ahlquist (1972: table 1), regarding difference between Gaviidae and Podicipedidae; S. L. Olson and Feduccia (1980b: table 1, character 33); Morlion (1985), regarding *Menura*; Livezey (1994), for basis of estimate for *Aptornis*; Livezey (1998b: appendix A, character 536); G. Mayr and Clarke (2003: appendix A, character 141); G. Mayr (2004a: appendix 1, character 68).

2814. Remiges crurales (**new term**), status et forma (**ordered**):
a. absent;
b. present, vexillae symmetric, limited curvature;
c. present, vexillae asymmetric, marked curvature.
Note.—See: Zhang and Zhou (2004).

2815. Remiges primarii, scapus pennae, vexillum pennae, margo, incisura vexilli, status generalis:
a. absent; **b.** present;
x. noncomparable by absence of true remiges (Sphenisciformes).
Note.—A small minority of flightless neognathous Neornithes show secondary reduction of incisurae vexillae (McGowan 1989: fig. 2; Livezey 2003). See: Padian and Chiappe (1998b); Chiappe et al. (1999: fig. 47).

2816. Remiges primarii, remex decimus (distalmost, tenth remex), scapus pennae, vexillum pennae, margo, incisura vexilli, status:
a. absent; **b.** present.
Note.—See: Livezey (1998b: appendix A, character 538). Sibley and Ahlquist (1972: table 4) listed that Tytonidae have no primaries "emarginate" on inner web (vexillum internum), whereas "one to six" primaries are "emarginate" on inner web (vexillum internum) in Strigidae.

2817. Remiges primarii, extremely marked proximodistal increase of elongation of lengths of vexillae, resulting in falchionate apex alae, status:
a. absent; **b.** present.
Note.—See: G. Mayr (2003c: appendix, character 27).

2818. Remiges secundarii, diastema remigum secundariae (i.e., sine remex secundarius quintus), status modalis:
a. absent, producing "**eutaxy**" or "quintocubitism";
b. present, producing "**diastataxy**" or "aquintocubitalism";
x. noncomparable (Dinornithiformes, Sphenisciformes).
Note.—Potential for artefactual homoplasy from misreferrals of diastataxy is comparatively high, in that apparent diastemae can result from shifts in relative positions and heterogeneous truncation of tectrices and remiges.

See: Goodchild (1886, 1891), early surveys of "cubital coverts"; Pycraft (1895, 1899c), including early correlative explanations including "degeneration" related to flightlessness; Mitchell (1899, 1913b); W. deW. Miller (1924); Steiner (1918, 1956, 1958); Stephan (1970); Sibley and Ahlquist (1972: 25–26); Jeikowski (1974); S. L. Olson and Feduccia (1980b: table 1, character 34); Raikow (1982: character 5); Sibley and Ahlquist (1990: 217); Livezey (1997a: appendix 1, character 111; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, character 380); G. Mayr et al. (2003: appendix 1, character 88); G. Mayr and Clarke (2003: appendix A, character 140); Dyke and van Tuinen (2004: appendix 1, character 105); G. Mayr and Ericson (2004: appendix I, character 87); G. Mayr (2004a: appendix 1, character 67).

2819. Remiges, ecdysis remigum primariae, modus definitivum:
a. sequential, annual;
b. synchronous or (rarely) *Staffelmauser*, i.e., stepwise.
Note.—Refers to chronicity of molt of remiges within individuals; great majority of taxa undergo remigial molt once per annual cycle. See: Stresemann and Stresemann (1966: 18–22); Sileo et al. (1977); Livezey (1986: appendix 1, character 1); Livezey (1997a: appendix 1, character 112; *corrigenda*, Livezey 1998a); Chu (1998: character 180); Livezey (1998b: appendix A, character 381); Giannini and Bertelli (2004: appendix 2, character 24).

2820. Remiges primarii et secundarii, scapus pennae, vexillum pennae (both vexillae interna et externa), status:
a. present, remiges vexillate;
b. absent, remiges avexillate, comprising stout rhachises only.
Note.—See: G. A. Clark (1993).

2821. Remiges primarii et secundarii, vexillum, status symmetria (**ordered**):
a. present; **b.** rudimentary;
c. absent, vexillae asymmetric.
Note.—Reduction of asymmetry of vexillae in ratites (McGowan 1989) evidently represents reversal(s). See: Hwang et al. (2004: character 1); Xu and Norell (2004: supplement, character 1).

2822. Remiges alulae, numerus modalis per ala (**ordered**):
a. zero, digitus alularis sine remigium;
b. one or two; **c.** three;
d. four; **e.** five to seven;
x. noncomparable, lacking remiges aut digitus alularis (Casuariidae, Apterygidae).
Note.—See: Nachtigall and Kempf (1971); G. A. Clark (1993: annotation 70); G. Mayr (1996); Chiappe (2001a: appendix 1, character 169); Chiappe (2002: appendix 20.2, character 169); Chiappe and Dyke (2002: fig. 12). Inferred absence in *Confuciusornis* based on assessment by Chiappe et al. (1999). Berlin specimen of *Archaeopteryx* was preserved adequately for characterization. Hypothetical basal polarity based on G. Mayr (1996). Precursory remiges alulares may occur in *Microraptor* (Xu et al. 2003).

2823. Remiges alulae, vexillum remigium, marked relative elongation, status:

a. absent;
b. present, length approximating that of tectrices dorsales remigium.
Note.—See: G. Mayr (1996).

2824. Tectrices remigium ventrales, status et numerus lineae (**ordered**):
a. absent;
b. present, single row—i.e., *comprising* only tectrices majores, mediae, *aut* minores ventrales;
c. present, two or more rows—i.e., *excluding* only tectrices majores, mediae, *aut* minores ventrales.
Note.—See: Goodchild (1886); A. C. Chandler (1916).

Integumentum Natalis

Note.—Characters of natal patterns and coloration were excluded, e.g., natal color patterns of Charadriiformes by Jehl (1968, 1971), Tinamiformes by Bertelli et al. (2002: appendix 2, characters 69–79), and Gruiformes by Livezey (1998b: appendix A, characters 363–373). Ontogeny of neossoptilae offers potential for interpretation of paedomorphosis (L. Jones 1907).

2825. Ontogenetic stage at hatching, gradus aut typus (**ordered**):
a. "super-precocial"—"toti-pterylous" (where definitively pennate), ambulatory, blindness and parental care absent following hatching;
b. "precocial"—"toti-pterylous," ambulatory, blindness virtually absent and little or no parental care following hatching;
c. "semi-precocial"—"semi-pterylous," nonambulatory, blindness obsolete but parental care significant following hatching;
d. "semi-altricial"—apterylous, nonambulatory, blindness brief but parental care significant following hatching;
e. "altricial"—apterylous, nonambulatory, blindness protracted and parental care significant following hatching.
Note.—Likely basal polarity based on nonavian theropods is either "a" (Elzanowski 1981, 1985) or "b" (Varricchio et al. 1997; J. M. Clark et al. 1999), the latter, adopted here, also being consistent with extant crocodylians. See: Cracraft (1985: character 40); Sibley and Ahlquist (1990); Livezey (1998b: appendix A, character 374); J. M. Starck and Ricklefs (1998); G. Mayr (2002a: legend fig. 9, node 4, character 5), concerning a purported fossil leptosomatid; G. Mayr (2003a: appendix I, character 51); G. Mayr (2003b: appendix I, character 20); G. Mayr (2004d: appendix 1, character 63).

2826. Rostrum mandibulare, pseudodenticulus natalis gnathothecae (**new term**), status:
a. absent; **b.** present.
Note.—Refers to ephemeral callosity of the rhamphotheca mandibulae or "egg tooth" (*Eischiele*), the diminutive Latin *dens* for "prong." See: G. A. Clark (1961), regarding variation in ages at ecdysis pseudodenticulae.

2827. Pluma natalis, neossoptilus, barba pennae, barbula rami, forma:
a. distinct from barbulae pennae definitivum or "teleoptilus" of respective conspecifics;
b. structurally similar to barbulae pennae definitivum or "teleoptilus."
Note.—See: A. C. Chandler (1916).

2828. Vagina pennae natalis, term of retention:
a. abbreviated, shed shortly after emergence;
b. protracted, retained in multiple pterylae for substantial interval after emergence, producing a generalized "pin-cushion" developmental stage in nestlings.
Note.—See: G. A. Clark (1993).

Apparatus Digestorius

Note.—A moderately rich descriptive literature on the digestive tract, much with a systematic perspective—Gadow (1879a–b), Mitchell (1901a), Swenander (1902), Beddard (1911), Gröbbels (1932a–b), R. L. Martin (1960)—provided some foundational resources for a comparatively limited number of structural characters for analysis.

Cavitas Oralis

2829. Cavitas oralis, saccus oris, status:
a. absent; **b.** present.
Note.—See: Murie (1868, 1869); Garrod (1874a–b); Bock et al. (1973).

2830. Cavitas oralis et pharynx, glandulae oris et pharyngealis, status glandulae:
a. present; **b.** vestigial or absent.
Note.—See: Antony (1920); McLelland (1993: annotation 9).

2831. Cavitas oralis et pharynx, glandulae oris et pharyngealis, disproportionate enlargement of glandulae associated with secretory refinement for adhesiveness, status et munus (**unordered**):
a. absent;
b. present, for construction of nests;
c. present, for enhanced lingual capture of prey;
d. present, for caching of ingesta as adhesive bolus.
Note.—See: McLelland (1979); G. Mayr (2003c: appendix, character 26).

Palatum

2832. Torus palatinus, status:
a. absent;
b. present, thick, highly vascularized.
Note.—See: Heidrich (1908); McLelland (1979; 1993: annotation 2).

Lingua

2833. Corpus linguae, conspicuous diminution, status:
a. absent;
b. present, triangular or hemi-elliptical vestigium.
Note.—See: Gadow (1892); F. A. Lucas (1896, 1897), for review; Beddard (1898a: 403); Mudge (1902); Beddard (1903a); Beddard (1903b: fig. 45); Mitchell (1913b); Gardner (1925), for survey; Jollie (1977c: fig. 198); McLelland (1979: fig. 3.2); Bock and Bühler (1988).

2834. Corpus linguae, forma *sensu* bilateral, rostrocaudal cartilagines aut ossa columnares in typically elongate, flexible corpus:
a. absent; **b.** present.
Note.—See: Gadow (1892); F. A. Lucas (1896, 1897), for review; Beddard (1898a: 403); Mudge (1902), regarding Psittaciformes; Beddard (1903a), regarding Acciptridae and Falconidae; Beddard (1903b: fig. 45), regarding Cathartidae; Gardner (1925), for survey; Jollie (1977c: fig. 198); McLelland (1979: fig. 3.2).

2835. Corpus linguae, dorsum corporalis, facies spinosus, status:
a. absent;
b. present, typically including margines linguae.
Note.—See: Gardner (1925), for survey; McLelland (1979: fig. 3.2).

2836. Alae linguae, caudolateral expansion relative to corpus medially united by membranous fascia, status:
a. absent or negligible;
b. present and distinct.
Note.—See: Gardner (1925), for survey; McLelland (1979: fig. 3.2); Heidweiller and Zweers (1990).

2837. Alae linguae, distinctly spinous dorsum in contrast with corpus, status:
a. absent; **b.** present.
Note.—Apomorphic state excludes mere caudal fringe of spinae. See: Gardner (1925), for survey; McLelland (1979: fig. 3.2).

2838. Apex linguae, bifurcatio, status (**ordered**):
a. absent; **b.** present, shallow;
c. present, deep.
Note.—See: Gardner (1925), for survey; McLelland (1979: fig. 3.2).

2839. Apex linguae, distinctly sagittate with recurved spinae, status:
a. absent; **b.** present.
Note.—See: Gardner (1925), for survey; McLelland (1979: fig. 3.2).

2840. Apex linguae, papilla of elongate filaments, status:
a. absent; **b.** present.
Note.—See: Gardner (1925), for survey; McLelland (1979: fig. 3.2).

2841. Margo linguae, dense filamentation, status:
a. absent, essentially smooth or variably spinous;
b. present.
Note.—See: F. A. Lucas (1896, 1897), for review; Gardner (1925), for survey; McLelland (1979: fig. 3.2).

2842. Torus linguae, status:
a. absent;
b. present, a smooth, rounded, basal eminentia.
Note.—See: Heidrich (1908); Gardner (1925); McLelland (1979).

Esophagus

2843. Saccus esophagi, status et forma (**unordered**):
a. absent;
b. present, as single, ingluviform distension in the mid-cervical region;
c. present, as paired organ of acoustic or visual display.
Note.—See: Murie (1868, 1869); G. A. Clark (1993: annotation 27); McLelland (1979: fig. 3.10; 1989; 1993: annotations 27–29); King (1989).

2844. Ingluvies, glandulae nutricium (**new term**), status:
a. absent;
b. present, as organ of involuntary ingestive accommodation.
Note.—New term refers to glands productive of "crop milk." See: McLelland (1979).

2845. Ingluvies, rugae ingluvei, status:
a. absent; **b.** present.
Note.—In Columbiformes, rugae (sulci) proventriculi also occur. See: McLelland (1993: annotation 33).

2846. Ingluvies, diverticulae ingluviei (dexter, sinistrum, et medianum), status:
a. absent; **b.** present.
Note.—See: Landolt (1987a–b); McLelland (1989: fig. 3.9).

Gaster

2847. Proventriculus gastris, regio glandularis, plicae proventriculi, glandulae proventriculares productive of odoriferous excretory products subject to voluntary (defensive) emesis, status:

a. absent;

b. present, used typically as defensive mechanism.

Note.—See: Matthews (1949); Bang (1966, 1971). Plicae also provide additional sites for glandulae and storage capacity.

2848. Proventriculus gastris, diverticulum proventriculi, status:

a. absent; **b.** present.

Note.—See: McLelland (1979).

Intestinum

2849. Intestinum tenue, duodenum, jejunum, et ileum, ansae duodeni, jejuni, et ilei, forma of ansae II et (possibly) III in terms of (*i*) **orientation**—sinistral ("left") *vs.* dextral ("right") *vs.* cyclical ("spiral")—and (*ii*) **occlusion**—confertus ("closed") *vs.* apertus ("open") (**unordered**):

a. dextro-confertus; **b.** dextro-apertus;

c. sinistro-apertus; **d.** sinistro-confertus;

e. cyclus.

Note.—Refers to configuration of ansae in segmentum intestini between (*i*) pars pylorica gastris, ostium pyloricoduodenale, and (*ii*) ileum, ostium ileocecale (McLelland 1979). See: Gadow (1877, 1879a–b, 1882a, 1889, 1891b, 1892), especially Gadow (1889: table, 308–310); Mitchell (1901a); Beddard (1911); Sibley and Ahlquist (1972: table 2); McLelland (1979).

Traditionally recognized types listed by Van Tyne and Berger (1976: fig. 23)—"isocoelous," "anticoelous," "antipericoelous," "isopericoelous," "cyclocoelus," "plagiocoelous," and "telogyrous" (last limited to Psittaciformes). Revised scheme was diagrammed by McLelland (1979: fig. 3.25), including "pericoelous" and "mesogyrous."

2850. Intestinum crassum, cecum, status:

a. present; **b.** absent.

Note.—See: McLelland (1993: annotation 81).

2851. Intestinum crassum, cecum, forma (bi)lateralis:

a. bilaterally, singly paired; **b.** unilateral.

Note.—See: Corti (1923); McLelland (1993: annotation 81).

2852. Intestinum crassum, cecum, diverticula ceci, status et/aut typus (**unordered**):

a. present, "intestinal";

b. present, "lymphoid";

c. present, "glandular";

d. vestigial, typus indeterminate;

e. absent.

Note.—Coding of states based principally on Clench and Mathias (1995).

See: Garrod (1874d); Beddard (1886c); Mitchell (1901a, 1896); Maumus (1902); Corti (1923); Lowe (1939b); Sibley and Ahlquist (1972: table 3); Van Tyne and Berger (1976); McLelland (1979); S. L. Olson and Feduccia (1980b: table 1, character 30); Raikow (1982: character 6); Bezuidenhout (1986); McLelland (1989); McLelland (1993: 315–316); Clench and Mathias (1995); G. Mayr (2002d: appendix 1, character 24); G. Mayr (2005b: appendix A, character 49).

2853. Intestinum crassum, cecum, paries, numerus modalis:

a. one; **b.** two;

x. noncomparable by bilateral asymmetry (Ardeidae).

Note.—See: Maumus (1902); McLelland (1993: annotation 81).

2854. Intestinum crassum, cecum, corpus ceci, forma generalis (**unordered**):

a. variably bilaterally subglobular;

b. unilaterally subglobular;

c. spiraliform; **d.** subtubular.

Note.—Compendium of minority variants, provisionally inferred here to represent apomorphic forms, is acknowledged to be incomplete. See: McLelland (1989).

2855. Intestinum crassum, cecum—basis, corpus, et apex ceci—external distinguishability of zonae related to profound development and differentiation, status:

a. absent; **b.** present.

Note.—See: McLelland (1989); McLelland (1993: annotation 82).

2856. Intestinum crassum, cecum, diverticula ceci, status:

a. present;

b. absent, rudimentary or vestigial.

Note.—See: McLelland (1993: annotation 83).

2857. Intestinum crassum, cecum, diverticula ceci cervicalis et thoracicus (associated with unique ruminant digestion), status:

a. absent; **b.** present.

Note.—See: Böker (1929); McLelland (1989).

2858. Intestinum crassum, cecum, ostia ceci sinistrum et dextrum, forma:

a. separate; **b.** unified.

Note.—See: Jacobshagen (1937).

2859. Hepar, lobus sinister hepatis, incisura lobaris, status:

a. absent or poorly developed;

b. deep, clearly defining partes lateralis et medialus.

Note.—See: Komárek et al. (1982a–b); McLelland (1993: annotation 100), in which uncertainty of inclusivity of apomorphic state is indicated.

APPARATUS RESPIRATORIUS

Regio Nasalis

Note.—See: Bang (1971); Bang and Wenzel (1985) for reviews of respiratory and olfactory morphology.

2860. Septum nasale, meatus nasalis, perforata, status:
a. absent, imperforate;
b. present, perforate.
Note.—Refers to perforatio septi nasalis transversus cum cartilagines et integumentum. See: Bang (1971); Sibley and Ahlquist (1972: table 2); Bang and Wenzel (1985: table I).

2861. Naris, concha nasalis rostralis, status (**unordered**):
a. present, voluminous;
b. vestigial; **c.** absent.
Note.—See: Bang (1971); this character required coding based on some nonexemplary confamilials.

2862. Naris, conchae nasales media et caudalis, status:
a. present; **b.** absent.
Note.—See: Bang (1971); Bang and Wenzel (1985).

2863. Naris, conchae nasales rostralis, media, et caudalis, forma:
a. prominent and large medialmost pair of passages directed dorsad and undertaking rounded, distinct lateral curvae or hamulae that terminate prior to significant anastomis laterobasalis;
b. large, dorsally directed, hamulate, medialmost pair of passages lacking or not terminating before turning lateroventrad to anastomis laterobasalis.
Note.—See: Bang (1971); King (1993: fig. 8.1a–c).

2864. Naris, concha nasalis septalis, status:
a. absent; **b.** present.
Note.—See: Bang (1966, 1971).

2865. Naris, concha nasalis atrialis, status:
a. absent; **b.** present.
Note.—See: Bang (1966, 1971).

2866. Glandula (loba) et ductus nasalis, ostia et ducti nasolacrimales lateralis et medialis, status et forma (**unordered**):
a. both ducti lateralis et medialis present, separate;
b. both ducti lateralis et medialis present, proximally separate, but distally unified as ductus communis;
c. ductus (et glandula) lateralis only;
d. ductus (et glandula) medialis only;
e. both ducti (and typically glandulae) lateralis et medialis absent.
Note.—Typically, status of lobus and respective ductus shared. See: Beddard (1898a); Marples (1932); Technau (1936); Staaland (1967); Bang (1966, 1971); Peaker and Linzell (1975); G. Mayr (2004d: appendix 1, character 61).

Larynx

Note.—One of the most neglected organs of avian anatomy (McLelland 1989), this organ is functionally important and ossified elements of the larynx are not uncommon in carefully prepared skeletal specimens. Notable exceptions are the works by Watson (1883), White (1975), Bock (1978), and Zweers et al. (1981). The comparatively uniform musculi laryngeales were described by Gadow and Selenka (1891) and Gröbbels (1932a–b).

2867. Mons laryngealis, forma superficialis:
a. papillate; **b.** smooth.
Note.—See: White (1975) *fide* McLelland (1989: 70).

2868. Cartilagines laryngeales, cartilago cricoidea, processus caudalis, status:
a. absent;
b. present, infrequently separate.
Note.—See: McLelland (1989: 73–74).

2869. Cartilagines laryngeales, cartilago cricoidea, corpus, crista dorsalis, status:
a. present, projecting dorsad into lumen laryngealis;
b. absent, corpus typically sulciform and uniting bilateral alae.
Note.—See: McLelland (1989: 69).

2870. Cartilagines laryngeales, cartilago cricoidea, corpus, crista dorsalis, forma:
a. median and projecting dorsad into lumen laryngealis;
b. median and extending length of cartilago cricoidea, forming incomplete septum dividing bilaterad the lumen laryngealis.
Note.—See: McLelland (1989: 70).

Trachea

2871. Ansae tracheales, status et forma (**unordered**):
a. absent;
b. present, extrasternal, intrafurcular;
c. present, intrasternal.

Note.—See: Rüppell (1933); Berndt (1938); Archey (1941); Amadon (1970); McLelland (1989); Livezey (1986: appendix 1, character 7); Livezey (1996a: appendix 1, character 77); Livezey (1997a: appendix 1, character 54; *corrigenda*, Livezey 1998a); Livezey (1998b: appendix A, characters 101 [extrasternal] and 102 [intrasternal]).

2872. Saccus trachealis, status:
a. absent; **b.** present.
Note.—See: Murie (1867); Rüppell (1933: fig. 42); McLelland (1989); King (1989); Livezey (1986: appendix 1, character 8); Livezey (1995c: character 41). Such features occur in some confamilials of exemplary taxa, e.g., *Oxyura* of Anatidae (Livezey 1995c: appendix II).

Syrinx

Note.—See: Forbes (1880b, 1881a); Wunderlich (1886 [1884]); Tymms (1913); Rüppell (1933); Warner (1972a–b); King (1989); McLelland (1989). Osseous aspects of syrinx treated under OSTEOLOGIA.

2873. Cartilagines syringeales, limited reduction lacking associated development of membrana tracheosyringealis, status et forma (**unordered**):
a. absent;
b. present, cartilagines all "C-shaped" with hiatae aligned dorsally;
c. present, limited to caudalmost cartilagines.
Note.—See: King (1989).

2874. Cartilagines syringeales, cartilagines accessoriae, cartilago membranosa ventralis, status:
a. absent;
b. present, opposed by cartilago membranosa dorsalis in minority.
Note.—See: King (1993: annotation 45).

2875. Ligamentum interbronchiale, foramen interbronchiale, status:
a. absent; **b.** present.
Note.—See: King (1989).

2876. Fenestra membrana tracheosyringealis, status (**unordered**):
a. absent; **b.** present, lateral;
c. present, dorsoventral.
Note.—Typically associated with hiatus, covered by membrana tracheosyringealis *in vivo*, resulting from dorsal or ventral reduction of cartilagines tracheosyringeales. See: King (1989); Livezey (1996a: appendix 1, character 78).

2877. Membrana tympaniformis medialis, status:
a. absent; **b.** present.
Note.—See: King (1989).

2878. Membrana tympaniformis lateralis, status:
a. absent; **b.** present.
Note.—See: King (1989).

2879. Fenestra cochleae, membrana tympanicas secundaria, structural isolation on laterobasis cranii by anulus tympanicus (comprising parts of ossa squamosum, exoccipitale, et basisphenoidale), status:
a. absent;
b. present, complete or partially interrupted by incisura quadratica.
Note.—See: Kühne and Lewis (1985). Partially complete, superficially similar anulus (involving only ossa exoccipitale et parasphenoidale) of some Galloanseromorphae are functionally different.

Bronchus Secundarii

2880. Septum interparabronchiale, status:
a. well developed;
b. poorly developed or absent.
Note.—See: King (1993: annotation 70).

Sacci et Diverticulae Pneumatici

2881. Saccus protrudens respiratorius, status et situs (**unordered**):
a. absent;
b. present, regio cervicalis;
c. present, regio gularis.
Note.—In cervical examples, typically involves diverticulae cervicocephalicae. See: G. A. Clark (1993: annotation 27); G. Mayr (2004b: appendix 1, character 56).

2882. Sacci pneumatici, saccus cervicalis, status:
a. present; **b.** absent.
Note.—See: Gier (1952); Duncker (1971); King (1993: annotation 77).

2883. Sacci pneumatici, sacci cervicales, claviculares, et abdominales, diverticulae subcutanea et extrathoracicae, status:
a. absent or extremely restricted;
b. present, variably extensive.
Note.—See: Beddard (1886d); Baer (1896); Schulze (1910); Gröbbels (1932a–b); Duncker (1971); S. L. Olson and Feduccia (1980b: table 1, character 14); Livezey (1986: appendix 1, character 3); King (1993: annotation 81); Livezey (1997a: appendix 1, character 100; *corrigenda*, Livezey 1998a).

2884. Diverticula cervicocephalica, recessus pneumatici cervicocephalica, extension as paired recessi around columna vertebralis, enclosing ingluvies, and resting sellariform on regio omalis, status:
a. absent; **b.** present.
Note.—See: Duncker (1971); Walsh and Mays (1984).

2885. Saccus abdominalis, status:
a. absent;
b. present, typically voluminous.
Note.—See: Beddard (1886d); Gröbbels (1932a–b); King (1966: 216); McLelland (1989: 264).

Pulmo

2886. Neopulmo, status:
a. present, typically approximating one-tenth the volume of paleopulmo;
b. absent.
Note.—See: Duncker (1971); McLelland (1989: 234), who noted that *Dromaius* possessed only minimal neopulmo, mentioning no other ratites.

Pericardium, Pleura, et Peritoneum

2887. Peritoneum, partitioning and relative expanse of septa posthepatica, horizontale, et obliquum (latter two being septae postpulmonaria), and related respiratory function, forma:
a. septa postpulmonaria weakly developed, with mm. diaphragmaticus et intercostales primary effectors of respiratory exchange;
b. septa postpulmonaria well developed, giving rise to septae horizontale et obliquum, with static-volumetric respiratory exchange effected by systema pulmo-diverticularale et mm. septocostales.
Note.—See: Duncker (1979); McLelland (1993).

Chromosomae et Karyotypae

Note.—More general assessments of avian karyotypes (e.g., Bloom 1969; de Boer 1975, 1976, 1980; R. M. Williams and Benirschke 1976; de Boer and Sinoo 1984; Ryttman et al. 1987; Ansari et al. 1988) were inadequately inclusive of taxa and summarized information as mere counts of elements without regard for homologous chromosomae conserved, divided, or lost.

2888. Ovum et spermatozoön, nucleus, chromosomae determinatorum sexus, typus (**ordered**):
a. homomorphy;
b. incipient heteromorphy;
c. heteromorphy.
Note.—See: de Boer (1975, 1980); Ansari et al. (1988); de Kloet and de Kloet (2003). Basal polarity among Neornithes remains problematic, given fossil status of closely related Theropoda and thermodetermination of sex among extant Archosauria (Crocodylia).

Apparatus Urogenitalis

Organa Genitalia Masculina

2889. Testis, spermatozoön, flagellum, pars intermedia, forma including (*i*) principally a great elongation, and (*ii*) secondarily a comparatively dense mass of granuli intermitochondriales (**new term**), status:
a. absent; **b.** present.
Note.—See: McFarlane (1971).

2890. Testis, spermatozoön, caput, acrosoma, forma:
a. comparatively small;
b. comparatively large.
Note.—See: McFarlane (1971); Raikow (1982: 438); Soley (1996).

2891. Testis, spermatozoön, flagellum, forma:
a. simple or "reptilian," comprising comparatively simple caput et flagellum, truncate;
b. complex or "passerine," comprising comparatively complex spiral or helical construction, elongate, "bundled" within.
Note.—See: McFarlane (1971); Lake (1981: 40); Raikow (1982: 438).

2892. Epididymis, ductulus efferens proximalis testis, size relative to that of distal counterpart (ductulus efferens distalis testis), status:
a. absent; **b.** present.
Note.—See: McFarlane (1971); King (1993: annotation 20).

2893. Epididymis, ductulus conjugens testis, status:
a. present; **b.** absent.
Note.—See: McFarlane (1971); King (1993: annotation 21).

2894. Apparatus copulationis, phallus masculinus, intromittence, status:
a. present, phallus protrudens, most with ligamentum elasticum phalli;
b. absent, phallus nonprotrudens.
Note.—Apterygidae and Tinamidae lack ligmentum elasticum phalli. See: Grimpe (1930); King (1981, 1993); Briskie and Montgomerie (1997); Coker et al. (2002).

2895. Apparatus copulationis, phallus protrudens, basis phalli, lymphobulbus phalli, corpus vasculare phalli, glomera corporis vascularis phalli, status:
a. present; **b.** absent.
Note.—See: Rautenfeld and Budras (1982).

2896. Apparatus copulationis, phallus protrudens, basis phalli, vasa lymphatica cloacalia, status:
a. present; **b.** absent.
Note.—See: Rautenfeld and Budras (1982).

2897. Apparatus copulationis, phallus protrudens, corpus phalli, sulcus phalli, status:
a. present; **b.** absent.
Note.—See: Rautenfeld and Budras (1982).

2898. Apparatus copulationis, phallus protrudens, corpus phalli, sacci phalli, status:

a. present; **b.** absent.

Note.—See: King (1981, 1993).

Organa Genitalia Feminina

2899. Organa genitalia feminina, gonadum dextrum, status (**unordered**):

a. present, typically functional ovarium dextrum, bilaterally symmetrical with gonadum sinister;

b. present, typically vestigial but at times approximating gonadum sinister in size;

c. present in minority, typically vestigial where present (significantly smaller than gonadum sinister), nonfunctional (exclusive of instances of pathology or loss of gonadum sinister), represented by gonadum dextrum vestigium.

Note.—Bilateral asymmetry of oviducti typical of Neornithes (Brode 1928). Basal polarity inferred from widespread condition of bilateral symmetry of gonadal development; vestigial states typically affects both ovaria et oviducti. Parallel vestigialization characterizes the oviductus dexter, which extends even to the Apterygidae, in which a functional ovarium dextrum persists; among Falconiformes, the oviductus dexter has been reported most frequently. See: Brode (1928); Kinsky (1971); A. B. Gilbert (1979); Chen et al. (1998); Sato et al. (2005).

Cloaca

2900. Proctodeum, phallus femininus, status et forma (**ordered**):

a. present, complete;

b. present, moderately developed, typically retaining semiephemeral rudimenta (especially among immature specimens) of corpus vasculare phalli, corpus phallicum medianum/laterale, et plicae lymphaticae;

c. present, vestigial; **d.** absent.

Note.—See: Komárek (1971); King (1981; 1993: 394); both states "a" and "b" include retention of all major components, including corpus vasculare phalli, corpora phallicum medianum et lateralium, and plicae lymphaticae.

2901. Ventus, labia venti, labium venti ventrale, glandulae internae labii venti, pars externus (**new term**), status modalis (**ordered**):

a. present, large; **b**. present, small;

c. vestigial or absent.

Note.—See: Quay (1967). Need to confirm status in Tinamidae, and to code ratites as well as multiple other families not sampled by Quay (1967), including entire orders (e.g., Gruiformes, Coraciiformes, Piciformes).

2902. Ventus, labia venti, labium venti ventrale, glandulae internae labii venti, pars internus (**new term**), status modalis (**ordered**):

a. present, large;

b. present, small or moderate;

c. vestigial or absent.

