Chapter 2

THE FOSSIL RECORD OF BIRDS

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I. Introduction

Avian paleontology has long been a poor stepsister to its mammalian counterpart, a fact that may be attributed in some measure to an insufficiency of qualified workers and to the absence in birds of heterodont teeth, on which the greater proportion of the fossil record of mammals is founded. Also acting to keep avian paleontology from being accorded its proper status is the highly popular trend among diverse writers to reiterate the idea that bird bones are hollow and light and therefore are seldom preserved, thus supposedly contributing to a meager fossil record for the class. Because such an introduction relieves a writer of the need to determine what actually is known about the fossil record of birds and of saying anything intelligent about the matter, such prefatory comments are unlikely to suffer the rapid quietus they deserve. The fact is, however, that the paleontological record of birds is already extensive and highly informative; the eventual exposition of the thousands of undescribed specimens already in museums and under study will make it even more so in the near future.

At the risk of appearing pretentious, I have sacrificed accuracy for simplicity in the title of this chapter. It would, of course, be quite impossible to treat the entire fossil record of birds here; instead, I have attempted to relate what I believe paleontology currently tells us about the first appearance and evolution of the major taxa of birds. Not all families receive equal attention, particularly those for which extensive revisions are necessary before any sense can be made of their fossil record. The need for such revisionary work continues to be very great, as I hope will be evident.

With certain exceptions, I have concentrated on the Mesozoic and Tertiary history of birds and have not gone into details about the Quaternary, for which there is a voluminous literature dealing largely with living genera and species. I have tried, however, to mention Quaternary taxa that expand our concepts of the diversity of certain groups and also to mention supposedly extinct genera that have lately been synonymized with those still living.

Quaternary avifaunas, as such, are beyond the scope of this work. Steadman (in Lundelius *et al.*, 1983) has summarized the avian fossil record for the last 15,000 years of the Pleistocene in North America. Most of the literature on Quaternary birds of the West Indies is covered in Olson (1978b) and Olson and Hilgartner (1982). Much of what is known about Pleistocene birds in South America may be found in K. E. Campbell's (1976b, 1979) studies in Ecuador and Peru, augmented by Eduardo Tonni's contributions from Argentina (e.g., Tonni, 1980a, and other papers published largely in the journal *Ameghiniana*). Quaternary avifaunas from Australasia are conveniently summarized by Rich and Van Tets (1982) and Fordyce (1982). There is no single overview of the very extensive literature on Quaternary birds from Europe, although one work that merits mention in this context is Mourer-Chauviré's (1975) comprehensive treatment of the middle and late Pleistocene birds of France.

The essence of this chapter is in a sense bibliographic, as there is no up-to-date source summarizing the explosion of recent literature on fossil birds. As testimony to the need for such a summary, it may be worth noting that of the 500 references cited herein, 178 (36%) were published in the decade from 1970 through 1979, and 145 (29%) appeared from 1980 onward. Or, in other words, 65% (323) of the titles cited were published after the last non-passerine part of Brodkorb's (1971b) "Catalogue of Fossil Birds" was submitted for publication. I have not necessarily provided references for taxa that are included in the "Catalogue," although I have attempted to cite the original source for those that were described subsequently, or that are listed only in the addenda in parts 2 to 4 of the "Catalogue"; the reference section is thus somewhat biased toward more recent publications.

The present work would have been far less useful had I not availed myself of considerable unpublished information and I have of necessity included numerous original observations of a sort that normally first appear in technical journals. Had I not done so, I would repeatedly have found myself being needlessly circumspect in addressing information and ideas that I knew would have to be altered. For example, I could hardly discuss the "terrestrial vulture" *Neocathartes grallator*, knowing that it is not a vulture at all, although this has not yet been documented elsewhere.

Unfortunately, the study of fossil birds has been, and continues to be, plagued by a good deal of what can only be called poor science. The idea that every scrap of fossil bird bone is a priceless gift to be treasured with veneration and treated as if diagnostic has infected avian paleontology down to the present. Although Wetmore (1959, p. 7) wrote that "the paleornithologist early learns to find enthusiasm in fragments of bone that to the uninitiated may appear without character or attraction," the charm of these fragments has very frequently exceeded their scientific merit. When misidentified they have invariably been more deceptive than instructive. Nevertheless, there is still a philosophy among certain workers that holds that every specimen of fossil bird can be identified to the species level and that every fossil deserves to be given a scientific name (for a critique of this credo, see Steadman, 1981). Indeed, certain recently published studies are considerably worse than those of some of the more notorious early workers, who had far more limited resources. The nominal taxa created in this process do little to advance our knowledge of avian evolution and are an undoubted hindrance to nonpaleontologists attempting to extract information from bare lists of fossil species.