Note.—Cloaca, an invaginatio multimeatus within the ventus cloacae, eminentia venti of the ventrum trunci—in turn within the crissum—ventus cloacae, manifests indications of phylogenetic signal in selected features. See: Quay (1967); Rautenfeld et al. (1974); King (1981, 1993).

GLANDULAE ENDOCRINAE

2903. Enzymus *S*-malate dehydrogenase, motilitas modalis approximans (**ordered**):

a. ~100; **b.** ~63;

c. ~55; **d.** ~27.

Note.—See: Kitto and Wilson (1966); Cracraft (1981a); G. Mayr and Clarke (2003: appendix A, character 146); G. Mayr (2004a: appendix 1, character 70).

SYSTEMA CARDIOVASCULARE

Note.—Hypotheses of basal polarity for cardiovascular characters based on inferences by Glenny (1955), including proposal for the condition of *Archaeopteryx* (Glenny 1955: 550–551), in part based on characters of Crocodylia. Hypotheses of ordering were based on relative anatomical position (e.g., lateral → coincident → medial) and ontogenetic corollaries (i.e., early ontogenetic ~ plesiomorphic, late ontogenetic ~ apomorphic). Detailed assessments by Midtgård (1981, 1982, 1984) required provisional assignments of majority states, *a priori* hypothesized to be plesiomorphic.

Preliminary surveys of vascular anatomy of the arteria carotis cerebralis et arteria sphenoidea—Edinger (1926, 1942, 1951), Baumel (1967), Baumel and Gerchman (1968), R. Pearson (1972)—despite weak sampling of taxa, manifested strong indications of additional phylogenetic signal.

See: Barkow (1829); Neugebauer (1845); D. W. Thompson (1890); Beddard (1898a, 1905); Ridgway (1901); Stresemann (1927–1934); Glenny (1944, 1947, 1955); R. S. Schmidt (1964); Sibley and Ahlquist (1972: tables 1–2); Raikow (1982: character 3), based on Van Tyne and Berger (1976: fig. 22); S. L. Olson and Feduccia (1980b: table 1, character 13); Prum (1988: character 30); Sibley and Ahlquist (1990); G. Mayr (2003b: appendix I, character 18).

2904. Arteria carotis communis, typus (**unordered**):

a. typus caroticus A—"bicarotid";

b. typus caroticus B-1 through B-4, or B-6—"'basic' unicarotid," in which the single arteria carotis is variably reduced and nonfunctional, persisting in some as vestigium ligamentosus or entirely absent;

c. typus caroticus B-5—"'superficial' unicarotid," in which the single arteria corresponding to arteria carotis is replaced by comparatively superficial arteria esophagealis ascendens, opposite vessel reduced or absent.

Note.—"Types" follow Glenny (1955: 544–548). See: Garrod (1873c); Krassnig (1913); Baumel and Gerchman (1968); Baumel (1993: annotation 10). The basic configuration of widest distribution among Neornithes, symbolized as "A-1 carotid, type-A coracoid, type-1 thoracic," was synonymized by Glenny (1945: 266) with that termed "aves bicarotidinae normales" of Garrod (1873a).

2905. Arteria carotis communis, a. subclavia—numerus modalis aa. sternoclavicularis ("coracoid arteries"), typus:

a. typus "A–C"—one arteria, typically sinister;

b. typus "D–F"—two arteriae, both sinister et dexter;

x. noncomparable (*Apteryx*).

Note.—"Typus coracoideus" of arteria carotis follows Glenny (1955: 543); codings derived from Glenny (1943, 1944, 1945, 1946, 1947, 1951, 1955, 1957, 1967). See also: Gadow (1891b); S. L. Olson and Steadman (1981: 3–4).

2906. Arteria carotis communis, arteria subclavia—situs arteria thoracica interna ("thoracic artery") relative to arteriae axillaris et sternoclavicularis, typus modalis:

a. typus thoracica "1–2"—(*i*) arteria thoracica interna lateral to arteria axillaris or (*ii*) between arteriae axillaris et sternoclavicularis;

b. typus thoracica "3–4"—(*i*) arteria thoracica interna opposite basis or (*ii*) united by common basal ramus to arteria axillaris;

x. noncomparable (*Apteryx*).

Note.—"Typus thoracica" of arteria carotis follows Glenny (1955: 544); types 5–6 were not represented among exemplars. Heliornithidae (*Heliornis*) manifested a unique subvariant of this character (Glenny 1967), therefore the assignment was necessarily provisional. See also: Gadow (1891b); S. L. Olson and Steadman (1981: 3–4).

2907. Arteria subclavia, a. esophagotrachealis, status:

a. absent; **b.** present.

Note.—This vessel supplements rami esophagealis et trachealis of a. esophagotracheobronchialis (Glenny 1951), and gives rise to rami pericardii in (at least) Meleagrididae.

2908. Arteria poplitea, aa. genicularis et cruralis medialis, forma basilaris:

a. arteriae genicularis et cruralis medialis derive from a. tibialis medialis;

b. arteriae genicularis et cruralis medialis continue from a. femoralis medialis, whereas a. tibialis medialis lacking.

Note.—Sphensciformes further distinguished by diametric subequality of aa. genicularis et cruralis medialis. See: Midtgård (1982). Basal polarity inferred by uniformity of most Aves with Crocodylia (Hochstetter 1906).

2909. Arteria iliaca externa, aa. ischiadica et femoralis, status *sensu* role as principal arterial vessel serving membri pelvici:

a. arteria ischiadica principal vessel;

b. arteria femoralis principal vessel, a. ischiadica reduced, primary circulation diverted from latter to former by anastomosis arteriosa ischiofemoralis.

Note.—See: Midtgård (1982). Basal polarity confirmed by uniformity of most Aves with configuration of most Reptilia).

2910. Arteria ischiadica, a. suralis lateralis, forma *sensu* size and distal conjoinment and functional transfer to a. tibialis cranialis:

a. arteriae suralis lateralis robust;

b. arteriae suralis lateralis reduced, supply supplanted by a. tibialis cranialis.

Note.—See: Midtgård (1982).

2911. Arteria poplitea, forma *sensu* comparative route of distad passage relative to m. popliteus (where present):

a. sharply craniad to m. popliteus;

b. semilinearly caudal to m. popliteus;

x. noncomparable by absence of m. popliteus (Passeriformes).

Note.—See: Midtgård (1982).

2912. Arteria poplitea, arteriae tibialis caudalis et cranialis, rete tibiotarsale, status et complexitas arteriolae et venae collateriae (**ordered**):

a. absent—rete tibiotarsale replaced by systema of venae comitantes;

b. present, simple—typically comprising fewer than ten arteria et 20 vena collateriae;

c. present, elaborate—typically comprising 15–45 arteriae et 20–40 venae collateriae.

Note.—See: Midtgård (1981).

SYSTEMA LYMPHATICUM

2913. Bursa cloacalis, typus (**unordered**):

a. antrum muralis cum proctodeum;

b. vestigium muralis cum proctodeum;

c. diverticulum proctodeus.

Note.—See: Jolly (1915); King (1981); Rose (1981); Rautenfeld and Budras (1982); C. Müller (1985); Rautenfeld (1993: annotation 12).

SYSTEMA NERVOSUM

Note.—Despite a primary literature on the brain of birds and some peripheral neuroanatomical structures (Turner 1891a–c; Künzi 1918; Boas 1934; Portmann and Stingelin 1961; R. Pearson 1972; Hopson 1977; Mlikovsky 1989; Rehkämper et al. 1991; Larsson et al. 2000), characters sufficiently detailed for an adequate number of taxa regrettably were few. This state of affairs is especially unfortunate in that available evidence suggests that a number of neuroanatomical features are evolutionarily conservative and phylogenetic trends indicated thereby confirmed broad patterns consistent with transformation series from basal Archosauria, progressively apomorphic Dinosauria, *Archaeopteryx*, basal Ornithurae (e.g., *Hesperornis*, *Ichthyornis*), and Neornithes (Hopson 1977; Jerison 1968; R. Pearson 1972; Domínguez Alonso et al. 2005).

Systema Nervosum Centrale

2914. Sectiones medullae spinalis, substantia grisea, cornu dorsale, apex et basis cornus dorsalis, typus neuro-histologicus:
a. unilobate, "leiocerate";
b. bicornuate, "schizocerate."
Note.—See: Woodbury (1998), for primary survey; G. Mayr and Clarke (2003: appendix A, character 145), including influential assumption of polarity and hypothetical codings for multiple taxa; Dyke and Van Tuinen (2004: appendix 1, character 108); G. Mayr and Ericson (2004: appendix I, character 91). Several types of "leiocerate" states exist (e.g., in conformation of lamina 4–9), perhaps reflective of substates.

Systema Nervosum Periphericum

2915. Pars somatica, nervi craniales, nervus trigeminus, primary subdivision into (*i*) a comparatively small part comprising nervus ophthalmicus, and (*ii*) comparatively large part comprising nervi maxillaris et mandibularis, status:
a. absent; **b.** present.
Note.—See: Dubbeldam (1993; annotation 8); polarity indeterminate. Extent of this division, related to radix sensoria, is reflected osteologically by the configuration of basis crani interna et fossae cranii media, tecti mesencephali, et ganglii trigemini (Baumel and Witmer 1993: fig. 4.3).

ORGANA SENSUUM

Organum Visus (Oculus)

Note.—Despite the diversity illustrated in the atlas by C. A. Wood (1917), variation in the fundus oculi and included parts proved uniformative.

2916. Tunica vasculosa bulbi, mm. ciliaris, m. ciliaris anterior, size relative to m. ciliaris posterior (**unordered**):
a. both present and of comparable size;
b. former small relative to latter;
c. former large relative to latter;
d. both components absent.
Note.—Mm. ciliaris (formerly designated m. sclerocornealis) may assume the appearance of one to four muscles, and typically overlapping or abutting in the vicinity of the ossa sclerae. Musculus ciliaris anterior also is known as Crampton's muscle, and m. ciliaris posterior also is known as Brucke's muscle; problems of homology persist relative to these former, traditional names (Rochon-Duvigneaug 1950). The former (anterior component) is of greatest size among diurnal and noctural raptors (Falconiformes and Strigiformes) and smallest in aquatic birds, being absent (together with the posterior counterpart) among the Phalacrocoracidae and Sulidae, the former lacking both components (Evans and Martin 1993: annotation 21). The status of the fibrae radiales (Müller's muscle) remains uncertain in most avian taxa, considered by some to be but fibers passing between "anterior" and "posterior" parts and not meriting nomenclatural designation. The posterior component is comparatively large among Sulidae.

2917. Tunica vasculosa bulbi, choroidea, spatium perichoroidale, inclusion, forma *sensu* density:
a. loose, variably vacuous;
b. dense, mucoid.
Note.—See: Walls (1942: 645).

2918. Iris, pupilla, forma:
a. vertically sublinear;
b. subcircular or ovate.
Note.—See: Zusi and Bridge (1981).

2919. Iris, tapetum lucidum iridis, status:
a. absent; **b.** present.
Note.—See: Chiasson and Ferris (1968).

2920. Tunica interna bulbi, retina, areae retinae, area giganto cellularis, status:
a. absent; **b.** present.
Note.—See: B. Hayes et al. (1991), regarding apomorphic state as "…well-defined region in the dorsotemporal retina, close to the ora…characterized by the presence of ganglion cells which are both regularly arrayed and larger than those found in the rest

of the retina…[and] also have a large dendritic field of sparsely branched dendrites with much dendritic overlap between cells, thick axons, and dendrites confined to the proximal inner plexiform layer… similar to the α-cells of the retina in cats." These areae evidently facilitate detection of nearby prey on the surface of the sea.

2921. Tunica interna bulbi, retina, tapetum lucidum retinae, status:
a. absent; **b.** present.
Note.—See: Nicol and Arnott (1974), in reference to Caprimulgidae (*Caprimulgus*); Evans and Martin (1993: 598); extended to Caprimulgiformes by Holyoak (2001). Not homologous with the tapetum of Mammalia, which is derived from the choroidea of tunica vasculosa bulbi (L. D. Martin 1985).

2922. Tunica interna bulbi, retina, pecten oculi, typus (**unordered**):
a. conicus; **b.** vanellus;
c. plicatus.
Note.—See: Evans and Martin (1993: annotation 30). Provisional basal polarity for Aves as state "a" based on resemblance to form characteristic of modern lepidosaurian Reptilia.

2923. Tunica interna bulbi, retina, areae et foveae retinae, pecten oculi, pons pectinis, pigmentum, status:
a. present, at least in part; **b.** absent.
Note.—See: Evans and Martin (1993: annotation 30).

2924. Lens, pulvinus anularis (annularis) lentis, status:
a. absent;
b. present, centered around corpus centrale lentis and interposed vasicula lentis.
Note.—A structure unique to modern Aves but taxonomically variable. See: Evans and Martin (1993: annotation 34).

2925. Organa oculi accessoria, membrana nictitans (palpebra tertia), opacity and retarded mobility over cornea, status:
a. absent, translucent or transparent, rapidly moved;
b. present, membrana opaque white, slowly mobile.
Note.—Related characters, pertaining to mobility of palpebra dorsalis (A. M. Lucas and Stettenheim 1972: 14, 31) and absence of membrana nictitans in many taxa (Strauch 1985: character 24), were considered unreliable.

See: Goodge (1960); Evans and Martin (1993: annotation 37).

Labyrinthus et Cochlea

2926. Ductus semicirculares, crus membranaceum commune, status:
a. present;
b. absent, canales semicirculares anterior et posterior entering utriculus separately.
Note.—See: Gray (1908).

2927. Cochlea, vestibulum, magnitudo:
a. large, comprising majority of labyrinthus;
b. small.
Note.—See: Gray (1908: 94–95).

2928. Cochlea, canales semicirculares ossei, situs relative to vestibulum:
a. canales surround vestibulum;
b. canales distant, dorsad to vestibulum.
Note.—See: Gray (1908: 94–95).

2929. Cochlea, canales semicirculares ossei, canalis semicircularis anterior (superior), forma:
a. dorsocaudal, "drooping" or "sloping caudad";
b. dorsoventral, "upright."
Note.—See: Gray (1908). This essentially bimodal variation represents subvariants of the generally "curving" form among Aves, which constitute a marked contrast with the "coiled" form characteristic of Mammalia.

2930. Cochlea, recessus scalae tympani et/aut vestibulum, pigmentum, status:
a. present; **b.** absent.
Note.—See: Gray (1908).

Auris Externa

2931. Asymmetria bilateralis cranii, status:
a. absent;
b. present, principally dorsoventral, enhancing audiolocation.
Note.—See: Stellbogen (1930); Kelso (1940); Norberg (1977, 1978); Feduccia and Ferree (1978: table 1); Evans and Martin (1993: 603); apomorphic state varies in degree in both Tytonidae and Strigidae.

2932. Pennae auriculares, plumae auriculares rostrales, forma:
a. unspecialized and comparatively dispersed;
b. forming discus acousticus facialis (**new term**) or "facial disc."
Note.—See: Kühne and Lewis (1985); Evans and Martin (1993: 603). Apomorphic state varies in degree in both families included, and also may pertain to at least one genus of Accipitridae (*Circus*). Sibley and Ahlquist (1972: table 4) noted that in Tytonidae the "facial disc" is cordiform, whereas it is subcircular in Strigidae. A minority of nonexemplary Falconiformes (e.g., *Circus*) and Caprimulgiformes (e.g.,

Caprimulgus) possess similar "facial discs" (Ilyichev 1961, 1975; Konishi 1973).

2933. Pennae auriculares, plumae auriculares rostrales et caudales, status:
a. absent, unspecialized;
b. present, acoustically redirecting buttress in taxa possessing or lacking facial auditory discs.
Note.—See: Ilyichev (1961, 1975); Konishi (1973); Evans and Martin (1993: annotation 59).

2934. Operculum auris, status:
a. absent; **b.** present.
Note.—See: Norberg (1978); Evans (1982); Evans and Martin (1993: annotation 60).

Organum Gustatorium

2935. Caliculus gustatorius (gemma gustatoria), numerus approximans:
a. low to moderate, typically 100–300;
b. high, 400–500.
Note.—See: Evans and Martin (1993: annotation 62).

Terminationes Neurales

2936. Organa somatosensoria, organa sensoria integumenta, terminationes sensorium apicis rostri, status:
a. absent; **b.** present, density variable.
Note.—See: Evans and Martin (1993: annotation 70). Integumentary nerves serving bill tip.

OOLOGIA

Note.—Most of the early works dedicated to description and comparison of egg shells were of extremely narrow taxonomic scope and anatomical superficiality (Tyler 1966). In recent years, however, broad taxonomic samples using standard comparative methods have become available for Archosauria (Grellet-Tinner and Chiappe 2004; Grellet-Tinner 2005) and Aves (Mikhailov 1992, 1995, 1997), making oological characters a source of significant phylogenetic signal. However, a number of comparatively basal character changes evident in plesiomorphic Aves (e.g., *Archaeopteryx* and *Lithornis*) and closely related Theropoda (e.g., Oviraptorosauria, Troödontidae, and *Deinonychus*)—notably described by Makovicky and Grellet-Tinner (2000), Grellet-Tinner and Chiappe (2004), and Grellet-Tinner (2005), were scored for only a modest number of taxa. Still others were scored for inadequate samples of taxa for inclusion, e.g., (*i*) numerus stratorum testae (Makovicky and Grellet-Tinner 2000; Grellet-Tinner and Chiappe 2004: appendices 9.2 and 9.3, character 4); (*ii*) ornamentum superficialis testae (Schönwetter 1960; A. B. Gilbert 1971, 1979; Currie and Horner 1988; Horner and Weishampel 1988; Mikhailov 1992, 1995, 1997; Norell et al. 1994, 2001; Horner 1997; Houde 1988: 23; Manning et al. 1997; Mateus et al. 1997; Chiappe et al. 1998; Grellet-Tinner 2001, 2003; Grellet-Tinner 2005: appendix 1, table 2, character C3); and (*iii*) strata primus et secundus testae, relative thicknesses (Mikhailov 1992, 1995, 1997; Grellet-Tinner 2005: appendix 1, table 2, character C14; Grellet-Tinner 2005: appendix 2, character 16); Grellet-Tinner and Dyke (2005).

The testa avium is characterized most frequently either in terms of organic and inorganic strata: *organic*—cuticula, stratum spongiosum, stratum mamillarium, and fiber layers; *inorganic*—stratum superficiale, stratum vallatum, conus mamillae (including galaerum basale mamillae). In addition, ova of many taxa are characterized by openings that extend through one or more layers and show diversity of branching patterns and "plugging" of atria externae, comprising porus testae and canaliculus testae. Also notable is the variable presence of a carbonate or phosphate tegmen (cover or coating) on the cuticula.

2937. Ovum, aequalitas formis, status:
a. symmetrical;
b. asymmetrical, with "neoavian" outline.
Note.—Symmetry quantified by some as aequalitas formis transversalis (planum transversum), primarily reflecting relative curvatures at polus acutus et polus obtusus. More sophisticated metrics have been developed for eggs of Neornithes (e.g., Preston 1953). See: Grellet-Tinner and Chiappe (2004: appendices 9.2 and 9.3, character 6); Grellet-Tinner (2005: appendix 1, table 2, character C1).

2938. Ovum, cella aeria, status et forma (**ordered**):
a. absent;
b. present, rudimentary "proto-cella";
c. present, fully developed "eu-cella."
Note.—See: Grellet-Tinner (2005: appendix 1, character 2).

2939. Testa, mineralogia, typus:
a. aragonite; **b.** calcite.
Note.—See: Grellet-Tinner and Chiappe (2004: appendices 9.2 and 9.3, character 1).

2940. Testa, mamillae testae, forma crystalinus (**ordered**):
a. acicular; **b.** elongate-laminar;
c. abbreviate-laminar.
Note.—Descriptor for state "b" refers to narrow meaning of term, i.e., "blade-shaped." See: Makovicky and Grellet-Tinner (2000); Grellet-Tinner and

Chiappe (2004: appendices 9.2 and 9.3, character 2); Grellet-Tinner (2005: appendix 2, character 15).

2941. Testa, stratum superficiale, cuticula, status:
a. present; **b.** absent.
Note.—See: A. B. Gilbert (1971, 1979); Currie and Horner (1988); Horner and Weishampel (1988); Mikhailov (1992, 1995, 1997); Norell et al. (1994, 2001); Horner (1997); Manning et al. (1997); Mateus et al. (1997); Chiappe et al. (1998); Grellet-Tinner (2001, 2003); G. Mayr and Clarke (2003: appendix A, character 148).

2942. Testa, stratum superficiale, cuticula, zona accessoria (**new term**), status et forma (**unordered**):
a. absent, or zona limited to polysaccharide tegmenta or traces;
b. present, tegmen ($CaCO_2$) microglobularis amorphosis (**new term**), comparatively thick (20–100 μm), continuous;
c. present, tegmen ($CaPO_3$) microglobularis amorphosis (**new term**), comparatively thin;
d. present, tegmen ($CaPO_3$) microglobularis amorphosis (**new term**), comparatively thick (20–100 μm), continuous.
Note.—Tegmentum limited to pulvinae or "covers" of Mikhailov (1997), and excludes fragmentary, polysaccharide tegmenta. See: A. B. Gilbert (1971, 1979); Currie and Horner (1988); Horner and Weishampel (1988); Mikhailov (1992, 1995, 1997); Norell et al. (1994, 2001); Horner (1997); Manning et al. (1997); Mateus et al. (1997); Chiappe et al. (1998); Grellet-Tinner (2001, 2003); G. Mayr (2003a: appendix 1, character 54); G. Mayr (2004a: appendix 1, character 69); G. Mayr (2004b: appendix 1, character 62).

2943. Testa, stratum spongiosum, zonae externa, forma:
a. narrow, vertically crystalline;
b. typically thick, prismatic.
Note.—See: A. B. Gilbert (1971, 1979); Currie and Horner (1988); Horner and Weishampel (1988); Mikhailov (1992, 1997); Norell et al. (1994, 2001); Horner (1997); Manning et al. (1997); Mateus et al. (1997); Chiappe et al. (1998); Grellet-Tinner (2001, 2003).

2944. Testa, mamillae testae, forma crystalinus (**ordered**):
a. acicular; **b.** elongate-laminar;
c. abbreviate-laminar.
Note.—Descriptor for state "a" refers to narrow meaning of term, i.e., "blade-shaped." See: Makovicky and Grellet-Tinner (2000); Grellet-Tinner and Chiappe (2004: appendices 9.2 and 9.3, character 2); Grellet-Tinner (2005: appendix 2, character 15).

2945. Testa, limitates stratorum primus et secundus, typus:
a. prismatic; **b.** aprismatic;
x. noncomparable by absence of at least one stratum (Sauropoda).
Note.—See: Grellet-Tinner and Chiappe (2004: appendices 9.2 and 9.3, character 5); Grellet-Tinner (2005: appendix 1, table 2, character C11).

2946. Testa, limitates stratorum secundus et tertius, typus:
a. aprismatic; **b.** prismatic;
x. noncomparable by absence of at least one stratum (Sauropoda, Dromornithidae).
Note.—See: Grellet-Tinner and Chiappe (2004: appendices 9.2 and 9.3, character 5); Grellet-Tinner (2005: appendix 1, table 2, character C12).

2947. Testa, stratum spongiosum (stratum inorganicum secundum), status:
a. absent; **b.** present.
Note.—See: Mikhailov (1991, 1992, 1997); Makovicky and Grellet-Tinner (2000); Chiappe and Grellet-Tinner (2000).

2948. Testa, stratum tertius, status:
a. absent; **b.** present.
Note.—See: Grellet-Tinner (2005: appendix 1, table 2, character C8).

2949. Testa, stratum quartus, status:
a. absent;
b. present, aprismatic delimitation.
Note.—See: Grellet-Tinner (2005: appendix 1, table 2, characters C9 and C13).

2950. Testa, stratum mamillarium, forma generalis:
a. comparatively broad, moderately dense;
b. comparatively narrow, densely compacted.
Note.—See: A. B. Gilbert (1971, 1979); Currie and Horner (1988); Horner and Weishampel (1988); Mikhailov (1992, 1995, 1997); Norell et al. (1994, 2001); Horner (1997); Manning et al. (1997); Mateus et al. (1997); Chiappe et al. (1998); Grellet-Tinner (2001, 2003); G. Mayr (2003a: appendix I, character 54); G. Mayr and Clarke (2003: appendix A, character 147).

2951. Testa, stratum mamillarium, conus mamillae, differentiated galerum basale mamillae, status:
a. present; **b.** absent.
Note.—See: Mikhailov (1992, 1995, 1997); Chiappe et al. (1998); Grellet-Tinner (2001, 2003).

2952. Testa, strata secundus et tertius, ratio of thicknesses of latter stratum divided by former stratum, magnitudo:
a. less than 0.10;
b. greater than 0.10;

x. noncomparable by absence of one or both strata (Sauropoda, Troödontidae, Dromornithidae).

Note.—See: Grellet-Tinner (2005: appendix 1, table 2, character C15); Grellet-Tinner (2005: appendix 2, character 17).

2953. Testa, porus, canaliculus testae, status:

a. present;

b. absent, or at least fail to penetrate surface.

Note.—See: King (1993: annotation 64); Mikhailov (1992, 1995, 1997); Norell et al. (1994, 2001); Horner (1997); Manning et al. (1997); Mateus et al. (1997); Chiappe et al. (1998); Grellet-Tinner (2001, 2003).

2954. Testa, porus, canaliculus testae, systema rami, forma (**ordered**):

a. complexus; **b.** bifurcatus;

c. singularis.

Note.—See: Mikhailov (1992, 1995, 1997); Norell et al. (1994, 2001); Horner (1997); Manning et al. (1997); Mateus et al. (1997); Chiappe et al. (1998); Grellet-Tinner (2001, 2003); Grellet-Tinner (2005: appendix 2, character 22).

DISCUSSION

The richness of characters compiled during this analysis of specimens and survey of the literature is significantly higher than any previous qualitative characterization of a group within Tetrapoda, let alone any limited to Aves. This wealth stemmed in part from the extensive anatomical literature available for consultation. The primary basis for this evidence, however, was our first-hand survey of variation (especially osteological) within Aves that was driven by: (*i*) the nomenclatural framework provided by Baumel et al. (1993); (*ii*) several series of synoptic specimens gathered from collections at the USNM and CMNH and several other institutions, as well as excellent private and institutional library resources; (*iii*) a goal to find variation amenable to characterization for all osteological features of modern birds named within the *Nomina*, to include all characters of paleontological origin that we found to be interpretable and informative, to include characters of other systems (e.g., cranial, pectoral, and pelvic myology, cardiovascular system, and integument) that were feasible given remaining logistical limits; (*iv*) the recognition that "autapomorphies" in an analysis of representatives of mid-order terminals correspond (given subsurveys to confirm distributions within terminals) to synapomorphies in analyses of species-level terminals; and (*v*) logistical opportunities offered by the host institutions of the authors to pursue this multi-year project and financial support and other accommodations provided by the National Science Foundation (NSF).

Despite our gratification in the success of this survey, it is appropriate to raise two caveats. First, the magnitude of anatomical characters compiled here notwithstanding, even a cursory assessment of potentially informative, unexplored sources of additional characters suggests that this study is but the first step toward a morphological synthesis relevant to avian phylogeny. This realization is supported by the great number of characters tabled for present purposes, but that clearly includes characters worthy of reconsideration by subsequent workers. Another indication of sampling of morphological evidence to date is that simple constraints of time prevented our assessment of characters suggested by material or the literature, e.g., arthrological refinements of the pelvic appendage in long-limbed raptors (Goslow 1972; Burton 1978) or apparently conservative characters of the lingual musculature (W. Müller and Weber 1998; Tomlinson 2000). A third corroboration is achieved by paging through any of a number of chapters in the *Nomina* (Baumel et al. 1993)—e.g., systema cardiovasculare, systema urogenitalis, systemae nervosum centrale et periphericum, systema digestorium, or organa sensuum—to tally the hundreds of annotations including documented variation, let alone named features never studied for variation, that has yet to be included as a character in a phylogenetic analysis. Many of these annotations are highly suggestive of signal, but data for most are limited to preliminary explorations of *Gallus* and *Anas*. Despite appearances, morphological characterization of birds for phylogenetic reconstruction still remains in its infancy.

Second, success of the companion phylogenetic analyses of these data—i.e., to resolve relationships and provide a reasonable, well-supported resolved tree—remains to be demonstrated. The ancillary, optimistic goal that the resultant reconstruction will share significant components with those of other, comparatively comprehensive analyses of independent data (especially molecular) must await two analytical stages for assessment. The forthcoming analysis of these morphological data, not only ours but those of others, should allow a reasonably reliable evaluation of success on all counts.

Our personal hopes are that subsequent use of our data set will not be limited to computational races for still-shorter trees or quasi-analytical refinements pertaining to ordering, etc., but that at least some investigators will illustrate their commitment to empirical rigor by objective refinements and vetting of the characters, their descriptions, and assignments of taxa. Although we think that these processes optimally are accomplished separately (as opposed to circular or prejudicial tactics), we also feel that significant improvements are most likely to be made by workers with expertise in both anatomical empiricism and phylogenetic analysis, as well as an openness to new directions for anatomical study.

The merging of the present morphological data with molecular data deriving from the associated "higher-theropod section" of the NSF Tree of Life initiative (Cracraft et al. 2004) will present an unparalleled opportunity to explore the power and limitations of hypotheses deriving from diverse databases or "total" evidence. Whatever the future holds for that collaboration and subsequent refinements is beyond our ability to predict, but we remain most optimistic.

ACKNOWLEDGMENTS

This research was supported by National Science Foundation (NSF) grant BSR-9396249 to Livezey, NSF grant DEB-9815248 to Livezey and Zusi, NSF grant TOL-0228604 to Livezey (multicollaborative), and National Museum of Natural History grant RI-85337000 to Zusi. B. DeWalt and P. Trunzo (CMNH) provided additional financial and logistic support. We thank the curators of the following museums for permitting study of their collections or for lending specimens: National Museum of Natural History (USNM); American Museum of Natural History (AMNH); The (British) Natural History Museum, Tring and London (BMNH); Muséum national d'Histoire naturelle, Paris (MNHN); National Museum of Natural History Te Papa Tongarewa, Wellington (NZNM); Museum of Central Australia (MCA); Forschungsinstitut Senckenberg, Frankfurt (FS); Canterbury Museum of Christchurch, New Zealand (CC); and Museum of Natural Science, Louisiana State University (LSU).

Figures were drawn and labeled by T. Litwak. Digital photographs of skeletal specimens provided the basis for outline drawings that were subsequently refined for detail and shading, and labeled, digitally. R. Panza assisted in creation of a synoptic series of skin specimens and recording of characters thereof. B. DeWalt, P. Trunzo, and J. R. Wible coordinated logistics of publication. M. A. Schmidt and T. Moore provided organizational and editorial assistance of the text for publication.

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APPENDIX 1

Neornithine Exemplary Taxa and Synoptic Specimens

	Voucher Specimen(s) for Primary Exemplars			
Primary Exemplary Taxon	Skull(s) or Skeleton(s)	Spirit	Juvenile Skulls or Skeleton(s)	Crania interna
Struthio camelus	560081	541232 616067	553658 BM 1952.3.1	34361
Rhea americana	227485	615364	614472 BM 1899.11.10.6	20285
Casuarius casuarius	429823	512900 540395	18217 BM 1972.1.11	614778
Dromaius novaehollandiae	500379	512770	346696 BM 1952.1.18	500849
Apteryx australis	500629	289857	AMNH 5372 BM (not registered)	614807
Eudromia elegans	612018	18956	CMNH 9648	227489
Chauna torquata	614547	508683	AMNH 3617 BM 1954.5.3	345218
Anseranas semipalmata	347638	508679	—	621019
Anser albifrons	430298	508073	*Cygnus atratus* 553111	7328
Anas crecca	430882	510469	AMNH 11547 (*Nettapus*) AMNH 8737 (Anatidae) BMNH 1986.48.1 (*Anas*)	225539
Megapodius freycinet	557008	506643	560789	557018 558276 (*Eulipoa*)
Ortalis canicollis	345803	541313 (*O. motmot*)	320124 (*Crax*)	320124 560144 (*Crax*)
Meleagris gallopavo	556354	512892 CMNH (uncatalogued)	611021 501018	556394
Canachites canadensis	612135	512851	100465	428561
Callipepla gambelii	499285	506199	36544 (*Cyrtonyx*)	501011
Francolinus capensis	558454	507600	558461	558460
Alectoris graeca	540255	605024 (*A. chukar*)	—	291250
Gallus gallus	560790	512870	610627 BM 3/1952.2.106	18959 10161
Numida meleagris	430657	19975	BM 1897.5.10.49	476
Diomedea nigripes	488173	508101	289167 (*D. immutabilis*)	554698
Puffinus pacificus	498313	616252 (*P. lherminieri*)	489522 (*Macronectes*) 556265	613909 560136
Pachyptila desolata	491835	511109	553245	321488
Oceanites oceanicus	559795	508762	—	559796
Pelecanoides urinatrix	490900	511799	—	553240 460837 (*P. magellani*)
Spheniscus magellanicus	490223	511774	18541 489508 (*Pygoscelis*)	227674
Gavia stellata	491290	540648	—	347806
Podiceps cristatus	560592	542645	560771 (*Tachybaptus*)	557532
Fregata minor	289127	502929	289130	490766
Anhinga anhinga	610590	505097	—	488772
Phalacrocorax urile	19655	540979 (*P. auratus*)	12730	610589 560253 (*P. auratus*)
Sula dactylatra	498133	502926	BMNH (5 unregistered)	558371
Pelecanus thagus	489427	505633	559663	18483
Phaethon rubricauda	498263	503092	289150	498262
Ardea herodias	346390	225179	490091	18616
Nycticorax nycticorax	488680	510432	—	345634
Tigrisoma lineatum	562521	507867	—	343839 32983
Botaurus lentiginosus	501939	511060 225181	—	019773
Cochlearius cochlearius	612256	510441	613843	431901 621016
Ajaia ajaja	289109	506403	614543 614544	—
Scopus umbretta	431670	507597	BMNH 1929.10.11.2	555705
Plegadis falcinellus	501957	542606	614532	614532
Ciconia ciconia	605010	540336	605014 322593 (*Bostrychia*)	18200
Phoenicopterus ruber	558418	506162	—	429075 557972

	Voucher Specimen(s) for Primary Exemplars			
Primary Exemplary Taxon	Skull(s) or Skeleton(s)	Spirit	Juvenile Skulls or Skeleton(s)	Crania interna
Balaeniceps rex	344963	510452	—	—
Accipiter striatus	553261	540646	611757 (*Haliaetus*)	—
Gyps africanus	431403	346317 (*Necrosyrtes*)	—	19992
Pandion haliaetus	561545	541683 541684	489413	499151
Falco sparverius	502729	615376	502227 (*F. peregrinus*)	7265
Caracara plancus	343846	511797	—	18456
Sagittarius serpentarius	431491 555730	505392	—	555124 500279
Cathartes aura	610725	541006	—	19774
Turnix suscitator	562147	541794	347288	347288
Mesitornis spp.	345128 290927 (*Monias*)	289725 (*M. variegatus*)	—	—
Afrotis afra	558479	507603	AMNH 10897 MCA 2905 (*Ardeotis*)	532238
Cariama cristata	321574	512890 19790	—	555731
Eurypyga helias	345805	504067	—	429735 613747
Rhynochetos jubatus	18964	288538	—	—
Psophia crepitans	321843	507874	—	429842
Aramus guarauna	610796	615393	614587	224277 11795
Grus canadensis	432581	511696	100399	498720 554776
Heliornis fulica	19159 321493 555614	509509 (*Heliopais*)	—	—
Porphyrio martinica	610788	511727	347866 (*Rallus*)	17683 488580
Pedionomus torquatus	555614	506063	—	—
Jacana jacana	614605	503676	—	unlabeled 612089
Rostratula benghalensis	613016	540450	BMNH 1897.5.10.32	291554
Dromas ardeola	491967	511092	—	—
Haematopus ostralegus	557726	319145	610813	610816
Ibidorhyncha struthersii	292765	511474	—	—
Himantopus himantopus	555256	507303	610819 81498	225276 498731
Cladorhynchus leucocephalus	553592	UMMZ 225835	—	—
Burhinus oedicnemus	614337	539070	603501 614336	432021 227828
Glareola nordmanni	430839	616334 (*G. pratincola*)	—	347361
Cursorius cursor	603507	540155	502183	603503
Pluvialis dominica	498352	uncatalogued	561371 (*Charadrius*) 610811 (*Charadrius*)	7370
Chionis alba	488297	508787	—	548050
Heteroscelus incanus	557551	542123	18085 (*Tringa*) 610839 (*Actitis*) 479321 (*Limosa*)	18569
Phalaropus tricolor	555268	428594	—	225721
Thinocorus rumicivorus	434098	511829	—	—
Uria lomvia	502368	508742	Zusi (1993)	500091
Stercorarius maccormicki	488321	508590 (*S. skua*)	432590	488259
Rissa tridactyla	500133	503288	500046	224194
Chlidonias niger	499661	508473	—	288221
Rynchops niger	610931	uncatalogued	490744 Zusi (1962)	499306
Pterocles gutturalis	430847	506579 (*P. decoratus*)	429080	344845
Columba livia	556277	540319	613812	20296
Zenaida macroura	499474	510394 (*Z. aurita*)	225771	18644
Geopelia striata	613025	509274	292303	322383
Didunculus strigirostris	017793	81605	—	—
Goura cristata	345081	507589	—	345078
Ducula aenea	562008	511657 (*D. pacifica*)	560659 (*Treron*)	344618
Raphus cucullatus	—	—	BMNH, London	—
Pezophaps solitaria	—	—	BMNH, London	—
Trichoglossus haematodus	347654	616027	—	unlabeled

Primary Exemplary Taxon	Voucher Specimen(s) for Primary Exemplars			
	Skull(s) or Skeleton(s)	Spirit	Juvenile Skulls or Skeleton(s)	Crania interna
Cacatua galerita	429841	343144 505166	MCA (uncatalogued) (*Calyptorhynchus*)	16639 615001
Amazona autumnalis	612297	541027	CMNH 15491 (*Ara*) 558857	612222
Melopsittacus undulatus	224815	616017	—	320893
Cuculus canorus	603559	539021	557148	343409
Coccyzus americanus	290158	542305	558867 (*Piaya*)	4903
Crotophaga ani	492389	512672	491703 (*C. sulcirostris*)	320959
Geococcyx californianus	346493	85250	—	501302
Centropus goliath	557152	507431	557165 613056 (*C. viridis*)	557167
Corythaixoides concolor	558533	290552 (*C. leucogaster*)	430305 430536 (*Tauraco*)	429090
Opisthocomus hoazin	431010	431267	223903	431012
Tyto alba	553887	539744	344477 343261	18953
Phodilus badius	20310	509512	—	—
Otus scops	603589	505074	603598 (*Athene*)	60359
Strix varia	612007	431144	556904 (*Asio*)	6454
Steatornis caripensis	560206	507798	BMNH (unpublished)	—
Podargus strigoides	612704	429760	AMNH 10384	611818
Nyctibius griseus	559134	504241	—	—
Aegotheles cristatus	612708	542627	—	—
Caprimulgus europaeus	603603	538055	LSU 113160 (*Chordeiltes*)	unlabeled
Hemiprocne comata	488343	505630 (*H. longipennis*) 290040	—	—
Cypseloides niger	555770	616113 511010	—	289436
Apus pallidus	582353	540245 507280 (*A. affinis*)	611836 (*A. affinis*) LSU 113152 (*Chaetura*)	582355
Glaucis hirsuta	562735	505480	USNM 288394 (*Chlorostilbon*)	unlabeled
Colius striatus	430538	507279 505105	—	291096 558549
Pharomachrus mocinno	347303	509816	—	615086
Trogon viridis	559345	506369 (*T. citreolus*)	Senckenberg 3669 (*T. viridis*)	345900 346640
Alcedo atthis	557190	223975	613062 610992 (*Ceryle*)	613063 291661
Halcyon sancta	561609	505847 (*H. chloris*)	—	613750
Todus subulatus	555806	510956	—	555803 unlabeled
Momotus momota	559488	343963	—	428664 613751
Merops apiaster	603619	540148	Senckenberg M1495 (*M. pusillus*) BMNH 1952.2.535 (*Nyctiornis*)	431680
Coracias garrulus	552950	510190	612716 (*Eurystomus*)	490568 430634
Brachypteracias leptosomus	223863 223864 (*Atelornis*)	—	—	—
Leptosomus discolor	291844	—	—	—
Upupa epops	603654	539180	—	603633 612622
Phoeniculus purpureus	322395	288588	—	502333 289548
Tockus erythrorhynchus	558554	290614	345443 (*Ceratogymna*)	322668
Galbula ruficauda	612057	541355	—	322980
Monasa nigrifrons	562215	541350	—	321539
Megalaima haemacephala	613078	510100	—	432019
Semnornis rhamphastinus	346961	509817	—	490614 610558
Indicator variegatus	428639	429673	—	429664 (*I. minor*)
Aulacorhynchus prasinus	346922	540590	—	431031
Ramphastos vitellinus	562739	508691	291970 (*R. sulfuratus*)	346728 553657
Jynx torquilla	602913	541124	BMNH 5/299	614833
Picoides villosus	555325	33708	613084 (*P. funebris*)	614405
Menura novaehollandiae	18265 19299	CMNH 1834	—	—

Primary Exemplary Taxon	Voucher Specimen(s) for Primary Exemplars			
	Skull(s) or Skeleton(s)	Spirit	Juvenile Skulls or Skeleton(s)	Crania interna
Pitta erythrogaster	562128	509234	—	612621 615027
Pitangus sulfuratus	554357	506400	—	555987
Ptilonorhynchus violaceus	612640	429715	—	559121
Aphelocoma ultramarina	553961	506316	614941 224532 (*Corvus*)	553904 11292 (*Corvus*)
Bombycilla cedrorum	561354	509820	—	321909
Parus atricapillus	556255	81680	—	4950 427814
Passer domesticus	612184	538929	502723	492860 502682

APPENDIX 2

Data Matrix

The enclosed compact disc contains the data matrix—35 outgroups + 150 ingroups = 185 taxa (rows) by 2,954 characters (columns)—that corresponds to the characters described in the present monograph and subsequently analyzed (Livezey and Zusi 2006). The matrix included (Macintosh OS IX-X) is a native MacClade (version 4) matrix, a user-friendly format used principally by the authors in the companion analyses and in which "essential" ordering of characters and other primary options were included (Livezey and Zusi 2006).

Columns and rows correspond to characters and taxa, respectively, and characters are sequenced using arabic numerals and states thereof by lower-case letters. Polymorphism codes appear, for example, as "a/b." Missing data are symbolized by "?." These options may undergo modifications in translation of the matrix from MacClade to Nexus versions, so users are advised to undertake such with caution.

Also provided, only in command form for MacClade, is a list (command format) specifying ordered (multistate) characters. Methodological details are given in the analytical work. However, note that multistate entries were read as "polymorphism" not as the default "uncertainty." Rooting was designated to use the outgroup as paraphyletic to the ingroup.

TABLE 1.—TERMS AND ABBREVIATIONS FOR FIGURES.

I—vertebrae synsacrales, sectio I—thoracicae, pt.
II—vertebrae synsacrales, sectio II—lumbares
III—vertebrae synsacrales, sectio III—(eu) sacrales
IV—vertebrae synsacrales, sectio IV—caudales, pt.
acrom.—acromion
ala parasphen.—ala parasphenoidalis
ala postacet. ilii—ala postacetabularis ilii
ala preacet. ilii—ala preacetabularis ilii
anc. lig. jugomand. ext.—ancora ligamenti jugomandibularis externus
anc. m. AME, pars cor.—ancora musculi adductor mandibulae externus, pars coronoidea
ang. basalar. proc.—angulus basalaris processi
ang. caud. corp.—angulis caudalis corporis
ang. caudomed. pal.—angulus caudomedialis palatini
ang. med. cor.—angulus medialis coracoidei
ang. postocul.—angulus postocularis
ang. subterm.—angulus subterminalis
ang. tom. max.—angulus tomialis maxillaris
ang. tom. premax.—angulus tomialis premaxillaris
annul. tymp.—annulus tympanicus
ansa costotransv.—ansa costotransversaria
aper. nas. oss.—apertura nasi ossea
apex car.—apex carinae
apex pubis
apex rostri
apon. oss.—aponeurosis ossificans
apon. zyg. oss.—aponeurosis zygomaticus osseus
apoph. furc.—apophysis furculae
arc. atlan.—arcus atlantis
arc. interzyg.—arcus interzygapophysialis
arc. jug.—arcus jugalis
arc. orig. m. extens. long. digiti maj.—arcus origo musculi extensor longus digiti majoris
arc. parameat.—arcus parameaticus
arc. suborbit.—arcus suborbitalis
arc. vert.—arcus vertebrae
arc. zygom.—arcus zygomaticus
area interart.—area interarticularis
art. intrapal.—articulatio intrapalatina
art. max.-arc.—articulatio maxillo-arcualis
art. pter.-basipter.—articulatio pterygobasipterygoidea
art. pter.-pal.—articulatio pterygopalatina
art. quad.-quadratojug.—articulatio quadrato-quadratojugalis
art. quad.-sphen.—articulatio quadrato-sphenoidalis
bulla intumescen. lumbo.—bulla intumescentia lumbosacralis
can. hypotars.—canalis hypotarsus
can. m. ext. dig. long.—canalis musculi extensor digitorum longus
can. m. flex. dig. long.—canalis musculi flexor digitorum longus
can. m. flex. hall. long.—canalis musculi flexor hallucis longus
can. n. hypogl.—canales nervi hypoglossi
can. ophthalm. ext.—canalis ophthalmicus externus
can. semicirc. rost.—canalis semicircularis rostralis
cap. fem.—caput femoris
cap. fib.—caput fibulae
cap. hum.—caput humeri
cap. phal.—caput phalangis
cap. rad.—caput radii
capit. cost.—capitulum costae
capit. otic.—capitulum oticum
capsul. nas. oss.—capsula nasalis osseae
car. iliac. dors.—carina iliacae dorsales
car. oss.—carina ossea
car. parasphen.—carina parasphenoidalis
car. ster.—carina sterni
cavum m. ethmomand.—cavum musculi ethmomandibularis
cavum nas. olfac.—cavum nasi olfactorii
cavum trach. ster.—cavum trachealis sterni
cavum tymp.—cavum tympanicum
choan. phar. oss.—choana pharyngealis ossea
clavicula
coll. cost.—collum costae
coll. fem.—collum femoris
coll. metacarp.—collum metacarpalis
concav. infracris.—concavitas infracristalis
concav. lat.—concavitas lateralis
cond. caud. quad.—condylus caudalis quadrati
cond. dors. hum.—condylus dorsalis humeri
cond. dors. uln.—condylus dorsalis ulnae
cond. lat. —condylus lateralis
cond. lat. quad.—condylus lateralis quadrati
cond. med.—condylus medialis
cond. med. quad.—condylus medialis quadrati
cond. occip.—condylus occipitalis
cond. vent. hum.—condylus ventralis humeri
cond. vent. uln.—condylus ventralis ulnae
corp. atlan.—corpus atlantis
corp. carpometacarp.—corpus carpometacarpi
corp. cost.—corpus costae
corp. fib.—corpus fibulae
corp. os. premax.—corpus ossis premaxillaris
corp. quad.—corpus quadrati
corp. rad.—corpus radii
corp. scap.—corpus scapulae
corp. ster.—corpus sterni
corp. vert.—corpus vertebrae
cost. vert.—costi vertebralis
cot. art.—cotyla articularis
cot. caud. mand.—cotyla caudalis mandibulae
cot. dors.—cotyla dorsalis
cot. hum.—cotyla humeralis
cot. lat.—cotyla lateralis

cot. lat. mand.—cotyla lateralis mandibulae
cot. med.—cotyla medialis
cot. med. mand.—cotyla medialis mandibulae
cot. quad. otici—cotyla quadrati otici
cot. quad. squam.—cotyla quadrati squamosa
cot. scap.—cotyla scapularis
cot. vent.—cotyla ventralis
cris. art. stern.—crista articularis sternalis
cris. basil. trans.—crista basilaris transversa
cris. bicip.—crista bicipitalis
cris. cnem. cran.—crista cnemialis cranialis
cris. cnem. lat.—crista cnemialis lateralis
cris. deltopect.—crista deltopectoralis
cris. fib.—crista fibularis
cris. fos. parabas.—crista fossa parabasalis
cris. front. int.—crista frontalis interna
cris. hypotars.—crista hypotarsalis
cris. iliac. dors.—crista iliaca dorsalis
cris. iliac. dorsolat.—crista iliaca dorsolateralis
cris. iliosynsac.—crista iliosynsacralis
cris. lat. spin. ilii—cristula lateralis spinae ilii
cris. lig.—crista ligamentosa
cris. margin. cerebel.—crista marginalis cerebelli
cris. med. car.—crista medialis carinae
cris. med. hypotars.—crista medialis hypotarsi
cris. medioplant.—crista medioplantaris
cris. m. depr. mand.—crista musculi depressor mandibulae
cris. m. scapulohum. caud.—crista musculi scapulohumeralis caudalis
cris. nuch. lat.—crista nuchalis lateralis
cris. nuch. transv.—crista nuchalis transversa
cris. otica dors.—crista otica dorsalis
cris. patell.—crista patellaris
cris. plant. lat.—crista plantaris lateralis
cris. plant. med.—crista plantaris medialis
cris. postocul.—crista postocularis
cris. postzygom.—crista postzygomatica
cris. procor.—crista procoracoidei
cris. sagitt.—crista sagittalis
cris. spin. synsac.—crista spinosa synsacri
cris. supracond. med.—crista supracondylaris medialis
cris. supraorb.—crista supraorbitalis
cris. tect. caud.—crista tecti caudalis
cris. temp. dors.—crista temporalis dorsalis
cris. temp. rost.—crista temporalis rostralis
cris. temp. vent.—crista temporalis ventralis
cris. tent.—crista tentorialis
cris. tibiofib.—crista tibiofibularis
cris. tom.—crista tomialis
cris. transvers. obl.—crista transverso-obliqua
cris. troch.—crista trochlearis
cris. trochant.—crista trochantericus
cris. vallec.—crista vallecularis
cris. vent.-med. pal.—crista ventromedialis palatini
dors. sell.—dorsum sellae
emin. costolat.—eminentia costolateralis
emin. intercond.—eminentia intercondylaris
epicond. dors.—epicondylus dorsalis
epicond. lat.—epicondylus lateralis
epicond. med.—epicondylus medialis
epicond. vent.—epicondylus ventralis
extrem. caud.—extremitas caudalis
extrem. dist. rad.—extremitas distalis radii
extrem. omal. cor.—extremitas omalis coracoidei
extrem. omal. furc.—extremitas omalis furculae
fac. art. antitrochant.—facies articularis antitrochanterica
fac. art. caud.—facies articularis caudalis
fac. art. clav.—facies articularis clavicularis
fac. art. cran.—facies articularis cranialis
fac. art. digiti alul.—facies articularis digiti alulae
fac. art. digiti maj.—facies articularis digiti majoris
fac. art. digiti min.—facies articularis digiti minoris
fac. art. fib. dist.—facies articularis fibulae distalis
fac. art. fib. prox.—facies articularis fibulae proximalis
fac. art. hum.—facies articularis humeralis
fac. art. intercost.—facies articularis intercostalis
fac. art. lat.—facies articularis lateralis
fac. art. med.—facies articularis medialis
fac. art. parasphen.—facies articularis parasphenoidalis
fac. art. radiocarp.—facies articularis radiocarpalis
fac. art. scap.—facies articularis scapularis
fac. art. uln.—facies articularis ulnae
fac. art. ulnocarp.—facies articularis ulnocarpalis
fac. art. zyg. caud.—facies articularis zygapophysis caudalis
fac. art. zyg. cran.—facies articularis zygapophysis cranialis
fac. carpometacarp.—facies carpometacarpalis
fac. caud.—facies caudalis
fac. cran.—facies cranialis
fac. dors.—facies dorsalis
fac. gastroc.—facies gastrocnemialis
fac. lat.—facies lateralis
fac. med.—facies medialis
fac. plant.—facies plantaris
fac. rad.—facies radialis
fac. uln.—facies ulnaris
fac. vent.—facies ventralis
fac. vent. rost.—facies ventralis rostri
fen. antorb.—fenestra antorbitalis
fen. caud. mand.—fenestra caudalis mandibulae
fen. infraspin. car.—fenestra infraspinosa carinae
fen. intercrist.—fenestra intercristalis
fen. interspin.—fenestra interspinosis
fen. ischiopub.—fenestra ischiopubica
fen. rost. mand.—fenestra rostralis mandibulae
fen. ventrolat.—fenestra ventrolateralis
fen. ventromed.—fenestra ventromedialis
fibula
font. interorb.—fonticulus interorbitalis

font. laterosphen.-pro.—fonticulus laterosphenoproöticus
font. occip.—fonticulus occipitalis
font. orbitocran.—fonticulus orbitocranialis
for. a. sphen.—foramen arteria sphenoidea
for. acetab.—foramen acetabuli
for. arcocost. caud.—foramen arcocostalis caudalis
for. arcocost. cran.—foramen arcocostalis cranialis
for. fos.—foramen fossae
for. ilioisch.—foramen ilioischiadicum
for. inteross. dist.—foramen interosseum distale
for. inteross. prox.—foramen interosseum proximale
for. intertransv.—foramen intertransversarii
for. magn.—foramen magnum
for. n. cochl.—foramen nervi cochlearis
for. n. facialis—foramen nervi facialis
for. n. max.-mand.—foramen nervi maxillomandibularis
for. n. oculomot.—foramen nervi oculomotorii
for. n. olfact.—foramen nervi olfactorii
for. n. ophthal.—foramen nervi ophthalmici
for. n. opt.—foramen nervi optici
for. n. supracor.—foramen nervi supracoracoidei
for. n. troch.—foramen nervi trochearis
for. n. vagi—foramen nervi vagi
for. neurovasc.—foramen neurovascularium
for. obtur.—foramen obturatum
for. orbitonas. lat.—foramen orbitonasalis lateralis
for. orbitonas. med.—foramen orbitonasalis medialis
for. pn.—foramen pneumaticum
for. pn. artic.—foramen pneumaticum articulare
for. pn. pal.—foramen pneumaticum palatini
for. ram. occip. a. ophthalm.—foramen ramus occipitalis, arteria ophthalmica
for. ram. pal.—foramen ramus palatinus
for. ram. sphenomax.—foramen ramus sphenomaxillaris
for. rost.—foramen rostri
for. transv.—foramen transversaria
for. v. occip. dorsomed.—foramen veni occipitalis dorsomedialis
for. v. occip. ext.—foramen veni occipitalis externus
for. vasc. dist.—foramen vasculare distale
for. vasc. prox.—foramen vasculare proximale
for. vert.—foramen vertebrale
fos. acust. int.—fossa acustica interna
fos. adit.—fossa aditus
fos. art. quad.—fossa articularis quadrati
fos. auric. cerebel.—fossa auricularis cerebelli
fos. cerebel.—fossa cerebelli
fos. condyl.—fossa condyloidea
fos. cran. caud.—fossa cranii caudalis
fos. cran. rost.—fossa cranii rostralis
fos. flex.—fossa flexoria
fos. gang. trigem.—fossa ganglii trigemini
fos. gl. nas.—fossa glandulae nasalis
fos. iliocaud.—fossa iliocaudalis
fos. infratroch.—fossa infratrochlearis
fos. intercot.—fossa intercotylaris
fos. m. AME, pars art., cap. ext.—fossa musculi adductor mandibulae externus pars articularis, caput externa
fos. m. brach.—fossa musculi brachialis
fos. metatars. I—fossa metatarsi I
fos. musc. temp.—fossa musculorum temporalium
fos. olecr.—fossa olecrani
fos. parabas.—fossa parabasalis
fos. parahypotars. med.—fossa parahypotarsalis medialis
fos. pneumotric.—fossa pneumotricipitalis
fos. poplit.—fossa poplitea
fos. renal.—fossa renalis
fos. renal., pars isch.—fossa renalis, pars ischiadica
fos. renal., pars pudenda—fossa renalis, pars pudenda
fos. retrocris.—fossa retrocristalis
fos. subcond.—fossa subcondylaris
fos. supratroch.—fossa supratrochlearis
fos. supratroch. plant.—fossa supratrochlearis plantaris
fos. tect. mesen.—fossa tecti mesencephali
fov. carp. cran.—fovea carpalis cranialis
fov. corp. nerv.—foveae corpusculorum nervosorum
fov. cost. capit.—fovea costalis capituli
fov. cost. tuberc.—fovea costalis tuberculi
fov. gang. vago-gloss.—fovea ganglii vagoglossopharyngealis
fov. lig. cap.—fovea ligamenti capitis
fov. lig. collat.—fovea ligamenti collateralis
fov. lig. vent.—fovea ligamenti ventralis
fov. subtroch.—fovea subtrochlearis
fov. tend. m. tibial. cran.—fovea tendinis musculi tibialis cranialis
ham. rostr. max.—hamulus rostri maxillae
hiatus labr.—hiatus labri
humerus
ilium
impr. lig. collat. lat.—impressio ligamenti collateralis lateralis
impr. lig. collat. med.—impressio ligamenti collateralis medialis
impr. m. brach.—impressio musculi brachialis
impr. m. coracobrach.—impressio musculi coracobrachialis
impr. m. depr. mand.—impressio musculi depressor mandibulae
impr. m. iliotrochant.—impressio musculi iliotrochantericus
impr. m. ischiofem.—impressio musculi ischiofemoralis
impr. m. obtur.—impressio musculi obturatorius
impr. m. pect.—impressio musculi pectoralis

impr. m. pseudotemp. prof.—impressio musculi pseudotemporalis profundus
impr. m. pter.—impressio musculi pterygoideus
impr. m. scapulotric.—impressio musculi scapulotriceps
impr. m. supracorac.—impressio musculi supracoracoideus
incis. cap.—incisura capitis
incis. caudolat.—incisura caudolateralis
incis. fos.—incisura fossae
incis. intercond.—incisura intercondylaris
incis. intercost.—incisura intercostalis
incis. intermed.—incisura intermedia
incis. intertroch.—incisura intertrochlearis
incis. intertroch. med.—incisura intertrochlearis medialis
incis. lat.—incisura lateralis
incis. margin.—incisura marginis
incis. med. cond.—incisura mediana condyli
incis. metacarp.—incisura metacarpalis
incis. sut. iliosyn.—incisura sutura iliosynsacralis
intumescen.—intumescentia
ischium
labr. cond. dors.—labrum condyli dorsalis
labr. ext. cor.—labrum externum coracoidei
labr. ext. ster.—labrum externum sternae
labr. int. cor.—labrum internum coracoidei
labr. int. ster.—labrum internum sternae
lac. interzyg.—lacuna interzygapophysialis
lam. arcocost.—lamina arcocostalis
lam. corporocost.—lamina corporocostalis
lam. ellipt. art.—lamina elliptica articularis
lam. ellips. lat.—lamina ellipsoidalis lateralis
lam. parasphen.—lamina parasphenoidalis
lamel. dors., choan. pal.—lamella dorsalis, pars choanalis palatini
lamel. vent., choan. pal.—lamella ventralis, pars choanalis palatini
linea intermusc. caud.—linea intermuscularis caudalis
linea intermusc. cran.—linea intermuscularis cranialis
linea intermusc. dorsolat.—linea intermuscularis dorsolateralis
linea intermusc. ventromed.—linea intermuscularis ventromedialis
linea m. latiss. dors.—linea muscularis latissimus dorsi
linea musc. vent.—linea muscularis ventralis
m. add. mand. oss. quad.—musculus adductor mandibulae ossis quadrati
m. AME, pars art., cap. ext.—musculus adductor mandibulae externus, pars articularis, caput externa
m. AME, pars art., cap. int.—musculus adductor mandibulae externus, pars articularis, caput interna
m. AME, pars coron., cap. med.—musculus adductor mandibulae externus, pars coronoidea, caput mediale
m. AME, pars coron., cap. temp.—musculus adductor mandibulae externus, pars coronoidea, caput temporale
m. AME, pars superf.—musculus adductor mandibulae externus, pars superficialis
m. AME, pars zyg.—musculus adductor mandibulae externus, pars zygomatica
m. depr. mand., pars prof.—musculus depressor mandibulae, pars profunda
m. depr. mand., pars sup.—musculus depressor mandibulae, pars superficialis
m. ethmomand.—musculus ethmomandibularis
m. prot. pter. et quad.—musculus protractor pterygoidei et quadrati
m. pseud. prof.—musculus pseudotemporalis profundus
m. pseud. sup., pars lat., cap. intramand.—musculus pseudotemporalis superficialis, pars lateralis, caput intramandibulare
m. pseud. sup., pars lat., cap. orb.—musculus pseudotemporalis superficialis, pars lateralis, caput orbitale
m. pseud. sup., pars lat., cap. temp.—musculus pseudotemporalis superficialis, pars lateralis, caput temporale
m. pseud. sup., pars med.—musculus pseudotemporalis superficialis, pars medialis
m. pteryg., pars lat., cap. caud.—musculus pterygoideus, pars lateralis, caput caudale
m. pteryg., pars lat., cap. rost.—musculus pterygoideus, pars lateralis, caput rostrale
m. pteryg., pars med., cap. caud.—musculus pterygoideus, pars medialis, caput caudale
m. pteryg., pars med., cap. rost.—musculus pterygoideus, pars medialis, caput rostrale
mandibula
marg. cost. ster.—margo costalis sterni
marg. dors. scap.—margo dorsalis scapularis
marg. med. cot. med.—margo medialis, cotyla medialis
marg. vent. scap.—margo ventralis scapularis
notar.—notarium
olecr.—olecranon
os basioccip.—os basioccipitale
os basisphen.—os basisphenoidale
os carpi radiale
os carpi ulnare
os coracoideum
os ecteth.—os ectethmoidale
os exoccip.—os exoccipitale
os front.—os frontale
os jug.—os jugale
os lacrim.—os lacrimale
os laterosphen.—os laterosphenoidale
os max.—os maxillare