I have repeatedly maintained that it is impossible to diagnose Paleogene birds on isolated fragments of limb bones. Even with complete skeletons, the affinities of early Eocene birds frequently prove remarkably difficult to ascertain. Various scraps of Eocene birds previously identified as rails, New World vultures, hawks, presbyornithids, ibises, procellariiforms, and musophagids, are now known to have come from paleognathous birds completely unrelated to any of these modern groups (P. Houde, personal communication). Thus I have been compelled to ignore many of the taxa newly proposed from the Eocene of England, for example, until these can be competently reassessed. In this chapter I have for the most part discounted taxa that I personally regard as having been too poorly documented or as being based on specimens too fragmentary to convey any meaningful information at this time.

It is, of course, important to refer to fossils in a context of geological time. The well-known Tertiary epochs, such as Eocene, Oligocene, and Miocene, were originally defined as marine sequences. The relative age of rocks is generally determined either by their contained fossils or their position relative to other strata with fossils assignable to a known epoch. Only recently has the advent of radiometric dating techniques provided absolute dates. Time within epochs is generally divided into "early," "middle," and "late," whereas rock strata themselves are referred to as being "Lower," "Medial," or "Upper." These subdivisions are rarely of equal duration.

More precise location in time is provided by the use of stages or ages (e.g., Aquitanian, Chadronian). These are of local application and may pertain to only a single basin or embayment, or to much larger areas, such as entire continents. As with epochs, stages were largely defined by occurrences of invertebrates in marine sediments. Such stages are of little use in continental deposits that do not interdigitate with marine facies, so stages based on fossil land mammals were brought into use. In North America there has been a heavy dependence on land mammal stages in vertebrate paleontology, as most of the better known fossiliferous deposits in the western United States, for example, cannot be directly correlated with marine stages. In Europe, where marine transgressions were generally more extensive, many continental deposits are still referred to by the names of marine stages, although land mammal ages are being refined and are coming into more general use, particularly for fissure fills that are impossible to correlate directly with marine stages.

When referring to a fossil taxon, I have usually attempted to mention its relative position within an epoch and also to refer to a particular marine or land mammal stage. Epoch boundaries tend to shift with refinements in dating and stratigraphic knowledge, but the stage name should generally allow one to determine a fossil's place in time. The correlation chart of Van Eysinga (1978), although in parts outdated or inaccurate, is a popular source for time/stratigraphic terminology. I have adopted the new divisions proposed by Fahlbusch (1981, and personal communication *fide* P. Ballmann), who places some of the more important Miocene and Pliocene fossil sites in Europe as follows (MU = mammal unit): Bouzigues (MU 2), Wintershof West (MU 3), and Vieux-Collonges (MU 4) are Lower Miocene; Sansan, Nördlinger Ries, Steinheim Basin, and Neudorf (all MU 6), and Beni Mellal (Morocco) (MU 7) are Medial Miocene; La-Grive-St.-Alban (MU 7 and 8) is Medial to Upper Miocene. The correlation charts in Ray (1976a,b) are useful for Tertiary birds from marine deposits of the North Atlantic and eastern North Pacific, and the chart in Tonni (1980a) may be consulted for the ages of Argentinian fossil birds.

Because it often proves impossible to interpret fossils when the higher-level systematics of living birds is incorrectly understood, I have had to address several contentious problems with the relationships of modern taxa. As I have indicated elsewhere (Olson, 1981a), the currently accepted arrangement of birds in no way reflects the probable evolutionary history of the class. Although we are still a long way from being able to promulgate a truly satisfactory classification, I have attempted here to arrange orders and families in what I believe is a more logical sequence than prevails at present. This is not to be construed as a classification per se, but is merely a "working arrangement" that I have found useful in trying to interpret fossils, in making some concordance of the osteological characters I have observed and of the various anatomical characters in the classical systematic literature, and in conceptualizing what the pattern of evolutionary diversification may have been like in the class Aves. I can see little use in continuing with a sequence that should have been replaced decades ago and against which there has long been much contrary information.

If we adopt the convention of beginning with primitive taxa and progressing to more specialized ones, it would hardly seem logical to start with such highly specialized families as penguins and loons, in the manner of Gadow (1893) and Wetmore (1960). This was done presumably because the relationships of such groups were not easily perceived, and it was therefore assumed that they must represent some "ancient" line within the class Aves.

The arrangement used here is predicated mainly on the assumptions that birds originated on land rather than in the water, and that highly specialized waterbirds are more derived than less specialized ones. These simple tenets will probably not be perceived as particularly insightful, even by ornithologists, yet they require a drastic alteration of the traditional Gadow–Wetmore sequence. My only other major innovation has been to rend asunder the six orders that are certainly or likely to be polyphyletic (viz., Gruiformes, Ciconiiformes, Falconiformes, Coraciiformes, Piciformes, and Apodiformes). The naturalness of each of these groups has been questioned for some time and I have only taken action where others have in the past been perhaps too timorous. Still, I have continued to use far more orders than should be admitted. The ordinal level taxa currently in use (following Wetmore, 1960) actually have little value in that most either are monotypic (or nearly so) and hence do not function to cluster groups of related organisms, or are polyphyletic, and thus do an even greater disservice. The only ordinal level taxa in the current scheme that do a proper job of associating more than two families into a monophyletic group are the Procellariiformes, Pelecaniformes, and Passeriformes. Clearly there is room for improvement here.