os meseth.—os mesethmoidale
os metacarp. alul.—os metacarpale alulare
os metacarp. maj.—os metacarpale majus
os metacarp. min.—os metacarpale minus
os nas.—os nasale
os pal.—os palatinum
os pariet.—os parietale
os preartic.—os prearticulare
os premax.—os premaxillare
os pter.—os pterygoideum
os quad.—os quadratum
os quad.-jug.—os quadratojugale
os squam.—os squamosum
os supraoccip.—os supraoccipitale
ost. can. carot.—ostium canalis carotici
ost. can. ophth. ext.—ostium canalis ophthalmici externi
ost. can. tubae pharyngotymp.—ostium canalis tubae pharyngotympanicae
ost. phar.—ostium pharyngeale
papill. remig. caud. dors.—papillae remigales caudales dorsales
papill. remig. vent.—papillae remigales ventrales
pars dors.—pars dorsalis
pars lat., cap. intramand.—pars lateralis, caput intramandibularis
pars lat., cap. orb.—pars lateralis, caput orbitale
pars lat., cap. quad.—pars lateralis, caput quadrati
pars lat., cap. subtemp.—pars lateralis, caput subtemporale
pars lat., cap. temp.—pars lateralis, caput temporale
pars lat. pal.—pars lateralis palatini
pars max. pal.—pars maxillaris palatini
pars med.—pars medialis
pars pal. pter.—pars palatina pterygoidei
pars vent.—pars ventralis
pes os lacrim.—pes os lacrimale
phalanx digiti alul.—phalanx digiti alulae
phalanx digiti min.—phalanx digiti minoris
phalanx dist. digiti maj.—phalanx distalis digiti majoris
phalanx prox. digiti maj.—phalanx proximalis digiti majoris
pila car.—pila carinae
pila cost.—pila costalis
pila ilioisch.—pila ilioischiadica
pila obliqua fos.—pila obliqua fossae
pila otica
pila supranas.—pila supranasalis
plan. transv. synsac.—planum transversalium synsacralis
pons max.-jug.—pons maxillarojugalis
pons supratend.—pons supratendineus
proc. access. pal.—processus accessorius palatini
proc. acrocor.—processus acrocoracoideus
proc. acrom.—processus acromialis
proc. alul.—processus alularis
proc. antitrochan.—processus antitrochantericus
proc. art. clav.—processus articularis claviculae
proc. art. sternocost.—processus articularis sternocostalis
proc. basipter.—processus basipterygoideus
proc. calcar.—processus calcaris
proc. carot.—processus caroticus
proc. coron.—processus coronoideus
proc. cost.—processus costalis
proc. craniolat.—processus craniolateralis
proc. dorsolat. nas.—processus dorsolateralis nasalis
proc. extens.—processus extensorius
proc. flex.—processus flexorius
proc. front. nas.—processus frontalis nasalis
proc. front. premax.—processus frontalis premaxillare
proc. interclav. dors.—processus interclavicularis dorsalis
proc. intermetacarp.—processus intermetacarpalis
proc. jug. max.—processus jugalis maxillare
proc. lat. cor.—processus lateralis coracoidei
proc. lat. mand.—processus lateralis mandibulae
proc. lat. parasphen.— processus lateralis parasphenoidalis
proc. m. bulbi ocul.—processus musculi bulbi oculii
proc. m. depr. mand.—processus musculi depressor mandibulae
proc. mand. quad.—processus mandibularis quadrati
proc. marg. caud.—processus marginis caudalis
proc. max. nas.—processus maxillaris nasale
proc. max. premax.—processus maxillaris premaxillare
proc. med. mand.—processus medialis mandibulae
proc. med. parasphen.—processus medialis parasphenoidalis
proc. odont.—processus odontoideus
proc. orb. lacrim.—processus orbitalis lacrimale
proc. orb. quad.—processus orbitalis quadrati
proc. otic. quad.—processus oticus quadrati
proc. pal. premax.—processus palatinus premaxillaris
proc. palat. max..—processus palatus maxillaris
proc. paroccip.—processus paroccipitalis
proc. pisif.—processus pisiformis
proc. postlat.—processus postlateralis
proc. postorb.—processus postorbitalis
proc. preacet.—processus preacetabularis
proc. premax. max.—processus premaxillaris maxillaris
proc. premax. nas.—processus premaxillaris nasalis
proc. procor.—processus procoracoideus
proc. pter. pal.—processus pterygoideus palatini
proc. retroart.—processus retroarticularis
proc. rost. pal.—processus rostralis palatini

proc. rostromed. pal.—processus rostromedialis palatini
proc. spin.—processus spinosus
proc. supracond. dors.—processus supracondylaris dorsalis
proc. supralabr.—processus supralabralis
proc. suprameat.—processus suprameatica
proc. supraocul.—processus supraocularis
proc. supraorb. lacrim.—processus supraorbitalis lacrimalis
proc. term. isch.—processus terminalis ischii
proc. transv.—processus transversarii
proc. uncin.—processus uncinati
proc. vent. corp.—processus ventralis corporis
proc. zygom.—processus zygomaticus
prom. musc. pal.—prominentia muscularis palatini
pubis
radius
ram. dors.—ramus dorsalis
ram. mand., caud.—ramus mandibulae, pars caudalis
ram. mand., interm.—ramus mandibulae, pars intermedia
ram. mand., symph.—ramus mandibulae, pars symphysialis
ram. vent.—ramus ventralis
recess. columel.—recessus columellae
recess. dorsocran. pn.—recesses dorsocraniales pneumatici
recess. infra-acrocor.—recessus infra-acrocoracoideus
recess. lat. corp. vert.—recessus lateralis corporis vertebrae
recess. pn. lat.—recessus pneumaticus lateralis
recess. tymp. caud.—recessus tympanicus caudalis
recess. tymp. dors.—recessus tympanicus dorsalis
recess. tymp. rost.—recessus tympanicus rostralis
retinac. extens. oss.—retinaculum extensorium osseum
rost. mand.—rostrum mandibulae
rost. max.—rostrum maxillae
rost. parasphen.—rostrum parasphenoidalis
scapula
scapus clav.—scapus claviculae
scapus isch.—scapus ischii
scapus pubis
sell. turc.—sella turcica
sept. interorb.—septum interorbitalis
sept. nas.—septum nasi
sesam. m. humerotric.—sesamoideum musculi humerotriceps
sesam. m. scapulotric.—sesamoideum musculi scapulotriceps
solum arcocost.—solum arcocostalis
spat. ilioisch.—spatium ilioischiadicum
spat. intermetacarp.—spatium intermetacarpale
spat. ischiopub.—spatium ischiopubicum
spin. comm.—spina communis
spin. ext. rost.—spina externa rostri
spin. fib.—spina fibulae
spin. supratransv. vert.—spina supratransversarii vertebrae
sternum
striae oss. transv.—striae ossis transversus
sulc. a. pal.—sulcus arteria palatini
sulc. antitrochant.—sulcus antitrochantericus
sulc. art. cor.—sulcus articularis coracoidei
sulc. car.—sulcus carinae
sulc. carot.—sulcus caroticus
sulc. extens.—sulcus extensorius
sulc. flex.—sulcus flexorius
sulc. hypotars.—sulcus hypotarsi
sulc. incis. transv.—sulcus incisurae transversus
sulc. intercnem.—sulcus intercnemialis
sulc. intercond.—sulcus intercondylaris
sulc. intercot.—sulcus intercotylaris
sulc. intercris.—sulcus intercristalis
sulc. inteross.—sulcus interosseus
sulc. m. humerotric.—sulcus musculi humerotriceps
sulc. m. scapulotric.—sulcus musculi scapulotriceps
sulc. m. sternocorac.—sulcus musculi sternocoracoideus
sulc. m. supracorac.—sulcus musculi supracoracoideus
sulc. n. olfact.—sulcus nervi olfactorius
sulc. nasi—sulcus nasi
sulc. olfact.—sulcus olfactorius
sulc. paratom.—sulcus paratomialis
sulc. patell.—sulcus patellaris
sulc. sellar. med.—sulcus sellaris medialis
sulc. supracor.—sulcus supracoracoideus
sulc. tend.—sulcus tendinis
sulc. tend. m. amb.—sulcus tendinis musculi ambientis
sulc. tend. m. long. coll. vent.—sulcus tendinis musculi longus colli ventralis
sulc. v. occip. ext.—sulcus veni occipitalis externus
sulc. v. semicirc.—sulcus veni semicircularis
sut. costouncin.—sutura costouncinatum
sut. frontonas.—sutura frontonasalis
sut. internas.—sutura internasalis
sut. par.-laterosphen.—sutura parietolaterosphenoidalis
symph. clav.—symphysis clavicularis
synchond. ischiopub.—synchondrosis ischiopubica
synost. ansae costotransv.—synostosis ansae costotransversariae
synost. metacarp. dist.—synostosis metacarpalis distalis
synsac.—synsacrum
term. spin.—terminus spinalis
tibiotarsus
torus dors.—torus dorsalis
trabec. caudodors.—trabecula caudodorsalis
trabec. caudolat.—trabecula caudolateralis

trabec. lat.—trabecula lateralis
trabec. med.—trabecula medialis
trach.— trachea
troch. art.—trochlea articularis
troch. cart. tib.—trochlea cartilaginis tibialis
troch. fib.—trochlea fibularis
troch. metatars. II—trochlea metatarsi II
troch. metatars. III—trochlea metatarsi III
troch. metatars. IV—trochlea metatarsi IV
trochant. fem.—trochanter femoris
tuberc. apical. procor.—tuberculum apicalis procoracoidei
tuberc. apon. vent.—tuberculum aponeurosis ventralis
tuberc. bicip. rad.—tuberculum bicipitale radii
tuberc. bicip. uln.—tuberculum bicipitale ulnae
tuberc. cap.—tuberculum capitis
tuberc. carp.—tuberculum carpale
tuberc. caud. quad.—tuberculum caudalis quadrati
tuberc. corac.—tuberculum coracoideum
tuberc. cost.—tuberculum costi
tuberc. dors.—tuberculum dorsalis
tuberc. extens.—tuberculum extensorium
tuberc. flex.—tuberculum flexorium
tuberc. labr. ext. ster.—tuberculum labri externi sternae
tuberc. m. AME., pars art., cap. ext.—tuberculum musculi adductor mandibulae externus, pars articularis, caput externus
tuberc. m. add. mand. oss. quad.—tuberculum musculi adductor mandibulae ossis quadrati
tuberc. m. delt., pars propat., pars caud., tend. brev.—tuberculum musculi deltoideus, pars propatagialis, pars caudale, tendo brevis
tuberc. m. gastroc. lat.—tuberculum musculi gastrocnemius, pars lateralis
tuberc. m. iliofib.—tuberculum musculi iliofibularis
tuberc. m. pron. sup.—tuberculum musculi pronator superficialis
tuberc. m. pseud. sup., pars lat.—tuberculum musculi pseudotemporalis superficialis, pars lateralis
tuberc. m. tib. cran.—tuberculum musculi tibialis cranialis
tuberc. preacet.—tuberculum preacetabulare
tuberc. retin. extens.—tuberculum retinaculi extensorii
tuberc. supracond. vent.—tuberculum supracondylare ventrale
tuberc. vent.—tuberculum ventrale
tum. pn. lacrim.—tumulus pneumaticus lacrimalis
ulna
vert. caud. lib.—vertebrae caudalis libre
vertex caudolat. ilii—vertex caudolateralis ilii
vertex craniolat. ilii—vertex craniolateralis ilii
vom.—vomer
zon. flex. craniofac.—zona flexoria craniofacialis
zon. flex. lat.—zona flexoria lateralis
zon. flex. med.—zona flexoria medialis
zon. flex. pal.—zona flexoria palatini
zyg. caud.—zygapophysis caudalis
zyg. cran.—zygapophysis cranialis

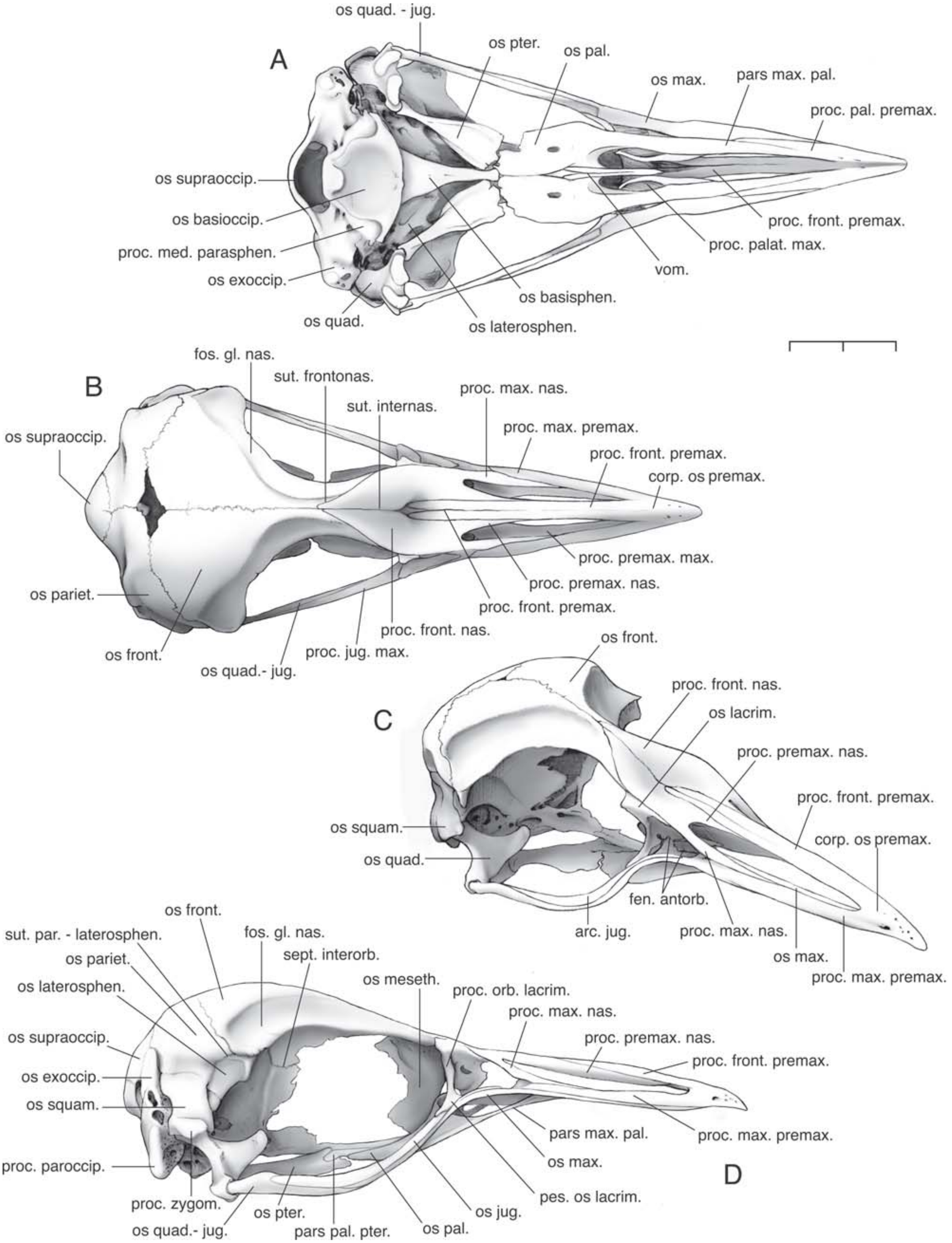


Fig. 1.—*Pygoscelis adeliae* (immature), cranium externum: (A) ventral view; (B) dorsal view; (C) craniodorsolateral view; and (D) lateral view. Unless otherwise noted: skulls are without mandibulae, appendicular elements are dextral, abbreviations are given in Table 1, and scale represents 2 cm.

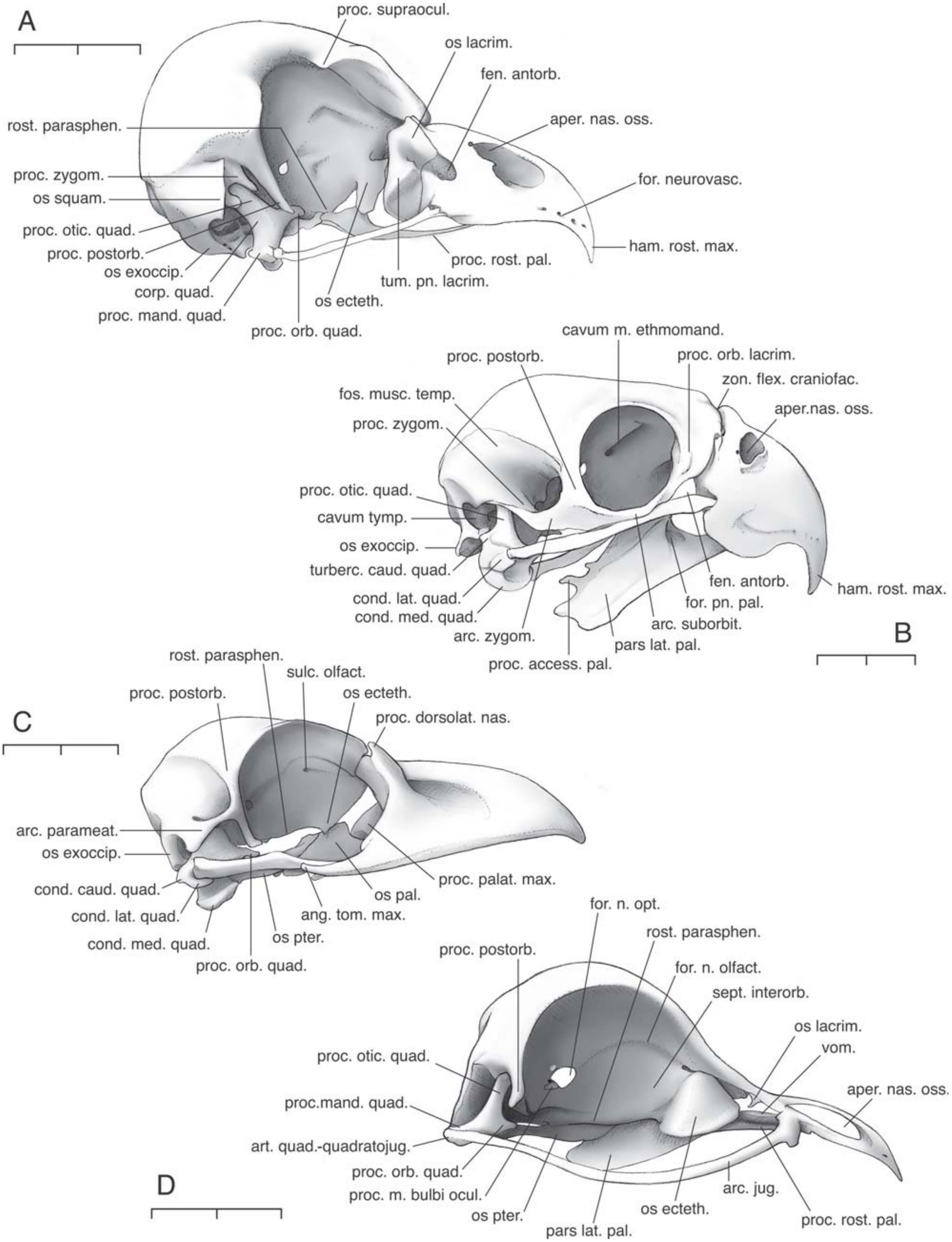
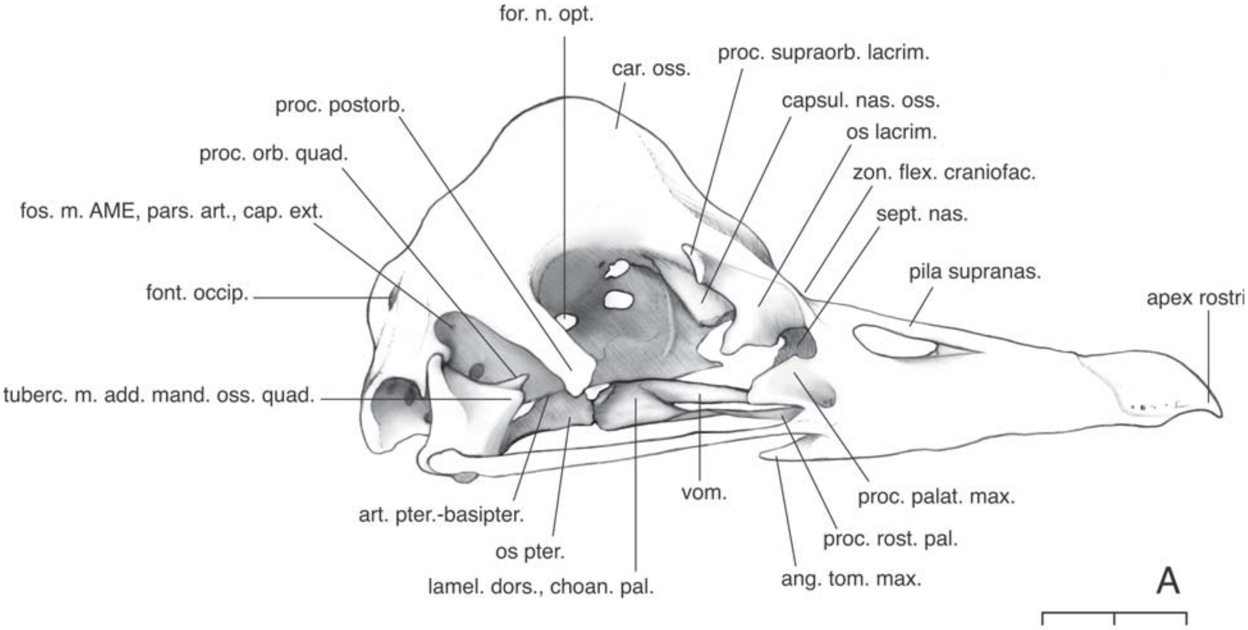


Fig. 2.—Cranium, externum, lateral view: (A) *Strix varia*; (B) *Cacatua galerita*; (C) *Podargus strigoides*; (D) *Nyctibius griseus*.



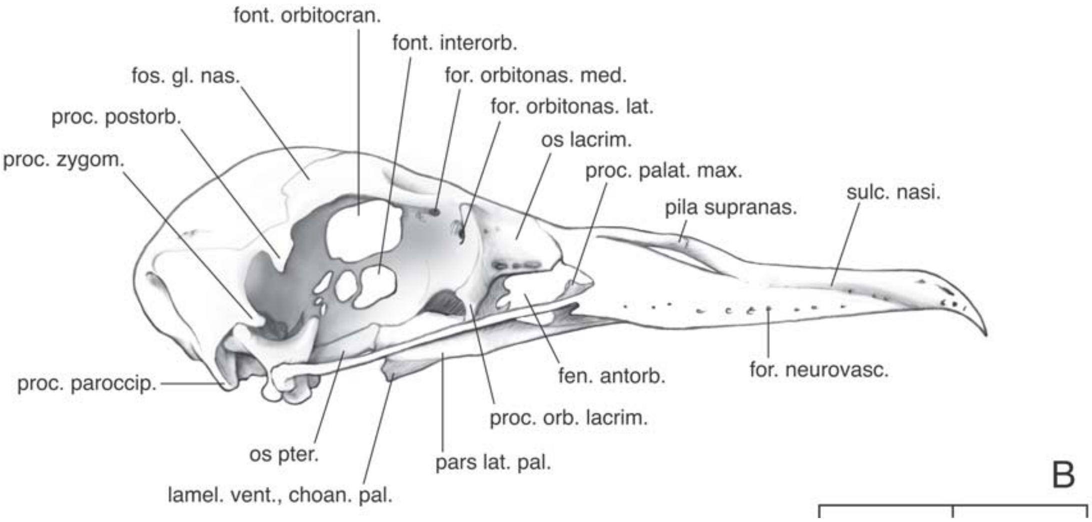


Fig. 3.—Cranium, externum, lateral view: (A) *Anseranas semipalmata*; (B) *Pachyptila salvini*.

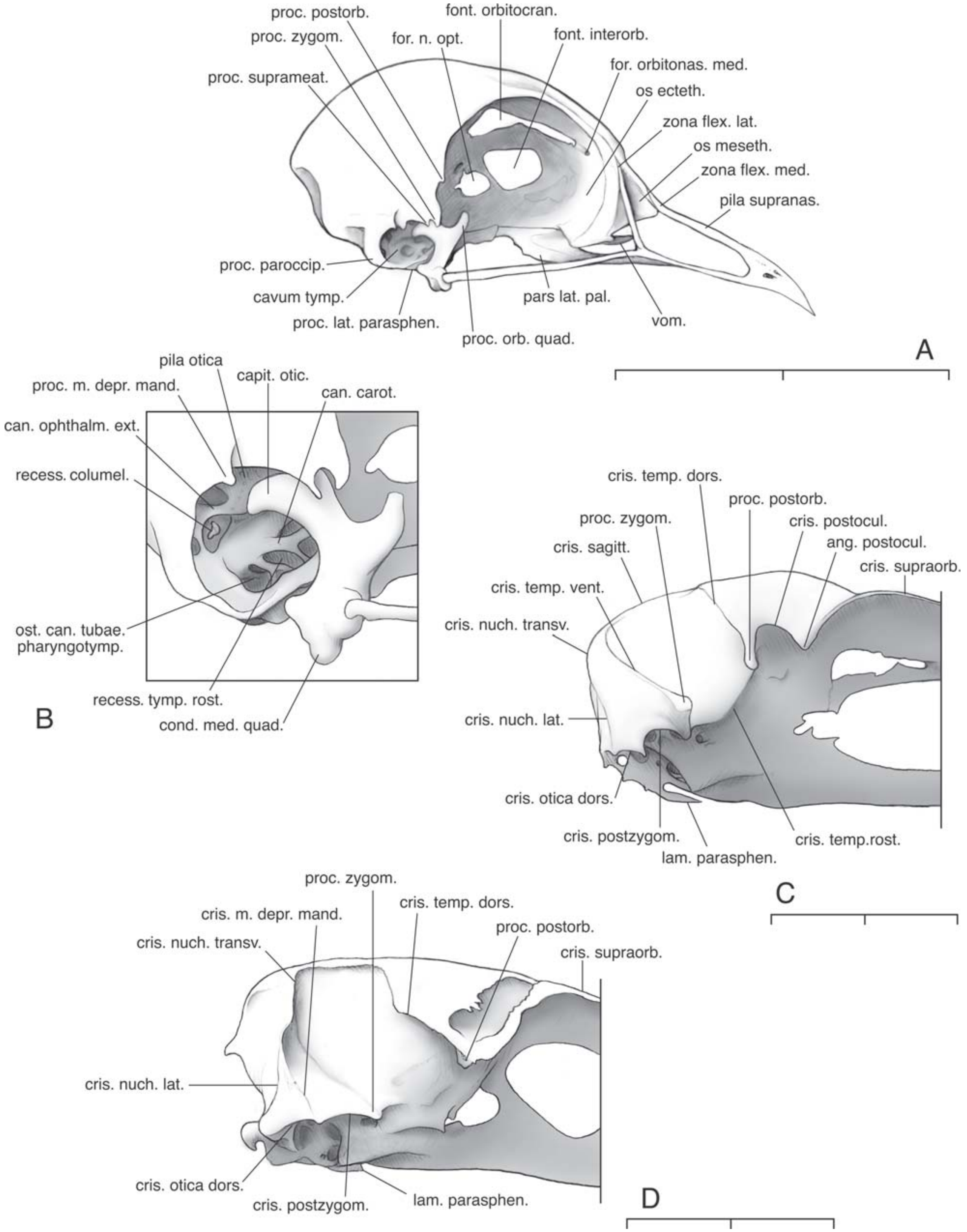


Fig. 4.—Cranium, externum, lateral view: (A) *Turnix suscitator*; (B) *Turnix suscitator,* cavum tympanicum enlarged; (C) *Nycticorax nycticorax*; (D) *Gavia stellata*.

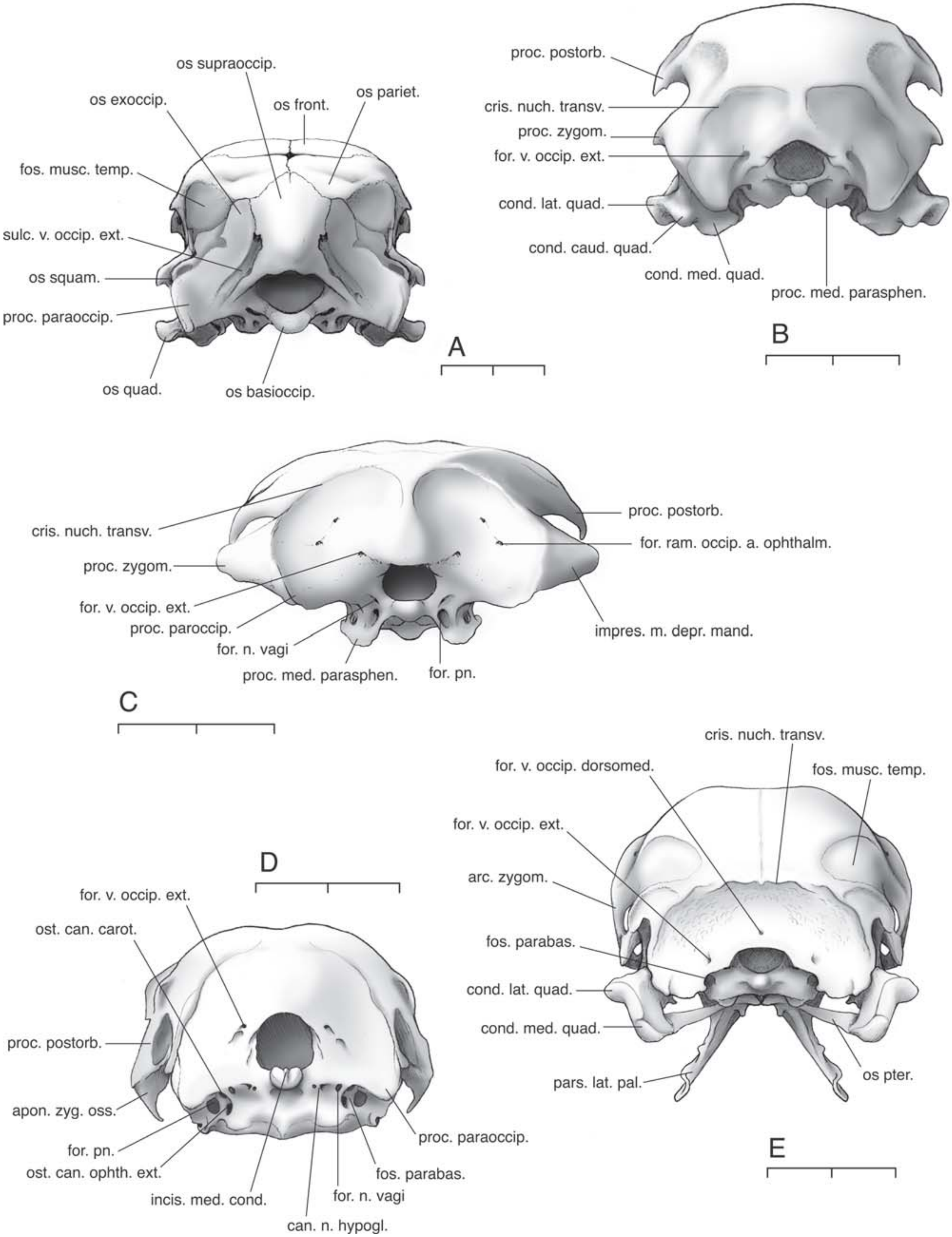


Fig. 5.—Cranium, externum, caudal view: (A) *Pygoscelis adeliae* (immature); (B) *Stercorarius maccormicki*; (C) *Phaethon rubricauda*; (D) *Meleagris gallopavo*; (E) *Cacatua galerita*.

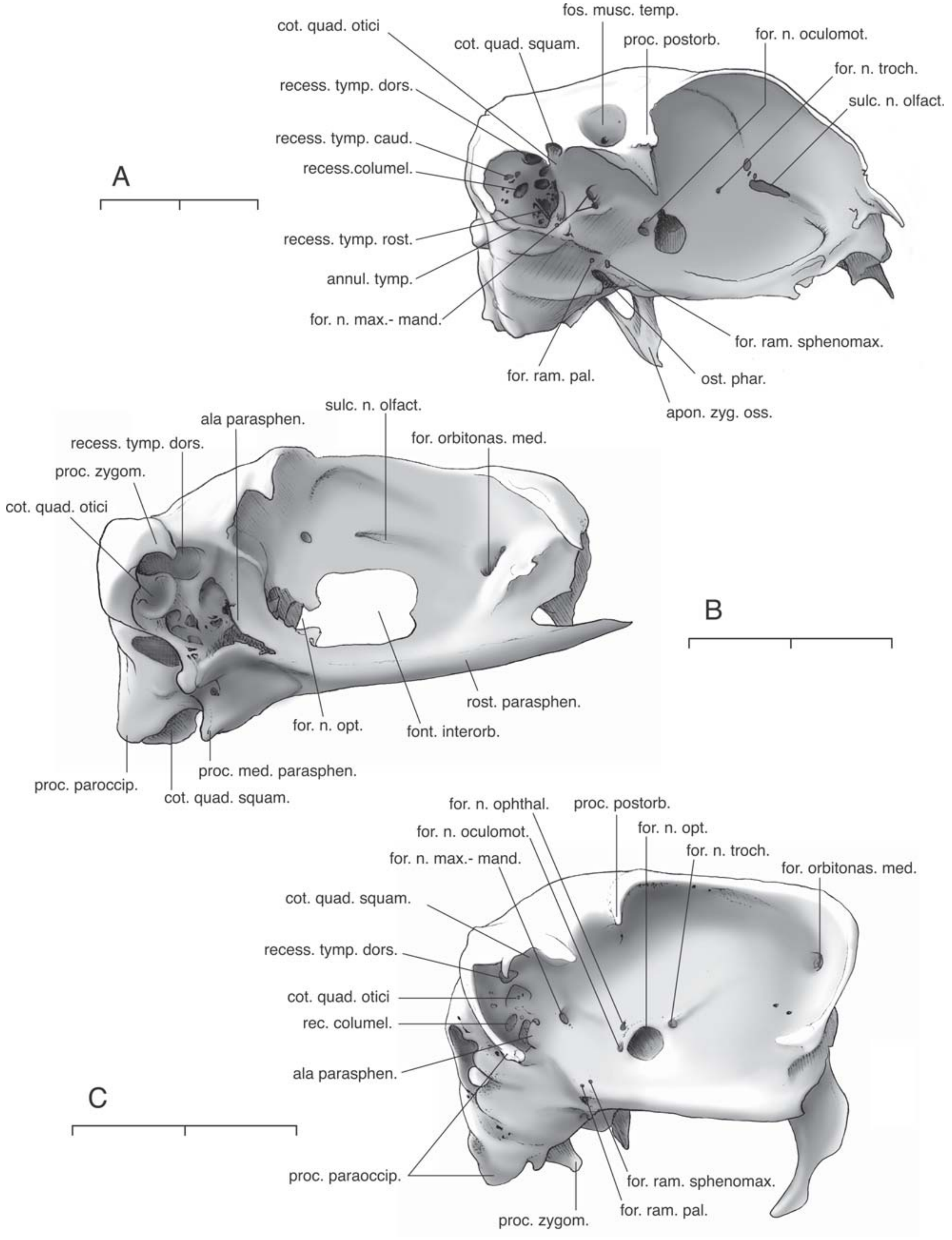
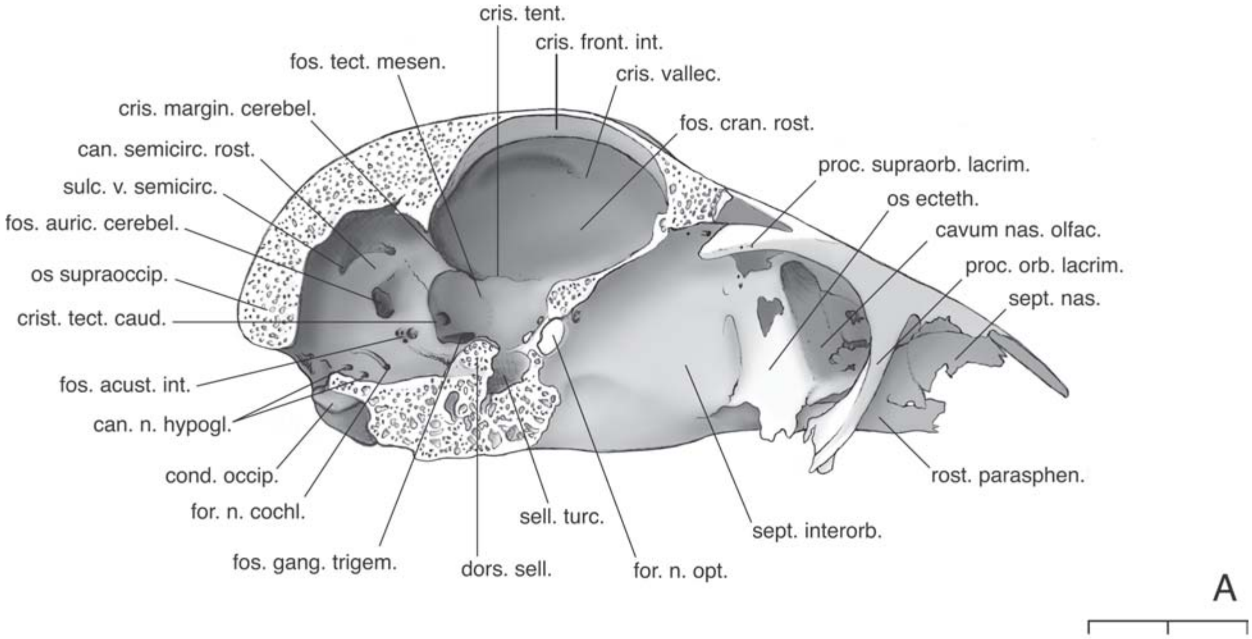


Fig. 6.—Cranium (ossa faciei excluded), externum, ventrolateral view: (A) *Meleagris gallopavo*; (B) *Phaethon rubricauda*; (C) *Ramphastos sulfuratus*.



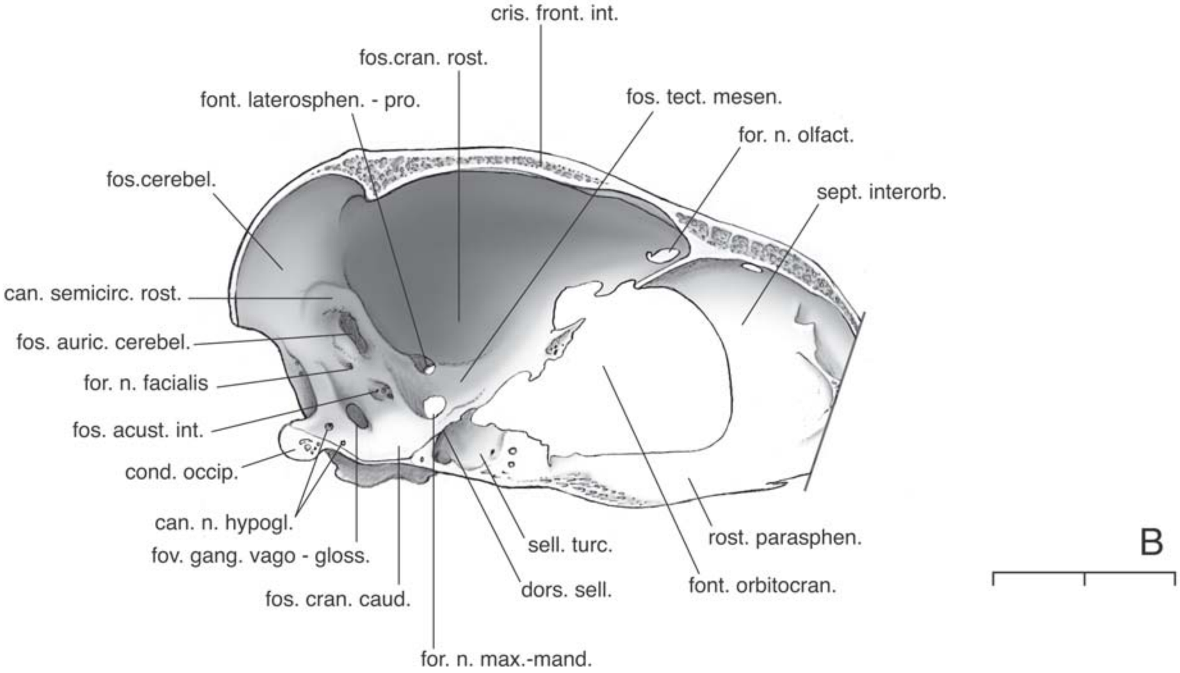


Fig. 7.—Endocranium (ossa facei and mandibula excluded), parasagittal exposure: (A) *Dromaius novaehollandiae*; (B) *Aptenodytes patagonicus*.

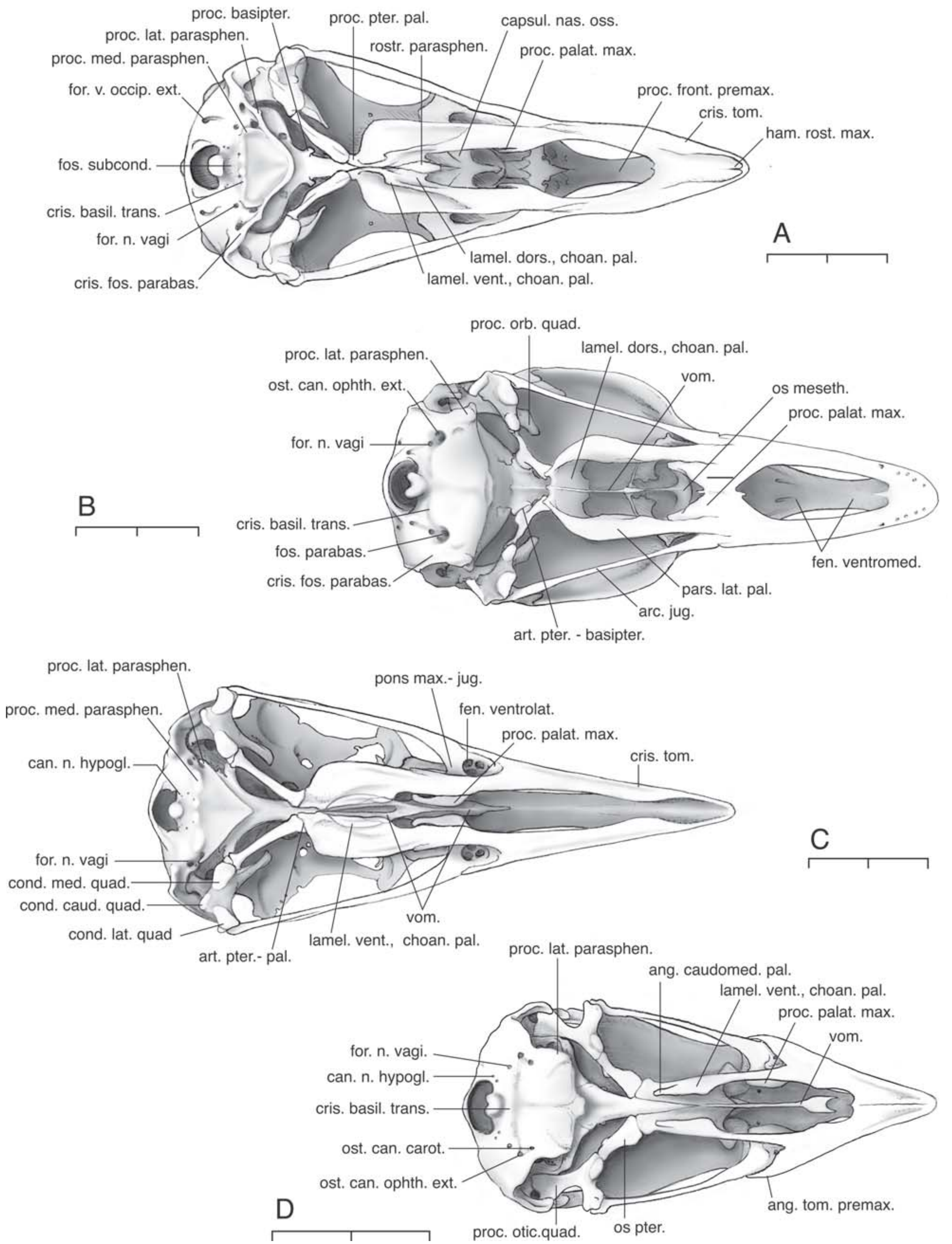


Fig. 8.—Cranium, externum, ventral view: (A) *Cathartes aura*; (B) *Chauna torquata*; (C) *Stercorarius maccormicki*; (D) *Opisthocomus hoazin*.

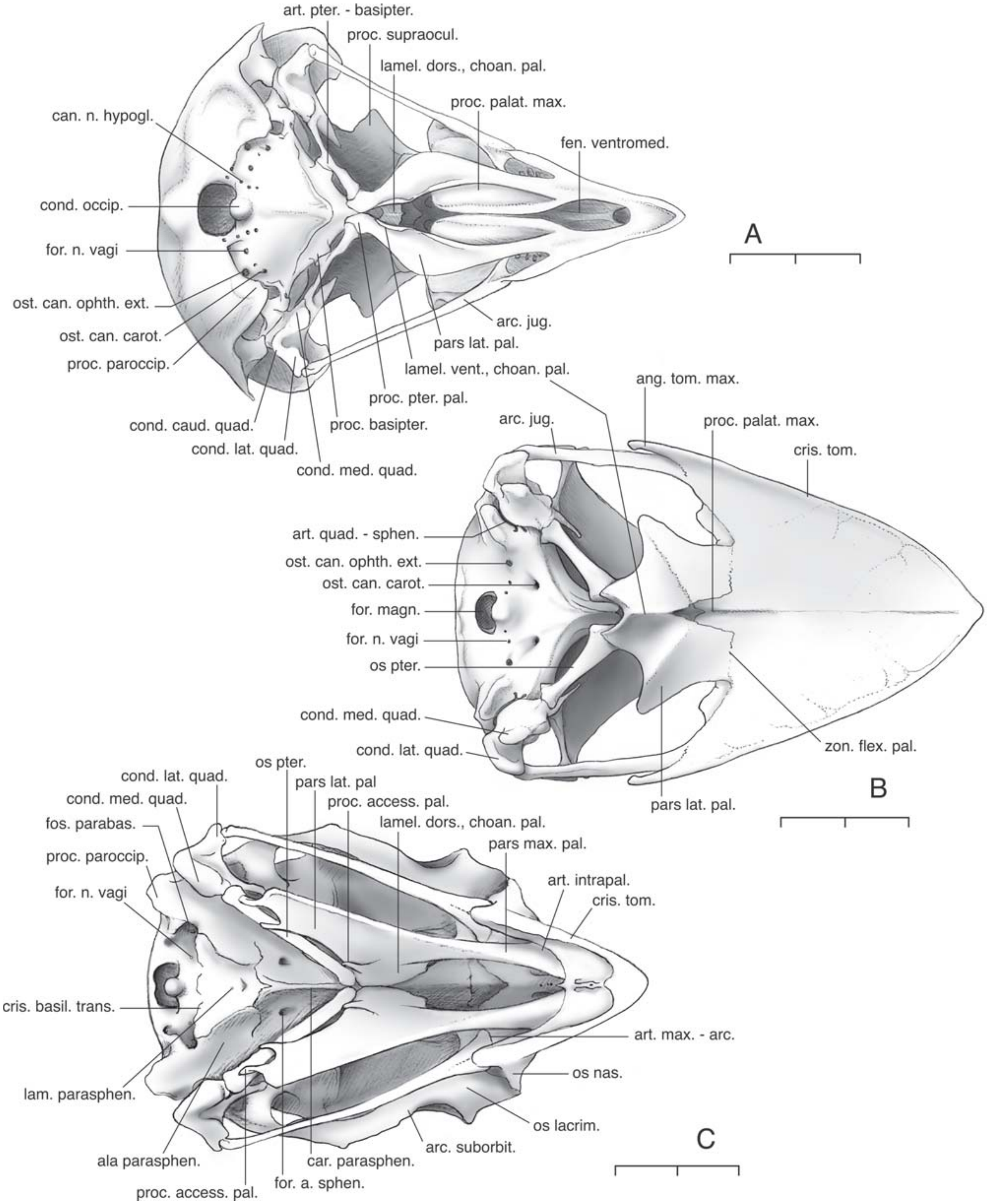


Fig. 9.—Cranium, externum, ventral view: (A) *Strix varia*; (B) *Podargus strigoides*; (C) *Cacatua galerita*.

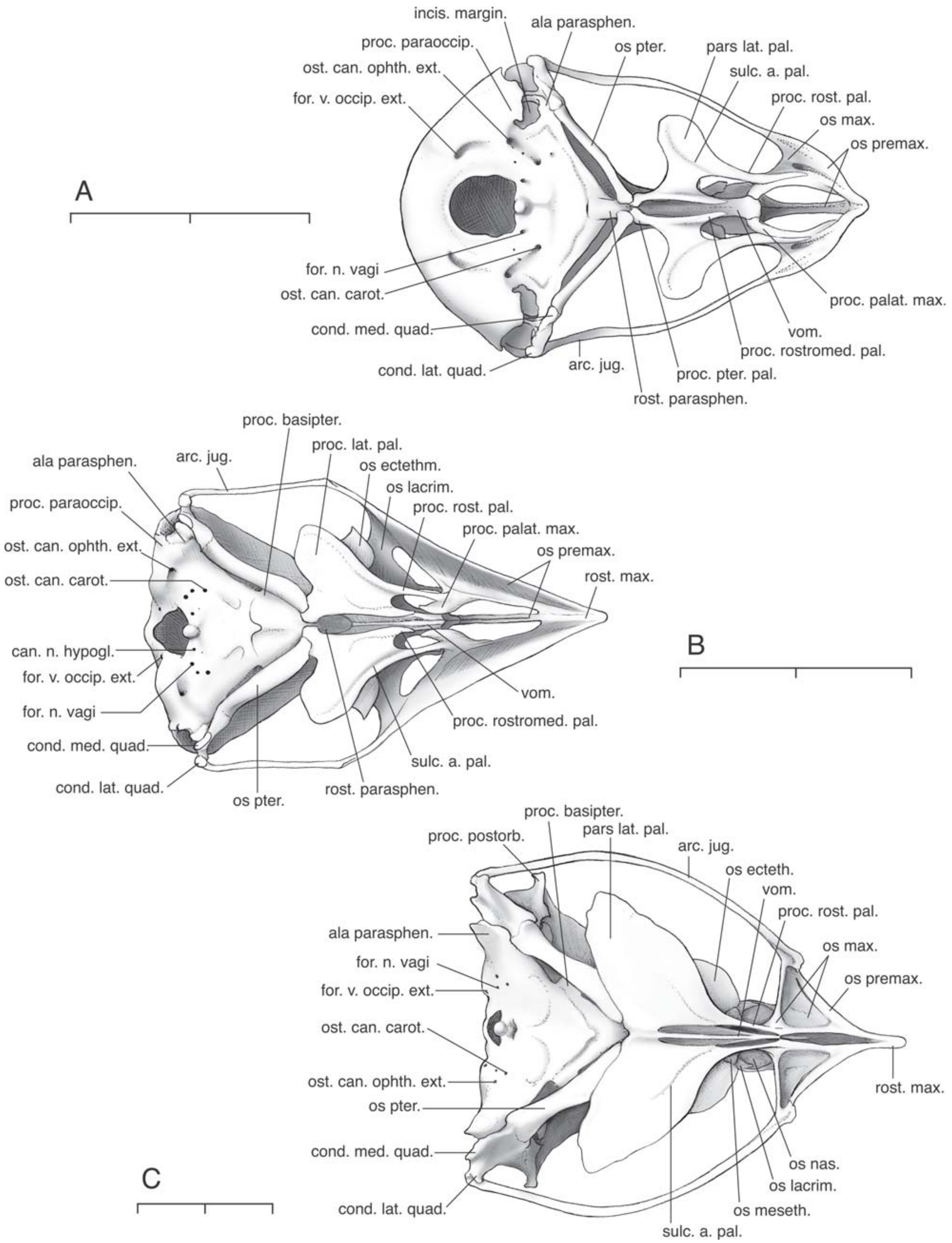


Fig. 10.—Cranium, externum, ventral view: (A) *Aegotheles cristatus*; (B) *Caprimulgus europaeus*; (C) *Nyctibius griseus*.

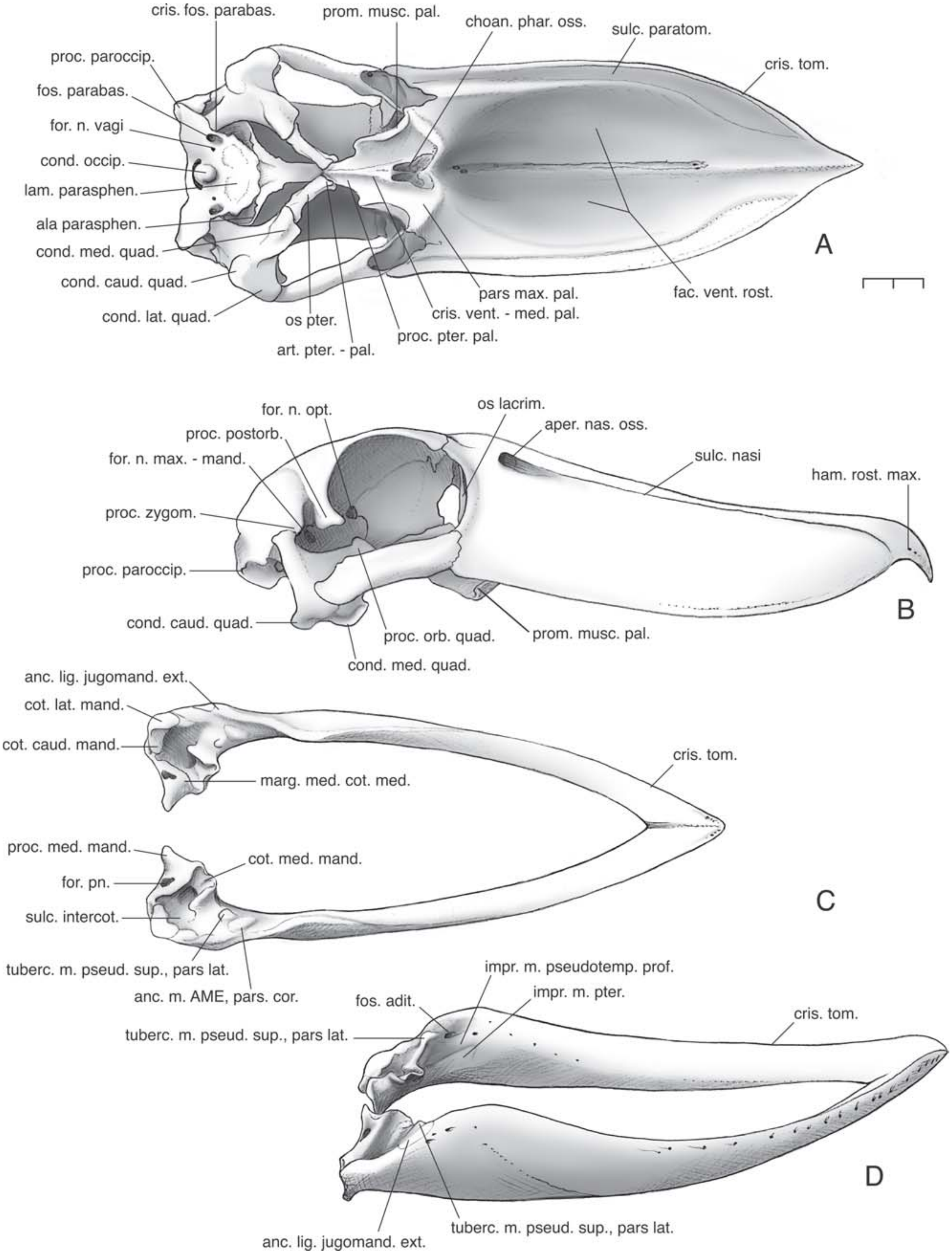


Fig. 11.—*Balaeniceps rex*: cranium, externum (A) ventral view; (B) lateral view; mandibula (C) dorsal view; (D) dorsolateral view.

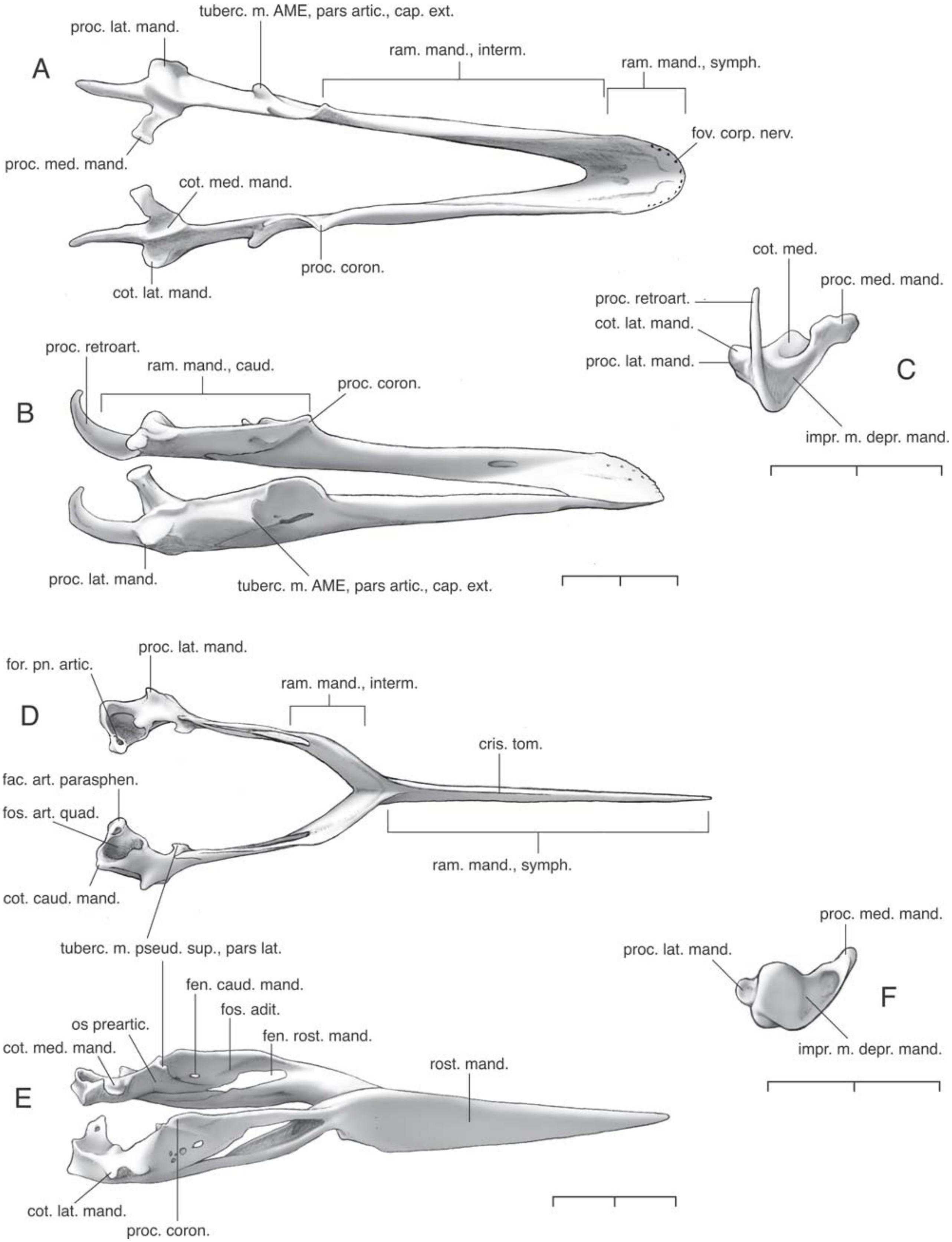


Fig. 12.—Mandibula: *Anseranas semipalmata*—(A) dorsal view; (B) dorsolateral view; (C) caudal view. *Rynchops niger*—(D) dorsal view; (E) dorsolateral view; (F) caudal view.

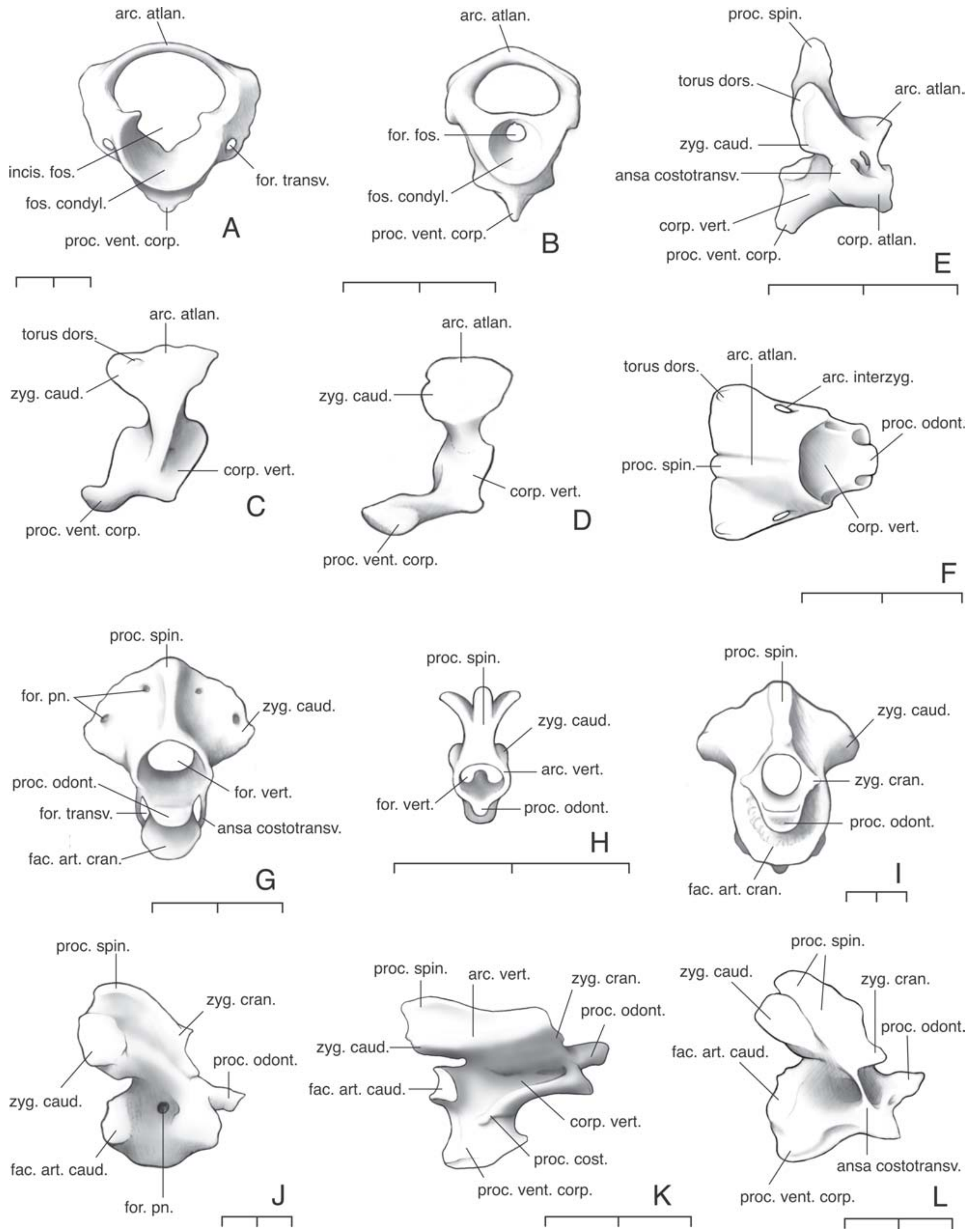


Fig. 13.—Vertebrae cervicales: atlas, rostral view—(A) *Struthio camelus*, (B) *Cacatua galerita*; atlas, lateral view—(C) *Struthio camelus*, (D) *Cacatua galerita*; atlas and axis, lateral view—(E) *Tockus erythrorhynchus*; axis, dorsal view—(F) *Opisthocomus hoazin*; axis, rostral view—(G) *Rhynochetos jubatus*, (H) *Indicator variegatus*, (I) *Balaeniceps rex*; axis, lateral view—(J) *Balaeniceps rex*, (K) *Podiceps cristatus*, (L) *Sagittarius serpentarius*.

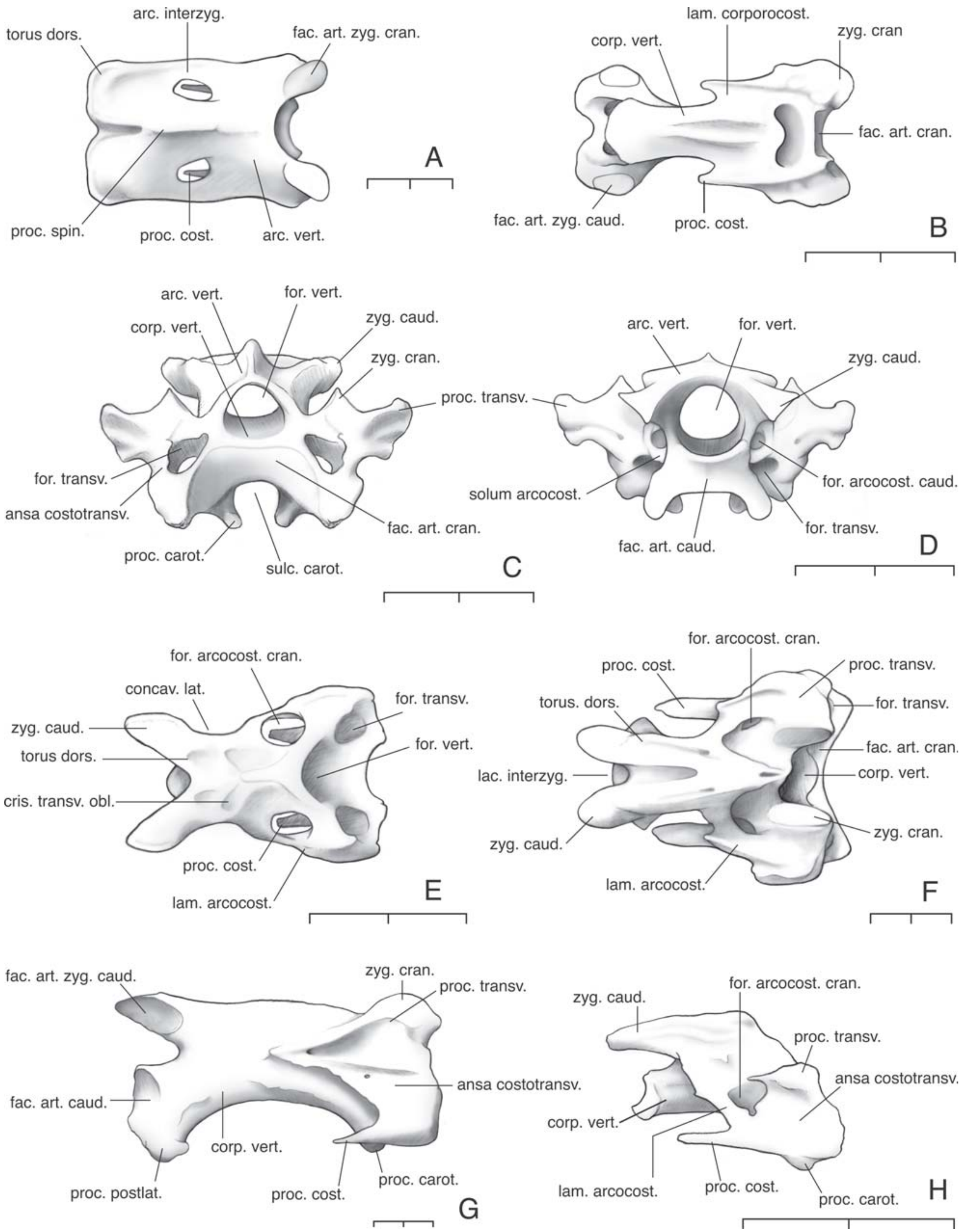


Fig. 14.—Vertebrae cervicales, sectio I—(A) *Meleagris gallopavo*, dorsal view; (B) *Nycticorax nycticorax*, ventral view. Sectio II—(C) *Rhynochetus jubatus,* cranial view; (D) *Rhynochetus jubatus,* caudal view; (E) *Opisthocomus hoazin,* dorsal view; (F) *Dromaius novaehollandiae*, dorsal view; (G) *Rhea americana*, lateral view; (H) *Burhinus oedicnemis,* lateral view.

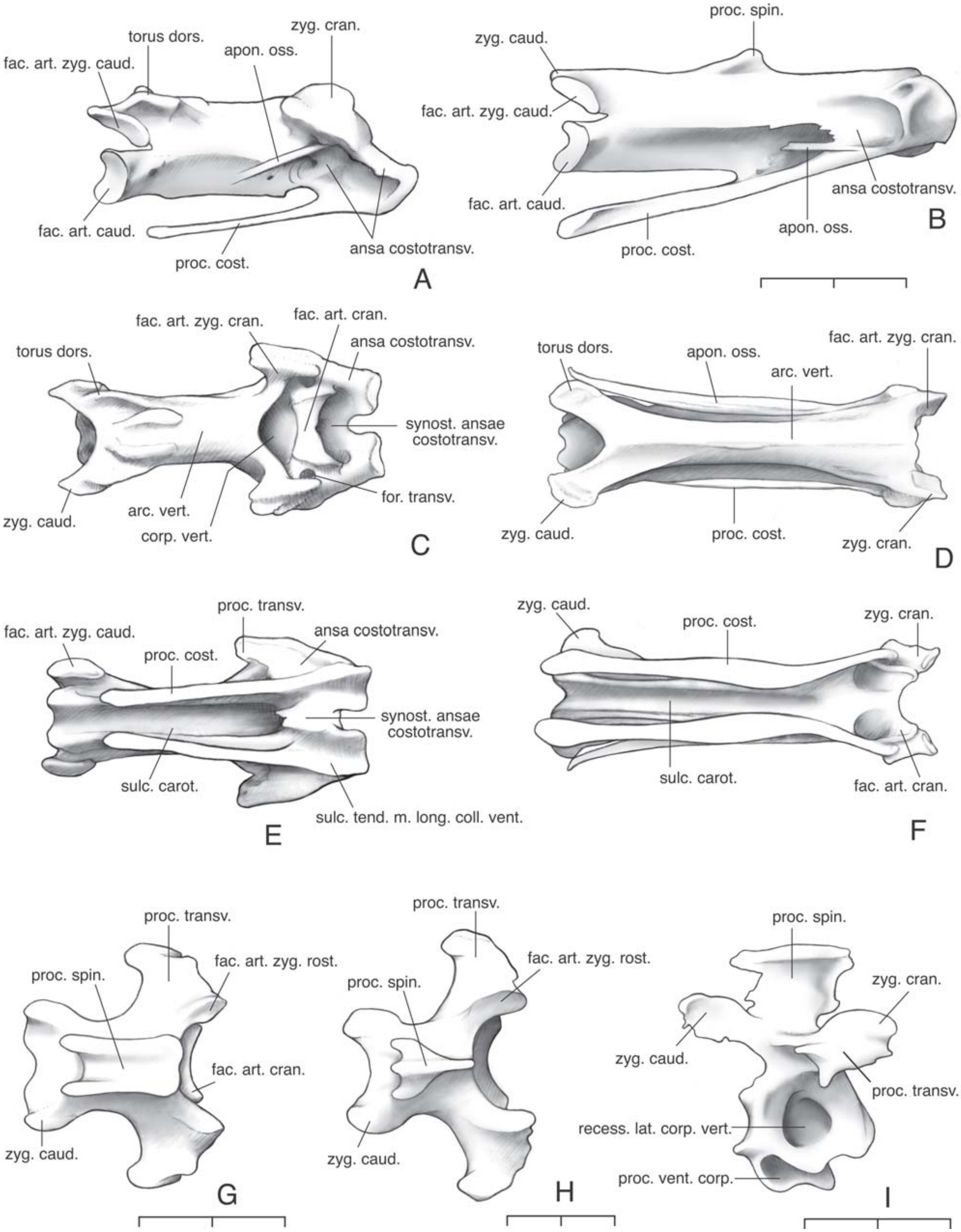


Fig. 15.—Vertebrae cervicales, sectio II: (A) *Anhinga anhinga*, vertebra 9, lateral view; (B) *A. anhinga*, vertebra 8, lateral view; (C) *A. anhinga*, vertebra 9, dorsal view; (D) *A. anhinga*, vertebra 8, dorsal view; (E) *A. anhinga*, vertebra 9, ventral view; (F) *A. anhinga*, vertebra 8, ventral view. Sectio III: (G) *N. nycticorax*, dorsal view; (H) *Sula dactylatra*, dorsal view; (I) *Haematopus ostralegus*, lateral view.

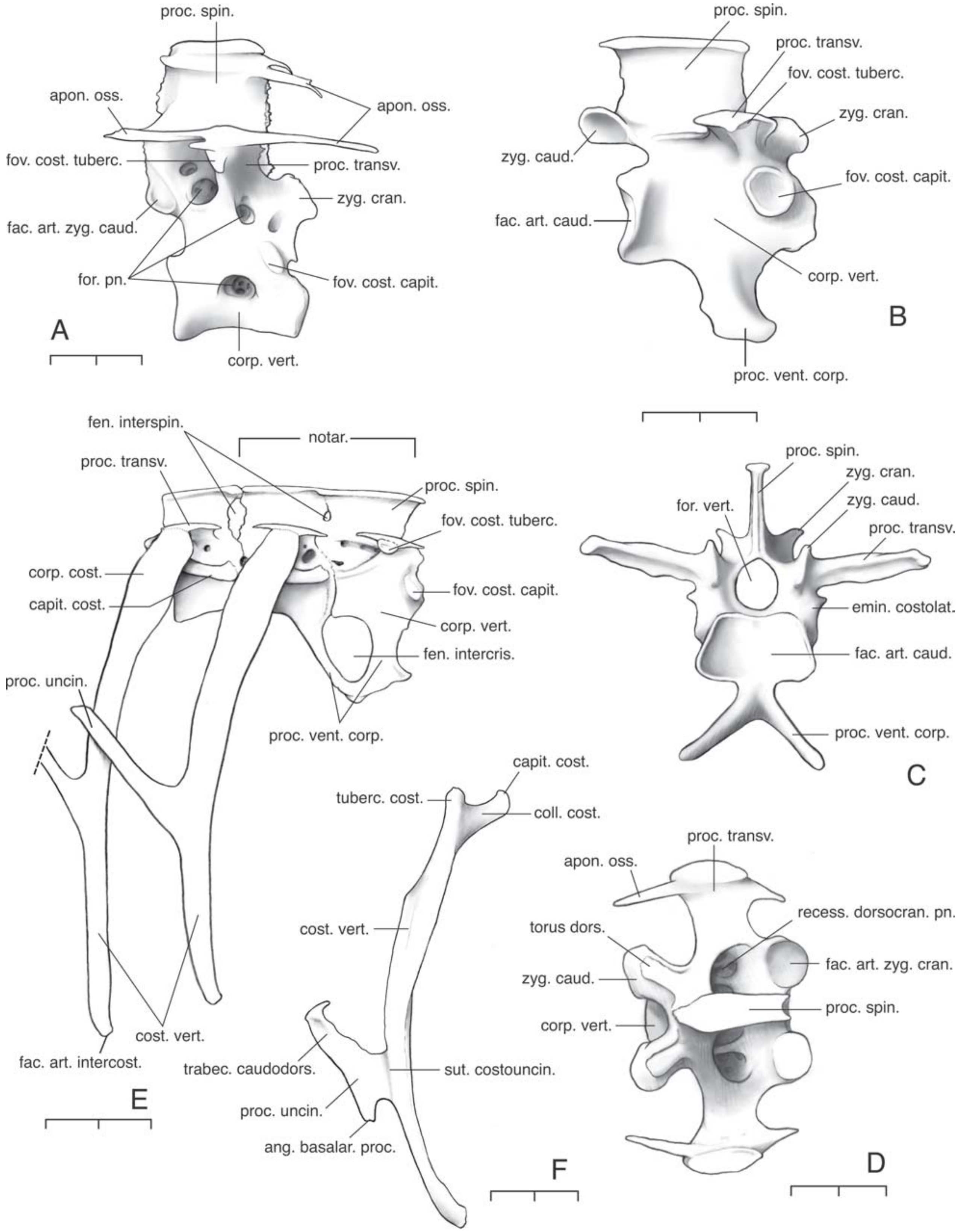


Fig. 16.—Vertebrae thoraciae: (A) *Chauna torquata,* lateral view; (B) *Spheniscus magellanicus,* lateral view (C) *Spheniscus magellanicus,* caudal view; (D) *Sagittarius serpentarius,* dorsal view. (E) *Steatornis caripensis,* vertebrae thoracicae and costae vertebrales, lateral view. (F) *Psophia crepitans*, costa vertebralis, lateral view.

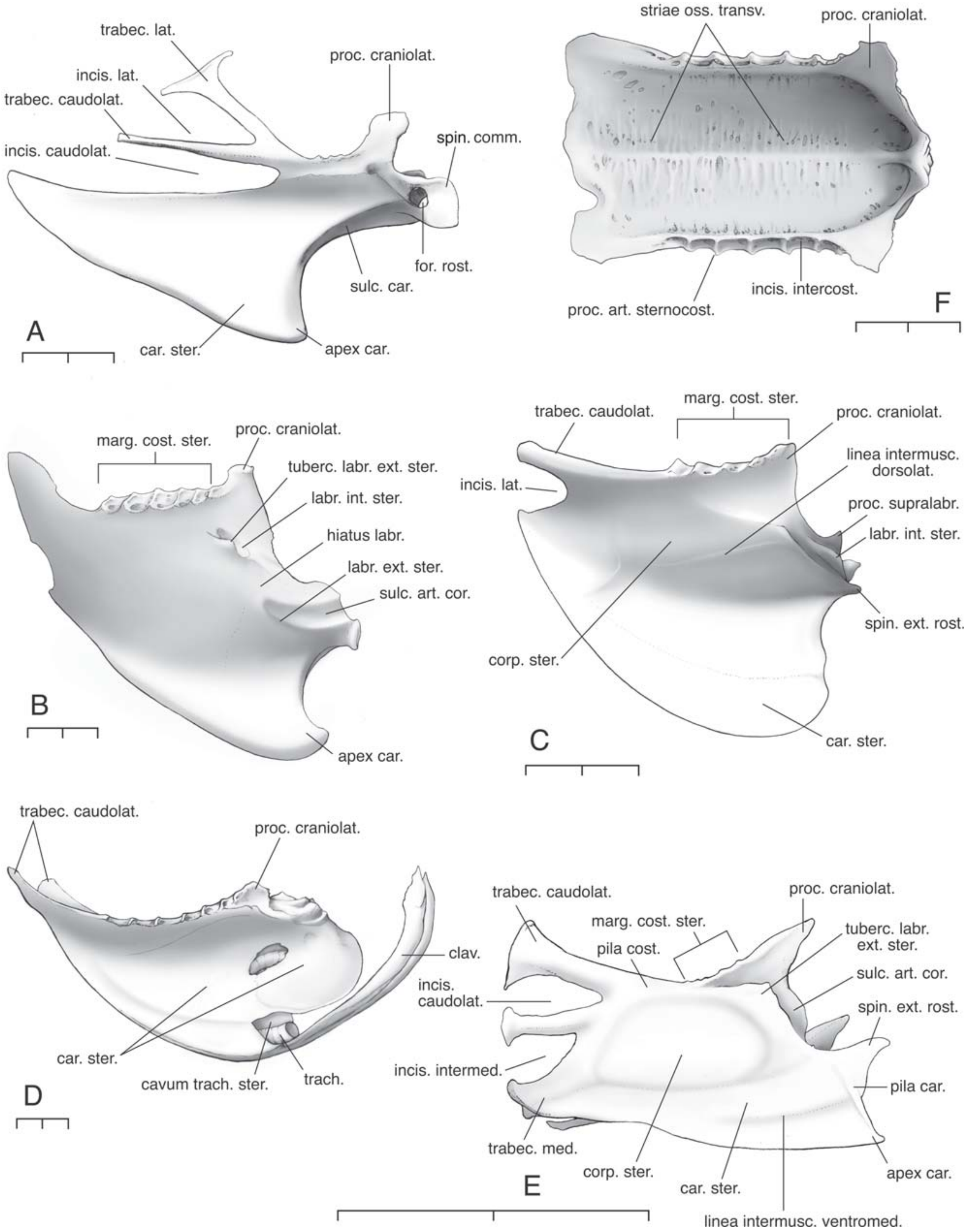


Fig. 17.—Sternum: (A) *Numida meleagris,* cranioventrolateral view; (B) *Diomedea nigripes,* cranioventrolateral view; (C) *Scopus umbretta,* cranioventrolateral view; (D) *Grus canadensis,* cranioventrolateral view; (E) *Alcedo atthis,* cranioventrolateral view; (F) *Anseranas semipalmata,* dorsal view.

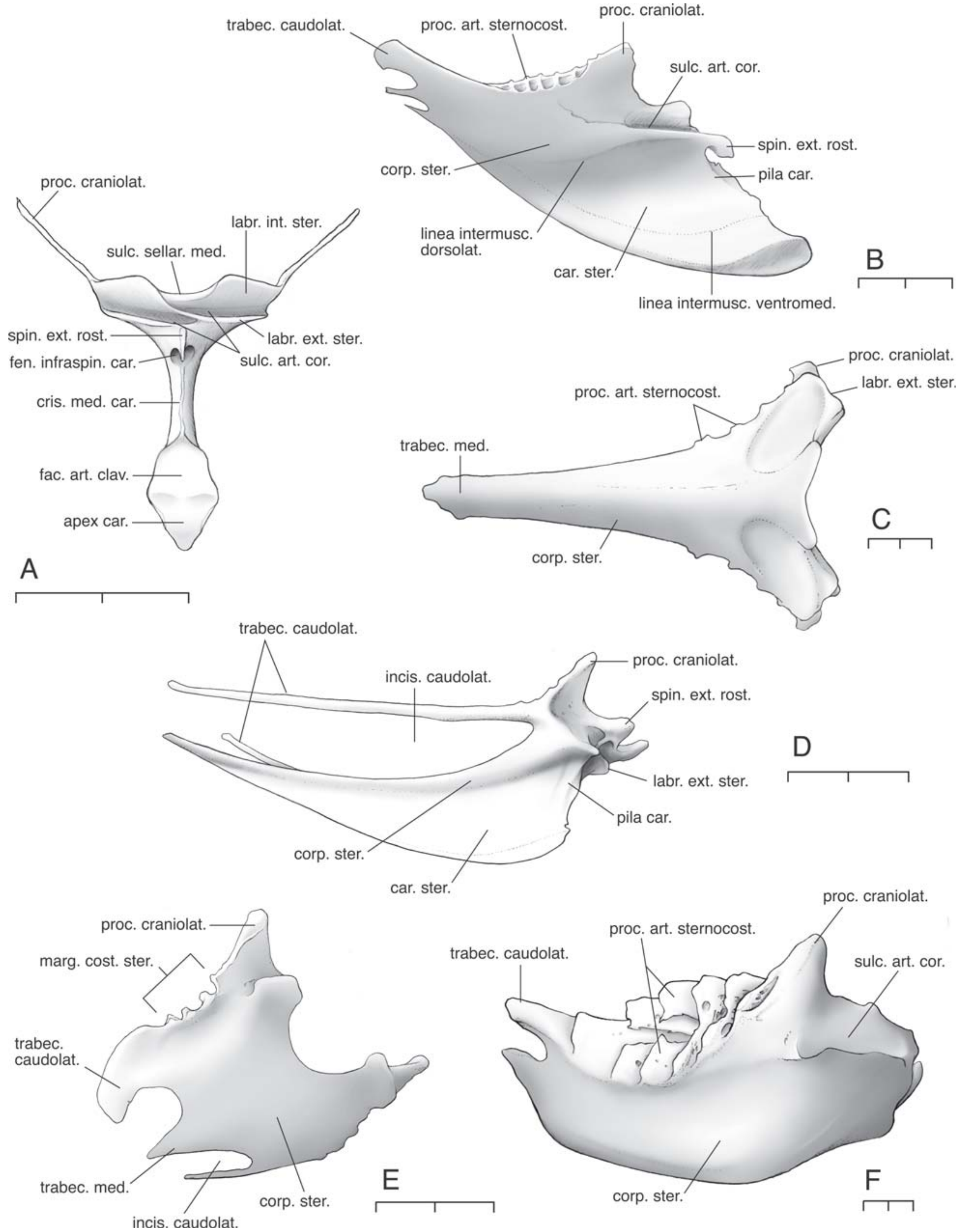


Fig. 18.—Sternum: (A) *Phaethon rubricauda,* cranial view; (B) *Phaethon rubricauda,* ventrocraniolateral view; (C) *Aptornis defossor,* ventral view; (D) *Eudromia elegans,* ventrocraniolateral view; (E) *Apteryx australis,* ventrocraniolateral view; (F) *Struthio camelus,* ventrocraniolateral view.

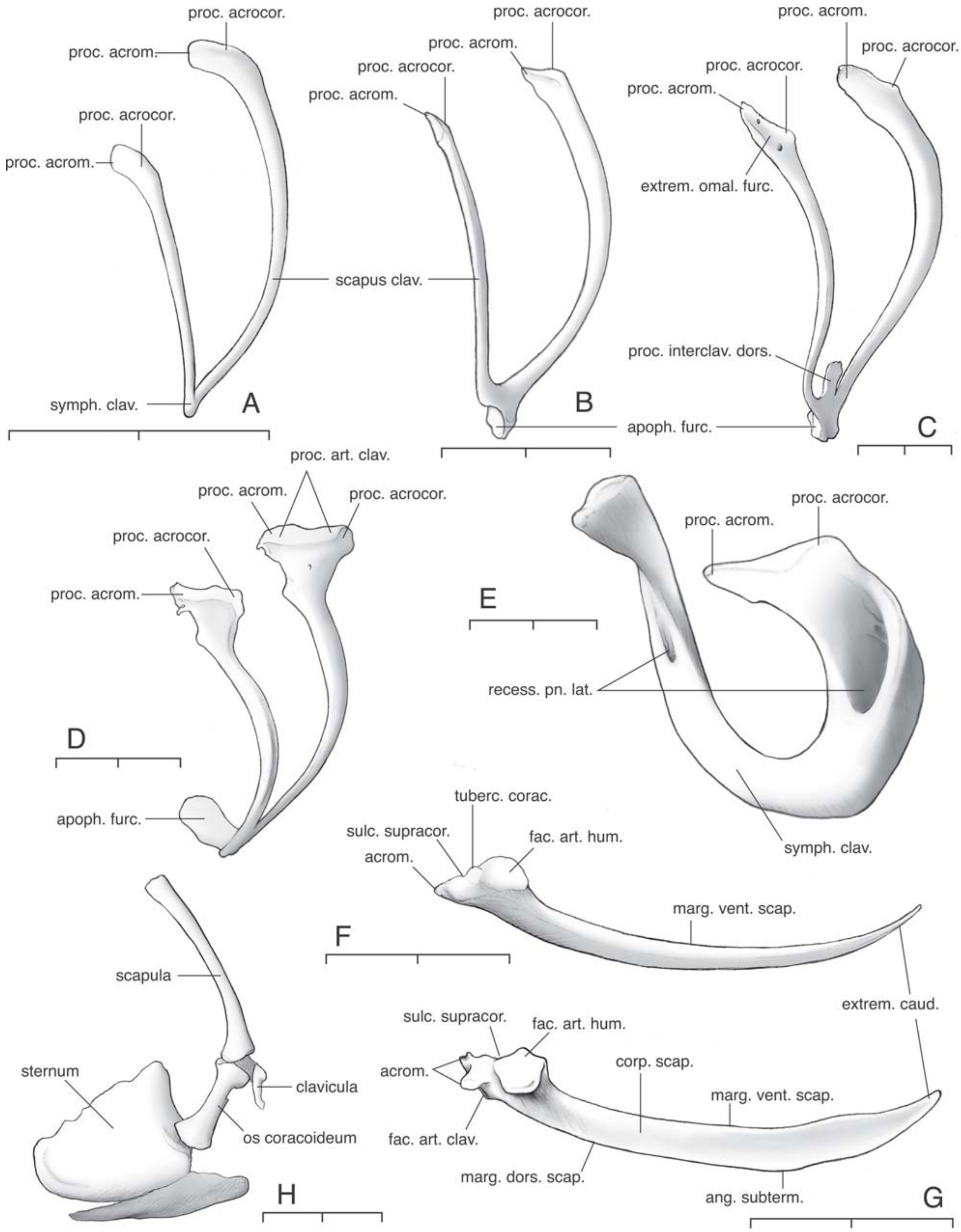


Fig. 19.—Clavicula: (A) *Eudromia elegans,* anterodorsal view; (B) *Megapodius freycinet,* anterodorsal view; (C) *Ardea herodias,* anterodorsal view; (D) *Ptilonorhynchus violaceus,* anterodorsal view; (E) *Chauna torquata,* caudodorsal view. Scapula, lateral view: (F) *Podiceps cristatus*; (G) *Corvus brachyrhynchos*. (H) Ossa cinguli membri thoracici: *Dromaius novaehollandiae* (immature), rostroventrolateral view.

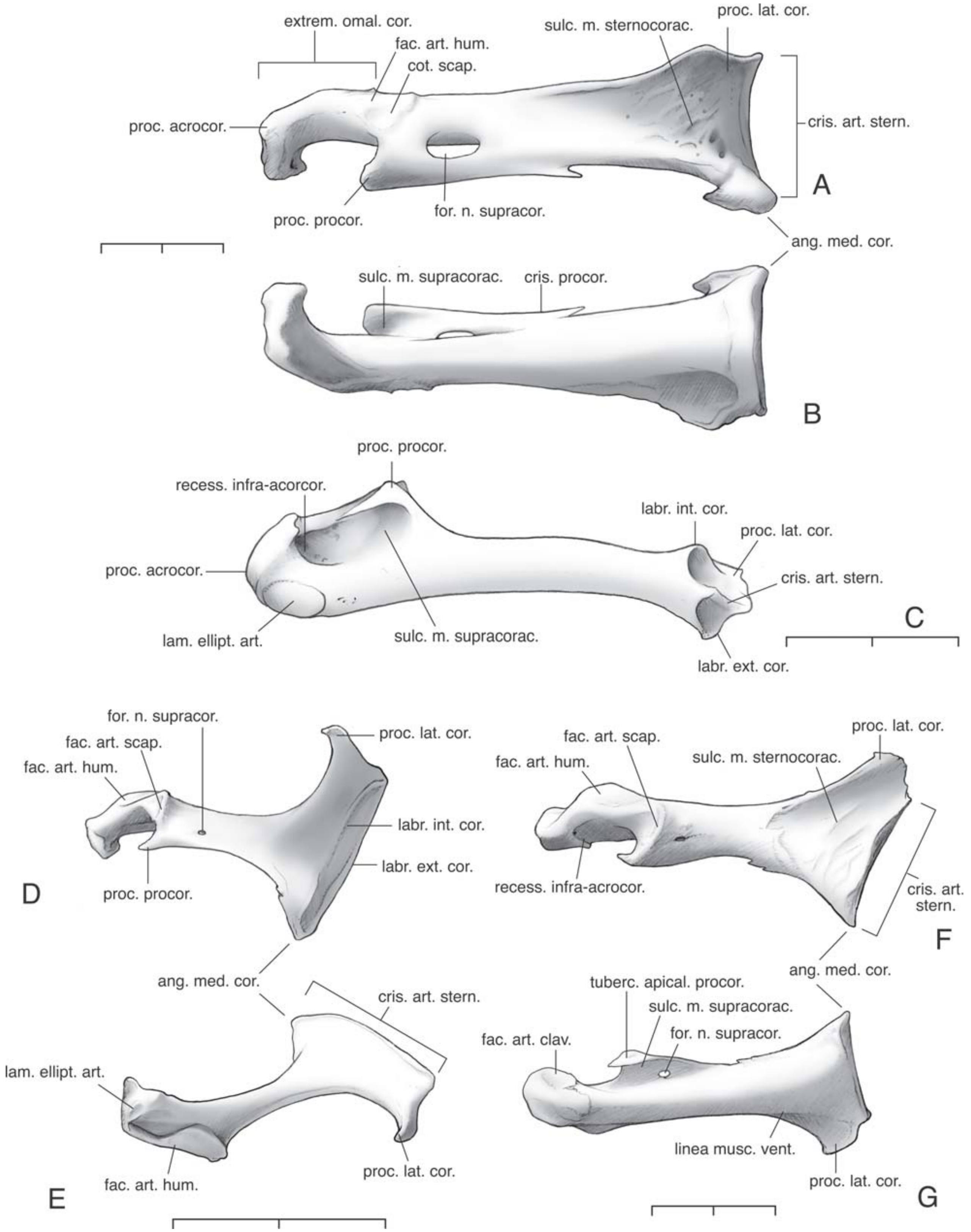


Fig. 20.—Coracoideum: (A) *Spheniscus magellanicus,* dorsal view; (B) *Spheniscus magellanicus,* ventral view; (C) *Sula dactylatra,* medial view; (D) *Puffinus pacificus,* dorsal view; (E) *Puffinus pacificus,* ventral view; (F) *Ajaia ajaja,* dorsal view; (G) *Ajaia ajaja,* ventral view.

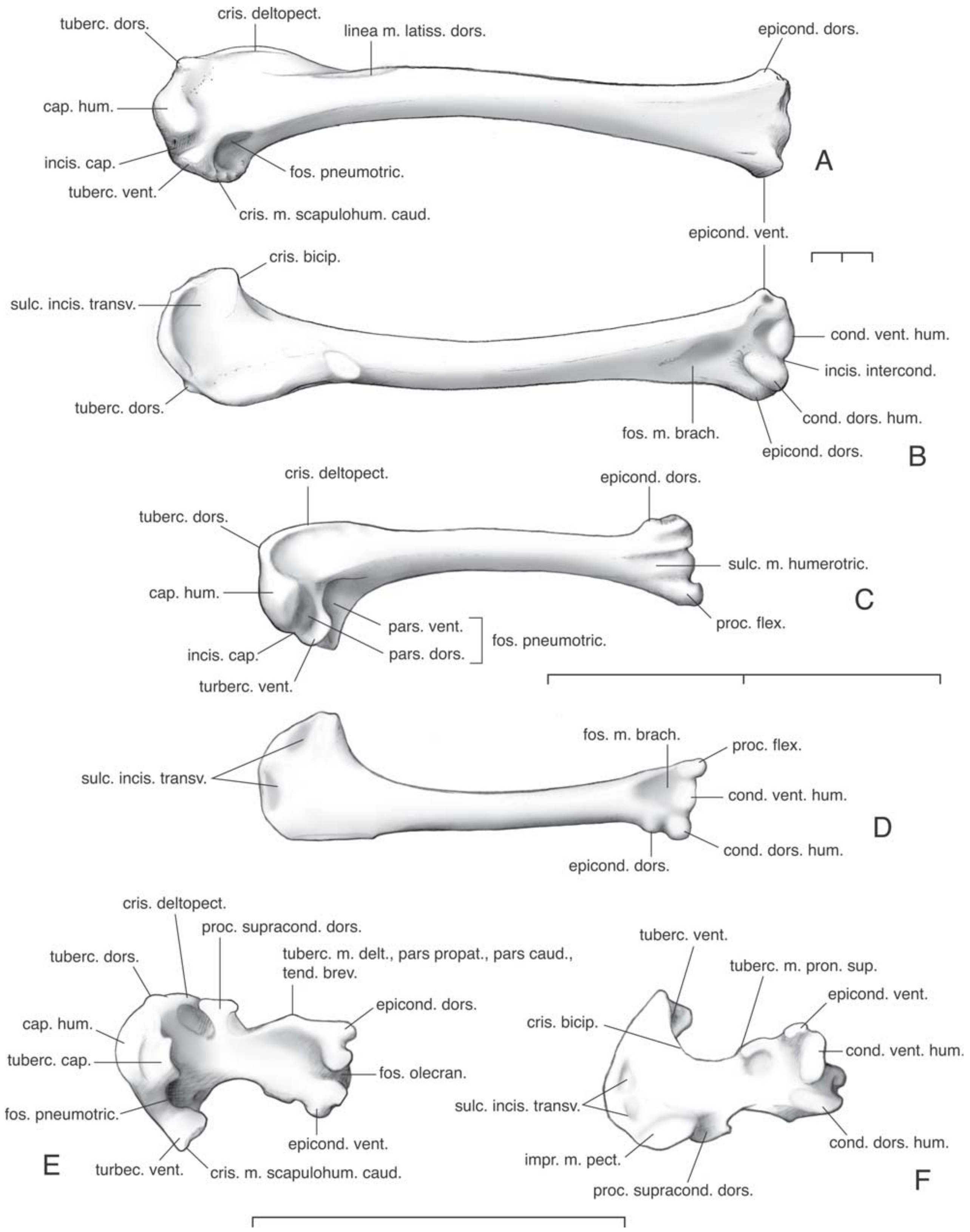


Fig. 21.—Humerus: (A) *Chauna torquata,* caudal view; (B) *Chauna torquata,* cranial view; (C) *Jynx torquilla,* caudal view; (D) *Jynx torquilla,* cranial view; (E) *Glaucis hirsutus,* caudal view; (F) *Glaucis hirsutus,* cranial view. Scale: (A–D) 2 cm, (E–F) 1 cm.

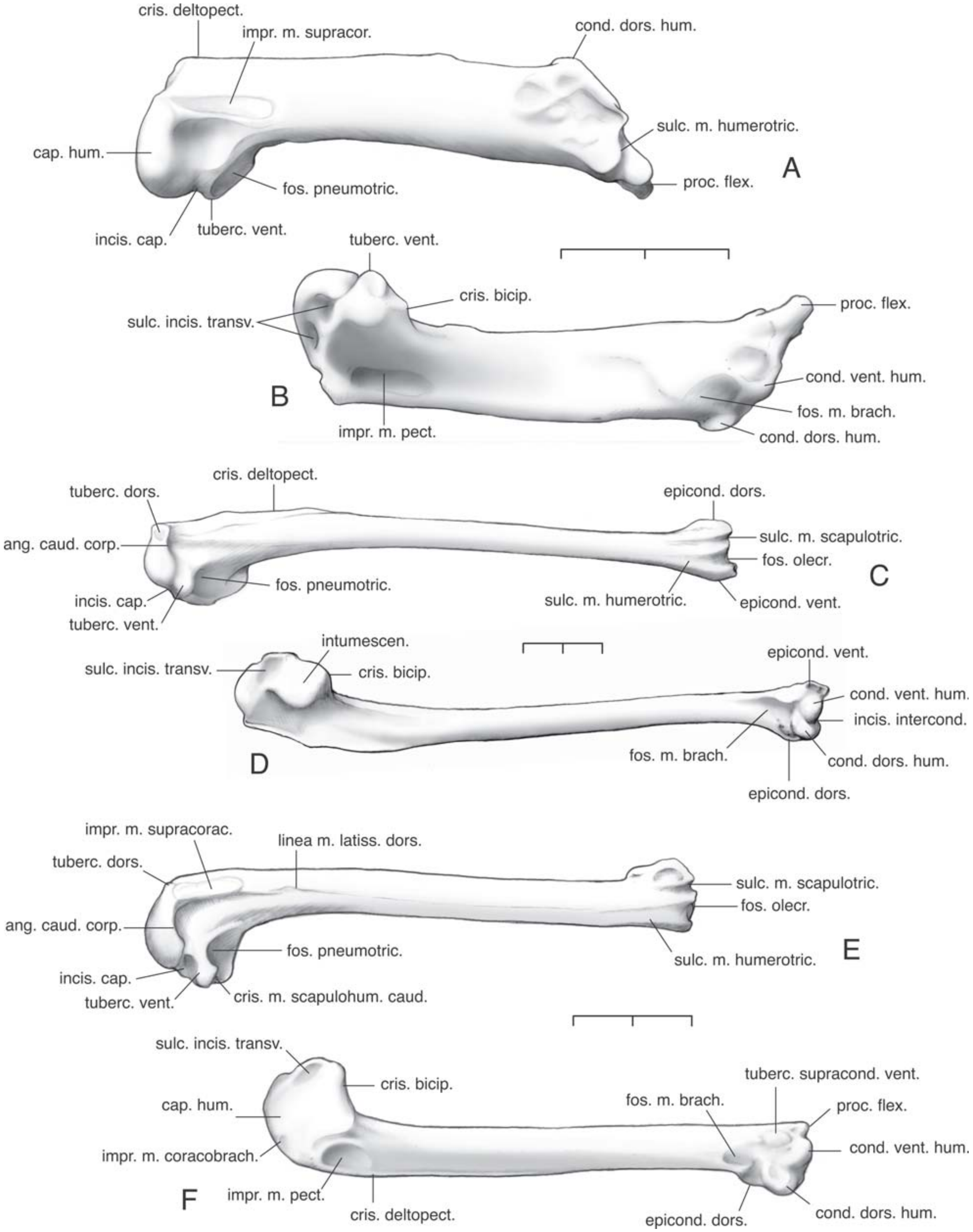


Fig. 22.—Humerus: (A) *Spheniscus demersus,* caudal view; (B) *Spheniscus demersus,* cranial view; (C) *Gavia stellata,* caudal view; (D) *Gavia stellata,* cranial view; (E) *Uria lomvia,* caudal view; (F) *Uria lomvia.* cranial view.

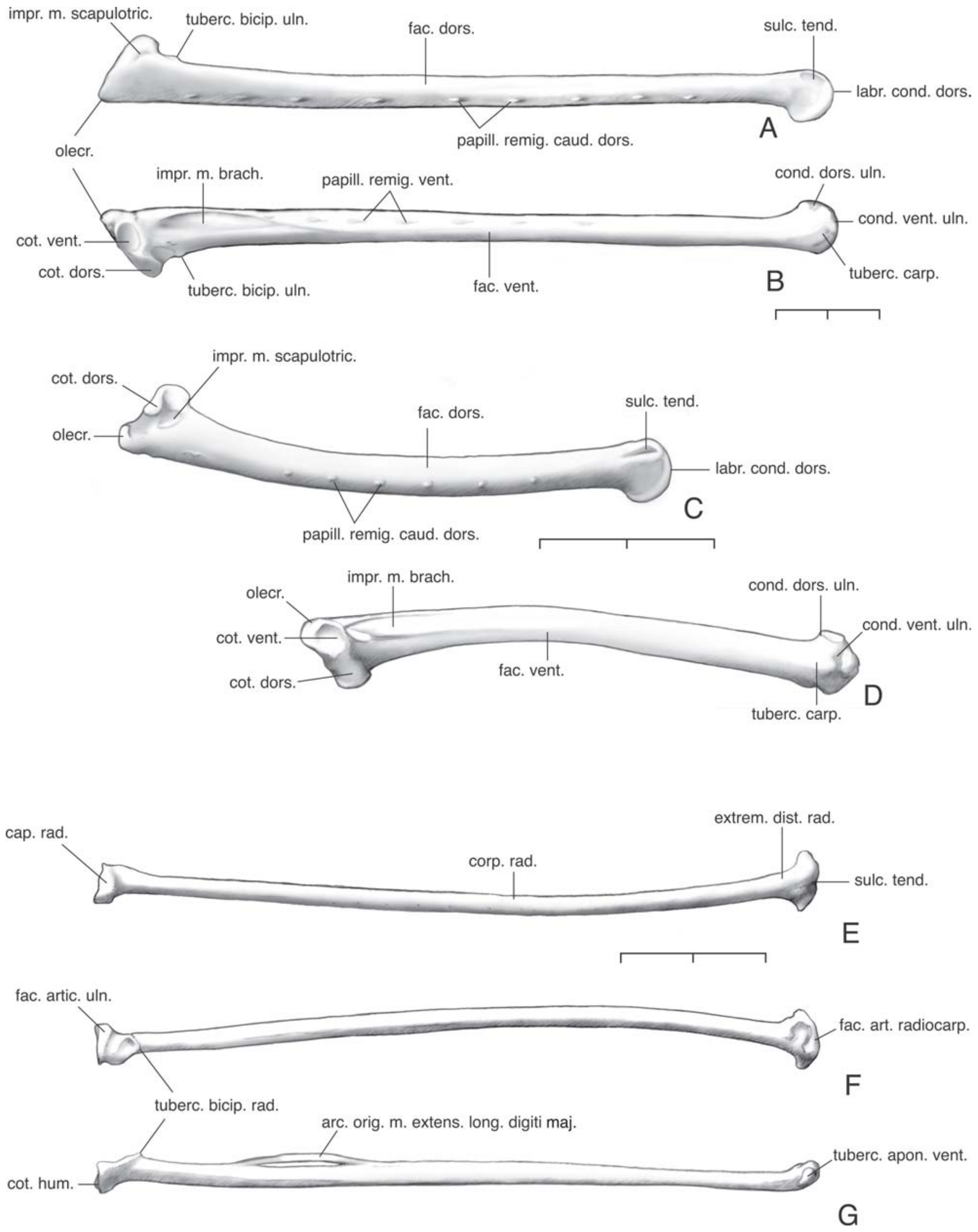


Fig. 23.—Radii and ulna: ulna—(A) *Anseranas semipalmata,* dorsal view; (B) *Anseranas semipalmata,* ventral view; (C) *Rhynochetos jubatus,* dorsal view; (D) *Rhynochetos jubatus,* ventral view. Radius, *Strix varia*—(E) dorsal view; (F) ventral view; (G) lateral view.

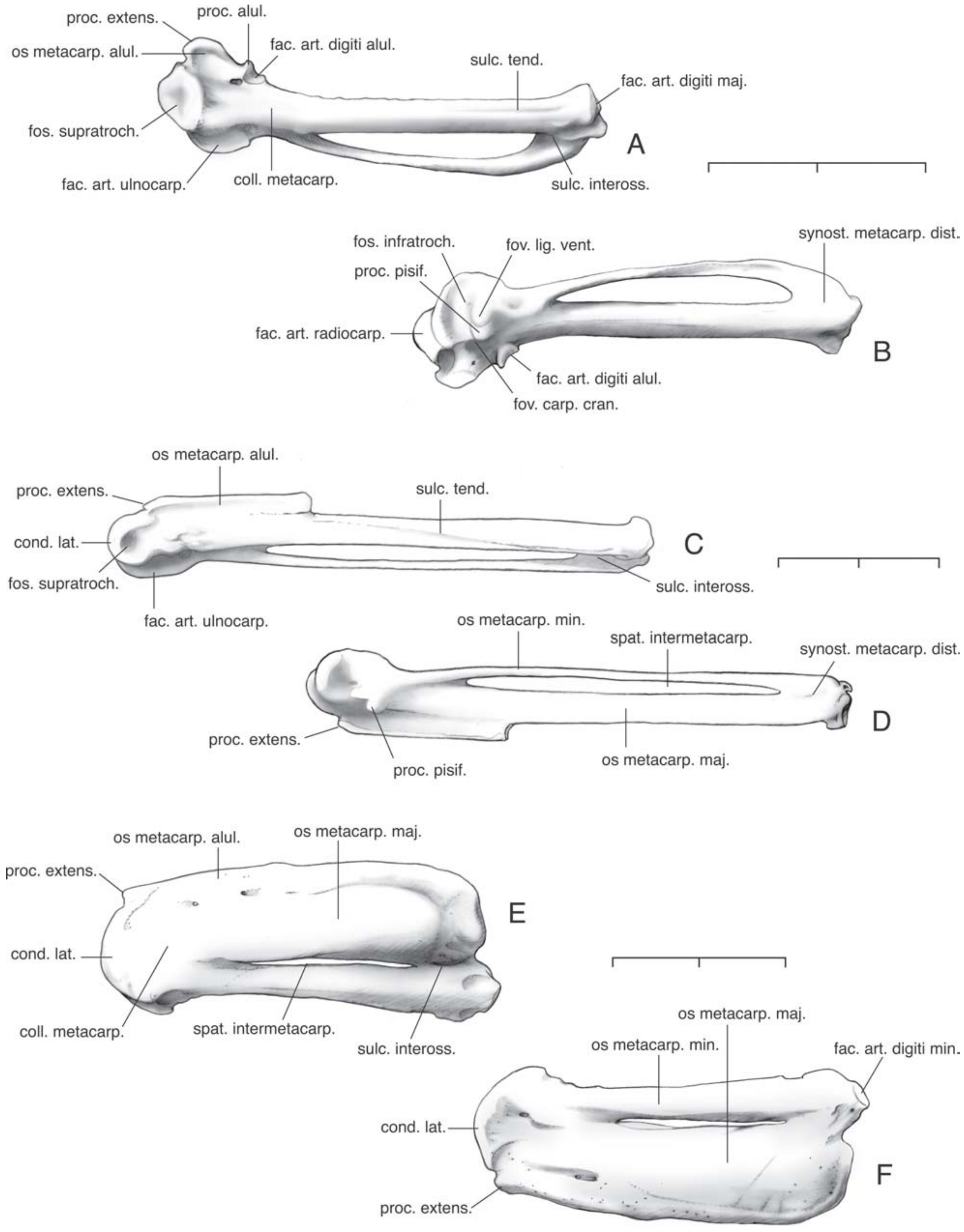


Fig. 24.—Carpometacarpus: (A) *Megapodius freycinet,* dorsal view; (B) *Megapodius freycinet,* ventral view; (C) *Gavia stellata,* dorsal view; (D) *Gavia stellata,* ventral view; (E) *Spheniscus magellanicus,* dorsal view; (F) *Spheniscus magellanicus,* ventral view.

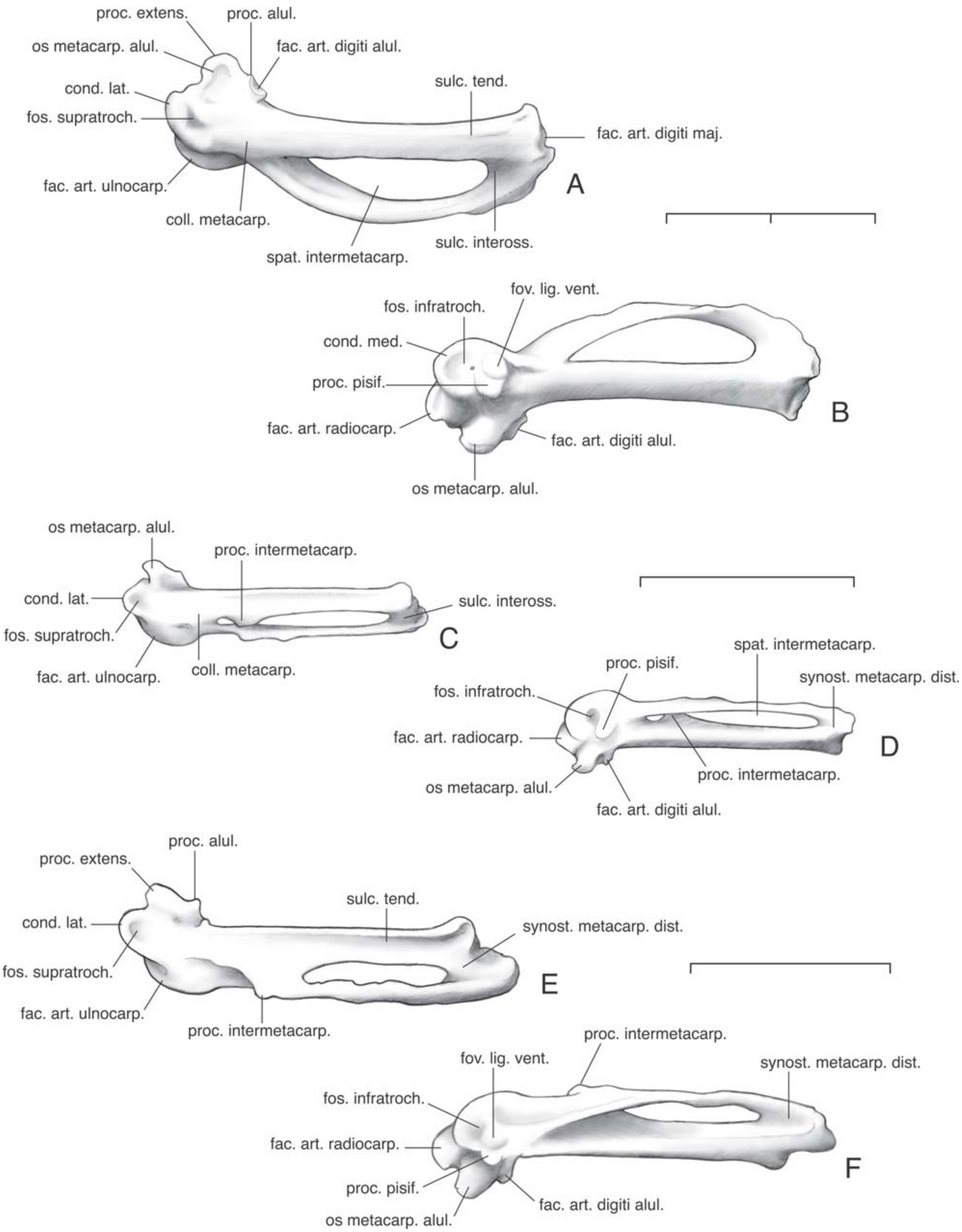


Fig. 25.—Carpometacarpus: (A) *Opisthocomus hoazin,* dorsal view; (B) *Opisthocomus hoazin,* ventral view; (C) *Todiramphus sanctus,* dorsal view; (D) *Todiramphus sanctus,* ventral view; (E) *Aphelocoma californica,* dorsal view; (F) *Aphelocoma californica,* ventral view. Scale: (A, B) 2 cm, (C–F) 1 cm.

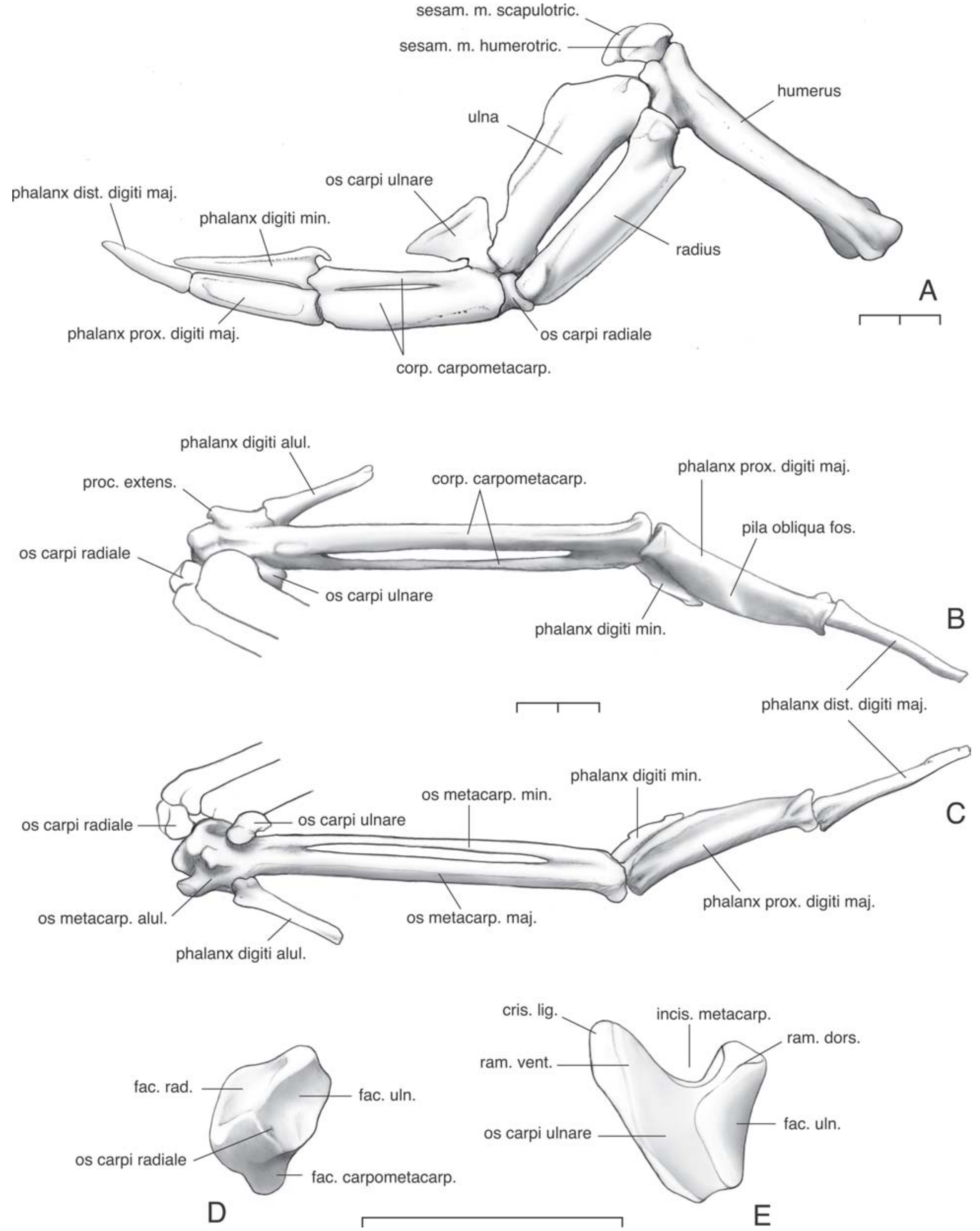


Fig. 26.—Ossa alae: (A) *Spheniscus magellanicus,* dorsal view. Skeleton manus: (B) *Phoenicopterus ruber,* dorsal view; (C) *Phoenicopterus ruber,* ventral view. (D) *Podargus strigoides,* os carpi radiale, proximal view; (E) *Podargus strigoides,* os carpi ulnare, proximal view. Scale: (A-C) 2 cm, (D -E) 1 cm.

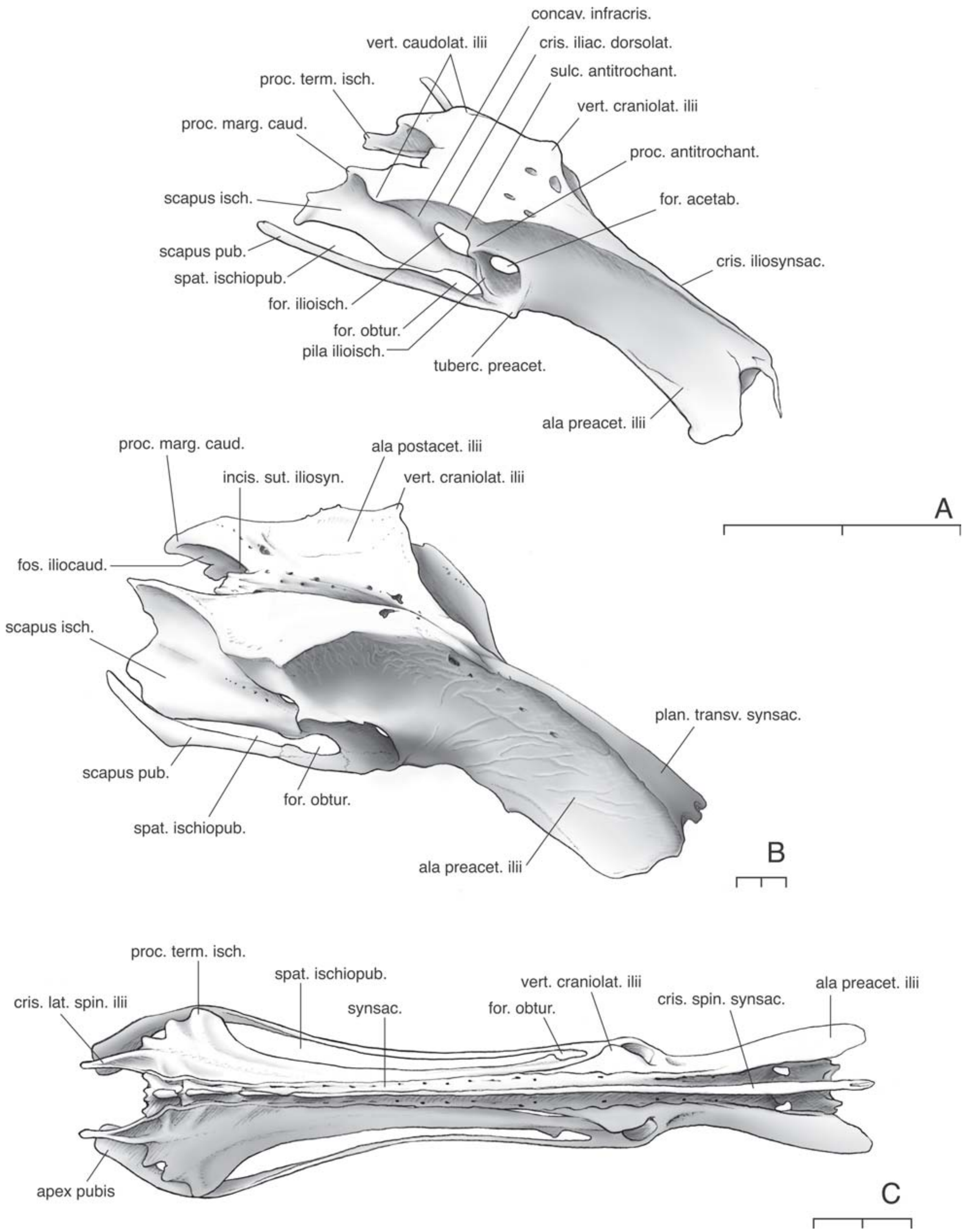


Fig. 27.—Ossa cinguli membri pelvici: (A) *Porphyrula martinica*, anterodorsolateral view; (B) *Aptornis defossor,* anterodorsolateral view; (C) *Gavia stellata*, dorsal view.

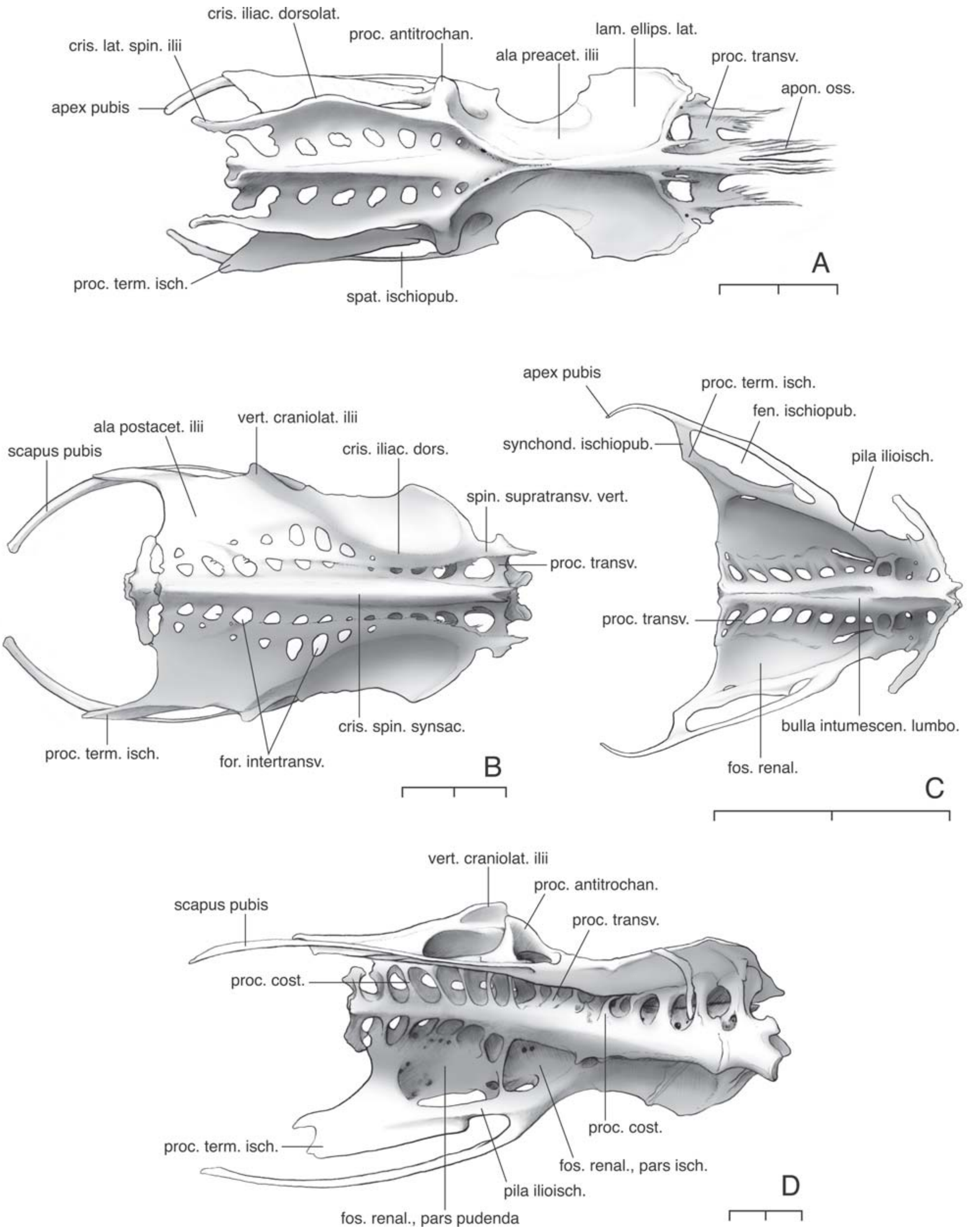


Fig. 28.—Ossa cinguli membri pelvici: (A) *Anhinga anhinga*, dorsal view; (B) *Fregata minor*, dorsal view; (C) *Apus apus*, ventral view; (D) *Ciconia ciconia*, ventrolateral view.

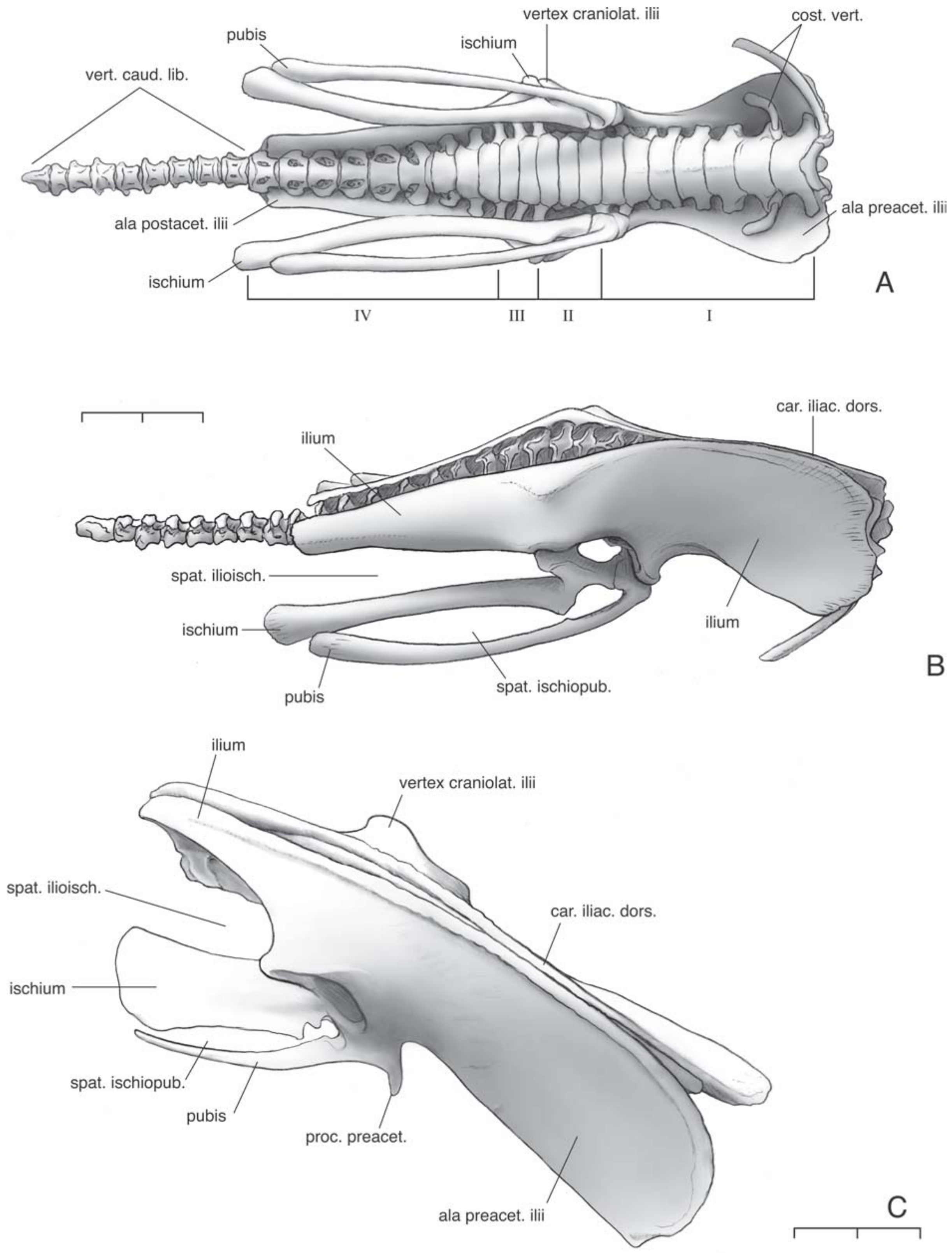


Fig. 29.—Ossa cinguli membri pelvici, synsacrum, and vertebrae caudales: (A) *Dromaius novaehollandiae* (immature), ventral view; (B) *Dromaius novaehollandiae* (immature), dorsolateral view. Pelvis: (C) *Apteryx australis,* anterodorsolateral view.

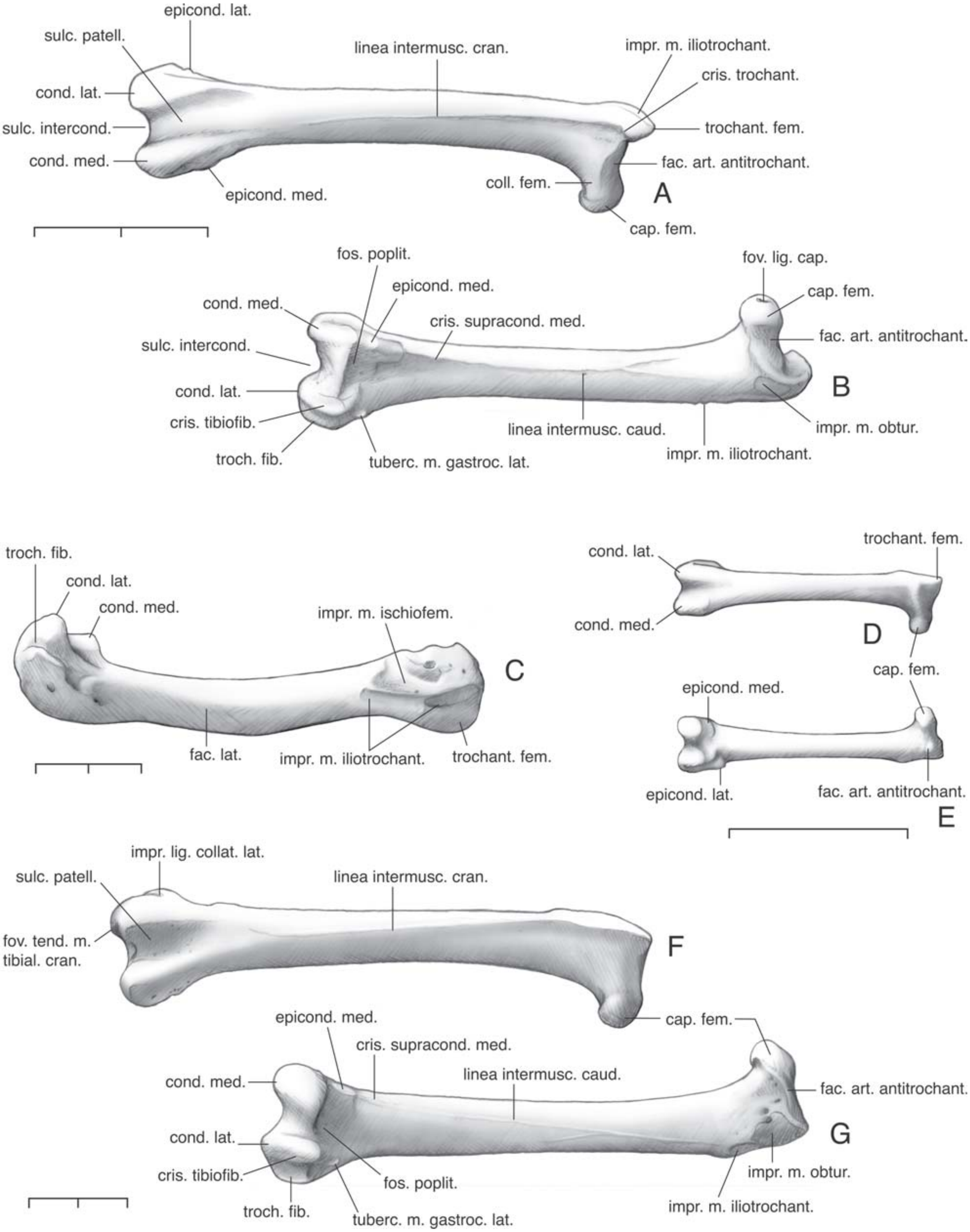


Fig. 30.—Femur: (A) *Megapodius freycinet,* cranial view; (B) *Megapodius freycinet,* caudal view; (C) *Apteryx australis,* lateral view; (D) *Galbula ruficauda,* cranial view; (E) *Galbula ruficauda*, caudal view; (F) *Balaeniceps rex,* cranial view; (G) *Balaeniceps rex,* caudal view. Scale: (A–C, F–G) 2 cm, (D–E) 1 cm.

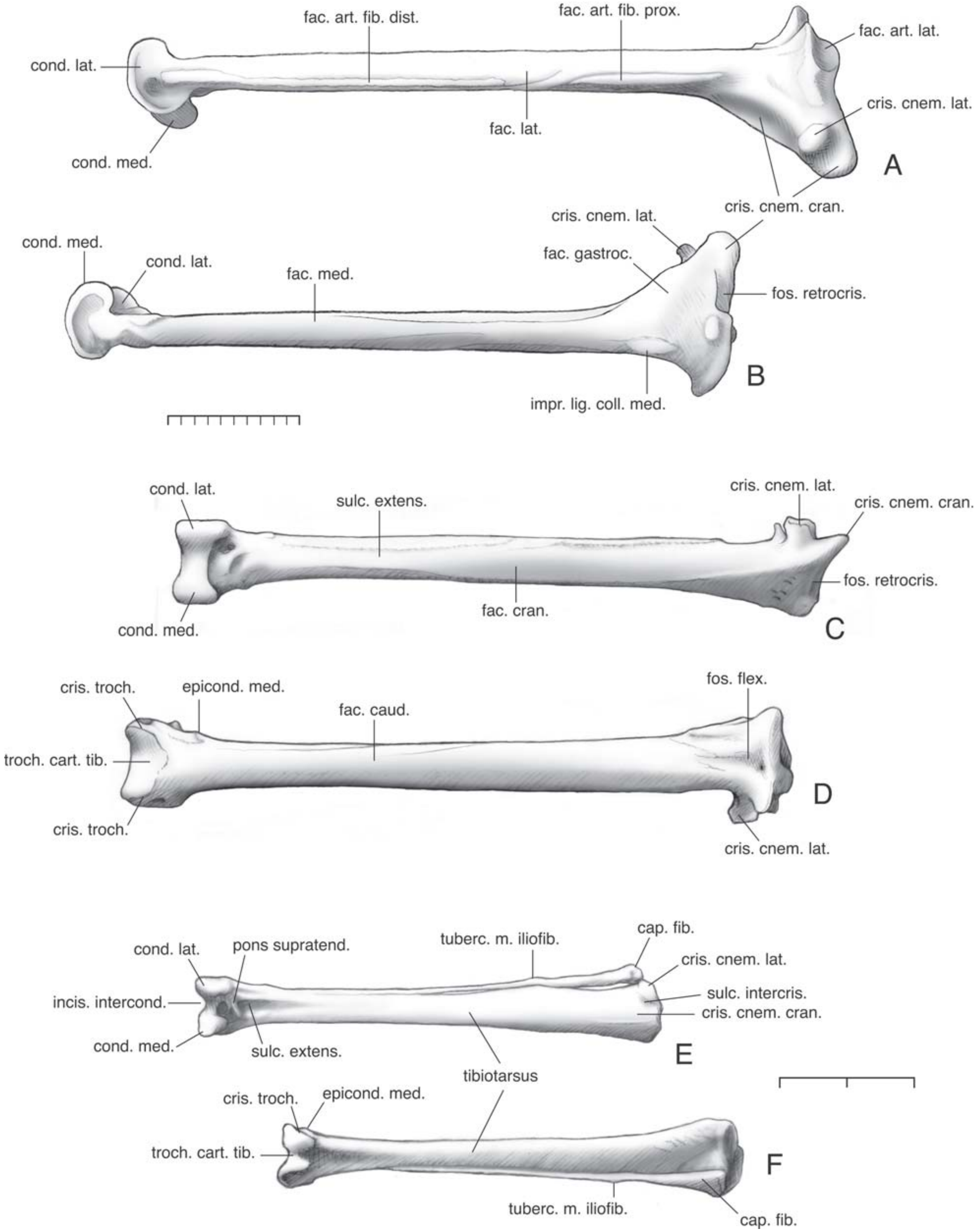


Fig. 31.—Tibiotarsus: (A) *Struthio camelus*, lateral view; (B) *Struthio camelus,* medial view; (C) *Struthio camelus,* cranial view; (D) *Struthio camelus,* caudal view. Tibiotarsus et fibula: (E) *Fregata minor,* cranial view; (F) *Fregata minor,* caudal view. Scale: (A–D) 10 cm, (E–F) 2 cm.

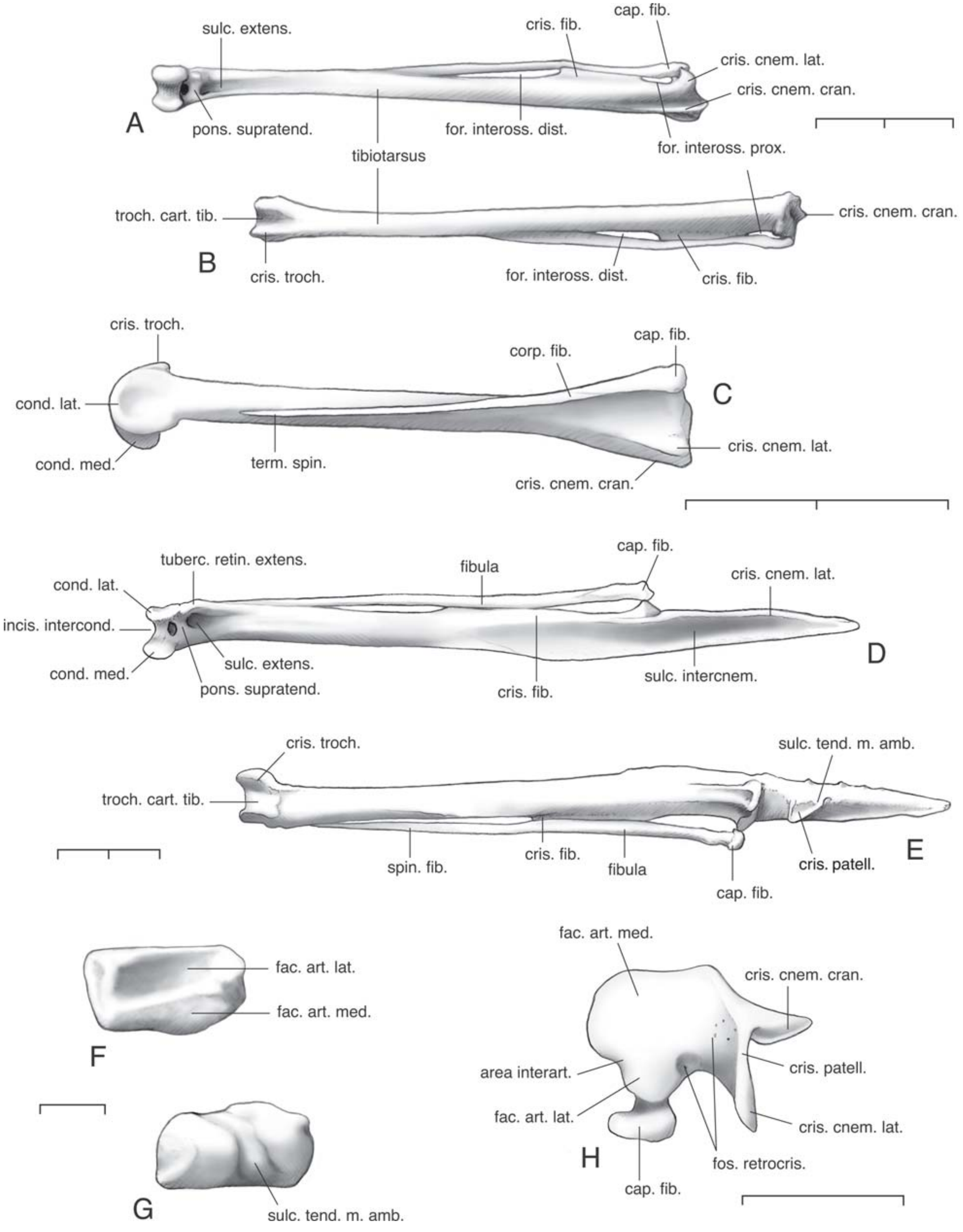


Fig. 32.—Tibiotarsus et fibula: (A) *Porphyrula martinica,* cranial view; (B) *Porphyrula martinica,* caudal view; (C) *Steatornis caripensis,* lateral view; (D) *Gavia stellata,* cranial view; (E) *Gavia stellata,* caudal view. Patella: (F) *Spheniscus magellanicus*, caudal view; (G) *Spheniscus magellanicus*, cranial view; (H) *Haematopus ostralegus,* proximal view. Scale: (A–E) 2 cm, (F–H) 1 cm.

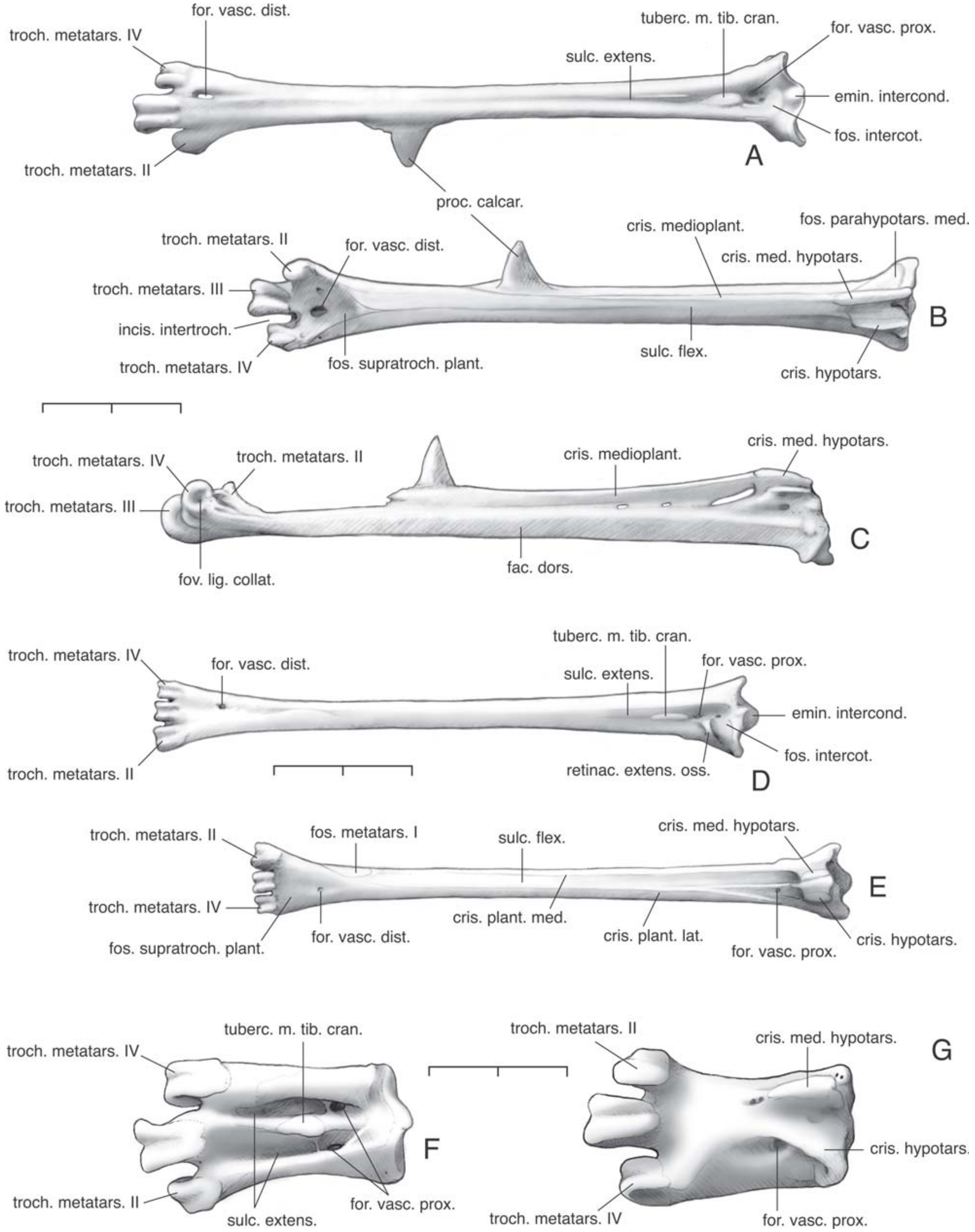


Fig. 33.—Tarsometatarsus: (A) *Meleagris gallopavo,* dorsal view; (B) *Meleagris gallopavo,* plantar view; (C) *Meleagris gallopavo,* lateral view; (D) *Menura novaehollandiae,* dorsal view; (E) *Menura novaehollandiae*, plantar view; (F) *Spheniscus magellanicus,* dorsal view; (G) *Spheniscus magellanicus,* plantar view.

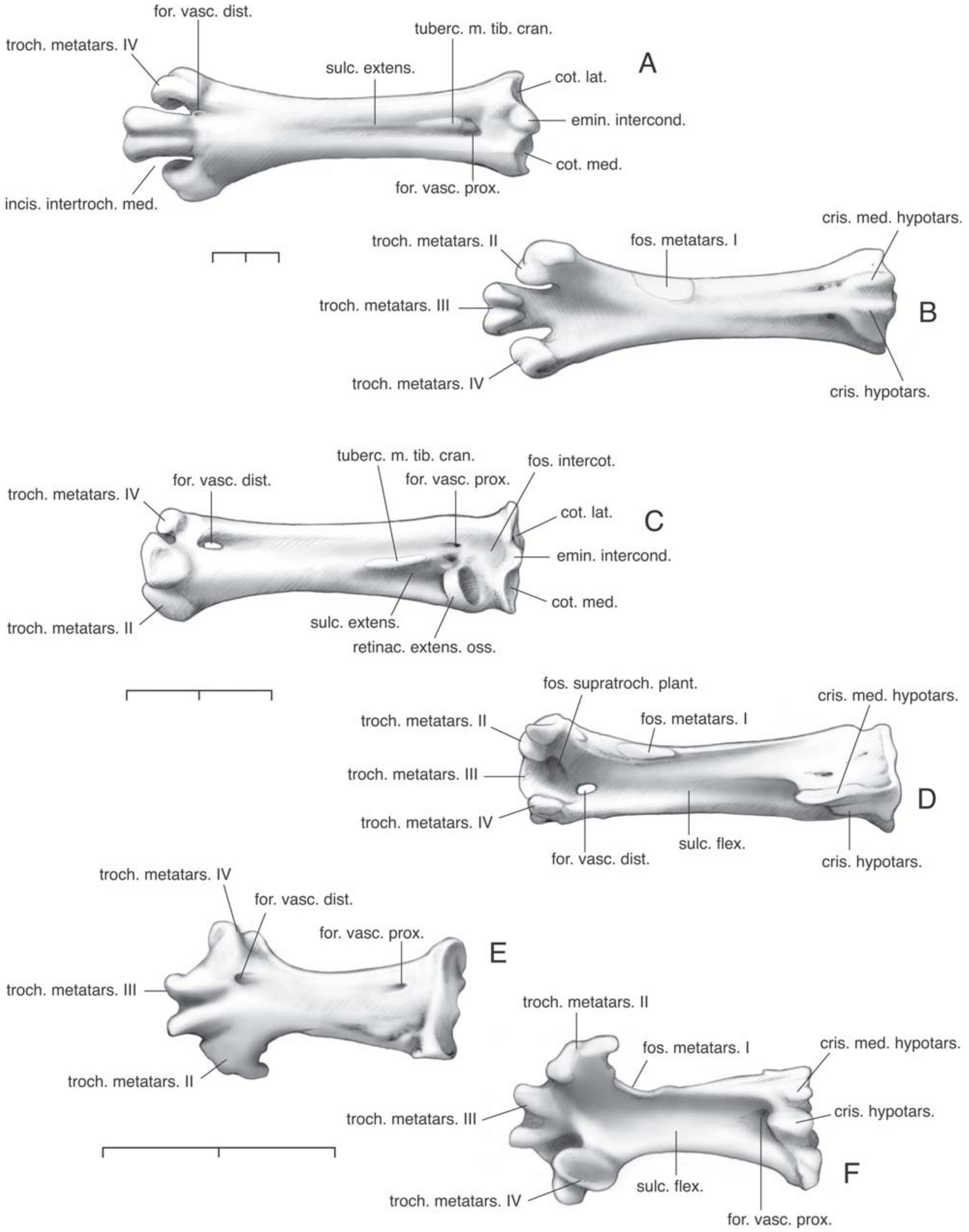


Fig. 34.—Tarsometatarsus: (A) *Apteryx australis,* dorsal view; (B) *Apteryx australis,* plantar view; (C) *Pandion haliaetus,* dorsal view; (D) *Pandion haliaetus,* plantar view; (E) *Cacatua galerita,* dorsal view; (F) *Cacatua galerita,* plantar view.

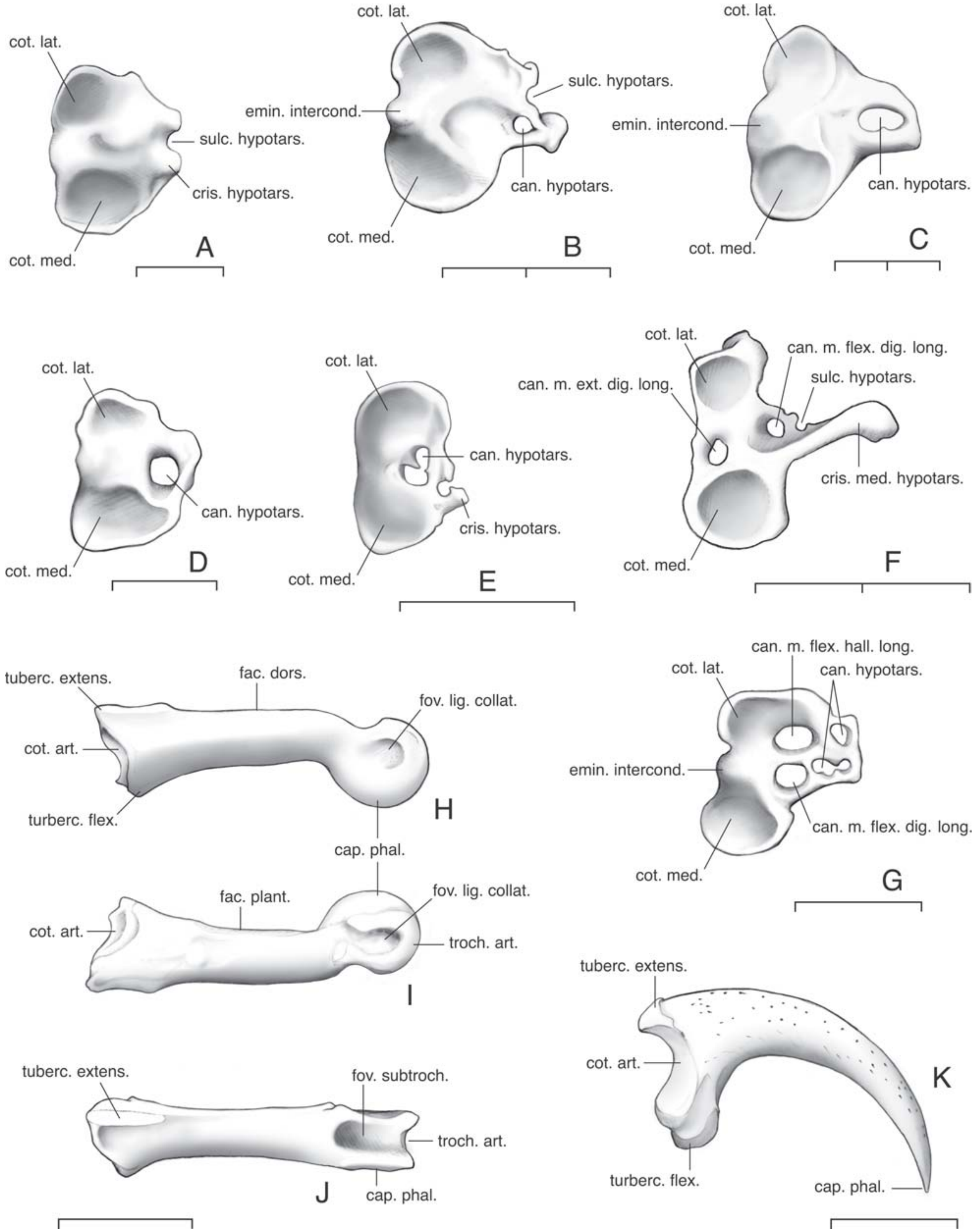


Fig. 35.—Tarsometatarsus et hypotarsus, proximal view: (A) *Apteryx australis,* (B) *Meleagris gallopavo,* (C) *Aptornis defossor,* (D) *Pandion haliaetus,* (E) *Cacatua galerita,* (F) *Eulampis jugularis,* (G) *Menura novaehollandiae*. *Pandion haliaetus,* digitus III pedis, phalanx proximalis—(H) lateral view; (I) medial view; (J) dorsal view. Digitus III pedis, phalanx ungualis—(K) lateral view. Scale: (A, D–E, G–K) 1 cm, (B–C) 2 cm, (F) 2 mm.

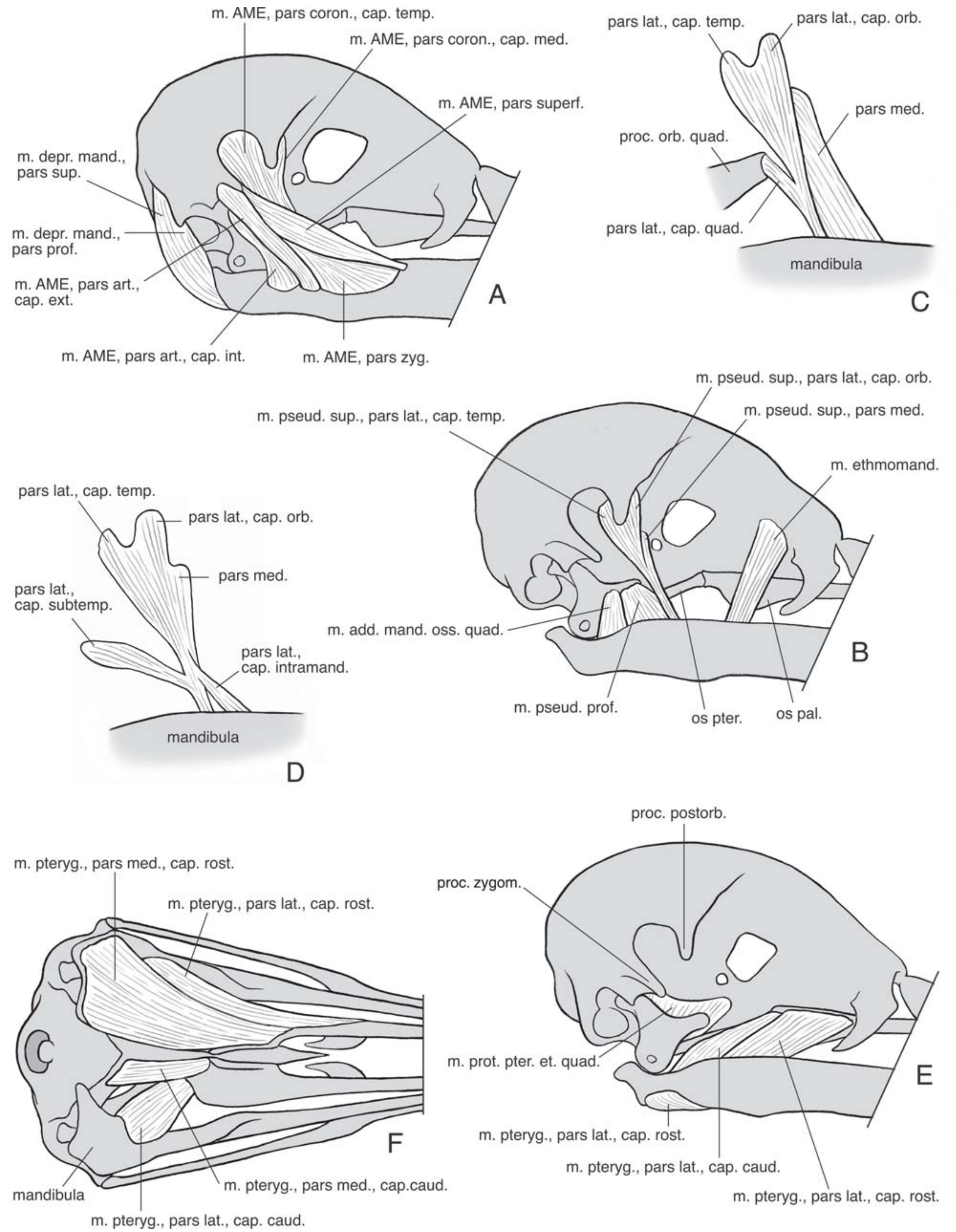


Fig. 36.—Musculi mandibulae, general topography and subdivisions: (A–B) lateral view. Musculus pseudotemporalis superficialis and subdivisions shown in isolation: (C–D), lateral view. Musculi mandibulae, general topography: (E) lateral view; (F) ventral view. Osteological features in gray; muscles lined.