From the discussions of the nature and origins of *Archaeopteryx*, a consensus has emerged that birds originated, if not in trees, certainly on land. Therefore, we should look for the most primitive taxa among the land birds. Although highly specialized in certain aspects of their morphology, the Hoatzin (*Opisthocomus*) and the Musophagidae are probably as close to the ancestral neognathous bird as any other birds now living and therefore I have begun my sequence with these taxa. They are followed by the remainder of what I have termed the "basal" land bird assemblage, including the Cuculidae, diurnal raptors (less the Vulturidae), Turnicidae, Galliformes, Columbiformes, and Psittaciformes. This assemblage is succeeded by the "higher" land birds, which correspond fairly closely with Garrod's (1874) "Anomalogonatae." (Section IX).

In any linear sequence, after reaching the end of one branch one must return to the base of another, so that some primitive birds necessarily appear in the middle of the sequence. In turning to the waterbird assemblage I have started with the Cariamidae and their relatives, as these have many osteological similarities with the Opisthocomidae and may provide a link between the land birds and some of the "waterbird" families included in the

Gruiformes, such as the Psophiidae. A close association between the Gruiformes and Charadriiformes has long been admitted and the Anseriformes have also been shown to be derived from this assemblage. Following these are the remainder of the waterbirds, ending with the most specialized group, the penguins, Spheniscidae.

II. *Archaeopteryx*

Many general discussions of the avian fossil record dwell extensively on the late Jurassic (Portlandian) specimens of *Archaeopteryx*, often to the virtual exclusion of other members of the class. Because I wish to concentrate on the *rest* of the fossil record of birds, I have deliberately curtailed discussion of the origin and relationships of *Archaeopteryx*, and the origin of birds as a whole, these topics actually being more herpetological in scope. Among the latest contributions to the ceaseless debate about the nature of *Archaeopteryx* and the origin of birds are the paper by Thulborn and Hamley (1982), the interchange between Martin (1983a) and Steadman (1983), and an additional review by Martin (1983b), which summarize the pertinent recent literature. In September 1984, the first International *Archaeopteryx* Conference was held in Eichstätt, the proceedings of which should contain the very latest views on the subject. After this chapter was submitted, three additional papers on *Archaeopteryx* appeared in the September–October 1984 issue (Vol. 82, no. 1–2) of the *Zoological Journal of the Linnean Society*.

The history of the five skeletal specimens and the single feather impression of *Archaeopteryx* from the Solnhofen limestone of Bavaria, and the considerable controversy surrounding the significance of these remains, has been dealt with in a lucid and fair manner by Feduccia (1980b). Helms (1982) has discussed the structure and manner of preservation of the feathers in the Berlin specimen. New preparation of the London specimen permitted Whetstone (1983) to describe in detail the braincase of *Archaeopteryx*, which he found to be more birdlike than had previously been supposed.

Brodkorb (1971c) showed that the skeletal proportions of *Archaeopteryx* are similar to those of modern arboreal birds such as chachalacas (Cracidae), hoatzins (Opisthocomidae), and turacos (Musophagidae). The asymmetry of the remiges of *Archaeopteryx* indicates that these feathers had an aerodynamic function (Feduccia and Tordoff, 1979), and *Archaeopteryx* also had a pectoral girdle that was probably capable of functioning in powered flight (Olson and Feduccia, 1979a). These and other arguments (Martin, 1983b) controvert Ostrom's (1976) contention that *Archaeopteryx* represents a preflight stage in the evolution of birds and that it was a terrestrial predator that used its wings to capture prey (Ostrom, 1979). Whatever the relationships of *Archaeopteryx* may be, it was surely volant.

It has been proposed that there was more than one species of *Archaeopteryx*, but no modern assessment of the species-level systematics of the genus has been attempted. Depending on whether or not *Archaeopteryx* had determinate growth, as in modern birds, the Eichstätt specimen of *Archaeopteryx* (F. X. Mayr, 1973), which is a third smaller than the celebrated London and Berlin specimens, could represent a species different from any of those previously named. Howgate (1984) has now named this as *Archaeopteryx recurva*, based primarily on characters of the teeth.

One of the most striking features of *Archaeopteryx* is that its feathers appear in every respect to be like those of modern birds. Parkes (1966) has argued that feathers evolved first for flight and secondarily for insulation. His is still the best and most reasonable analysis of the problem.

In discussions of the origins of feathers it is a curious fact that pterylosis is scarcely, if ever, mentioned; yet it is true of all birds that the feathers occur in rows (pterylae) separated by bare spaces (apteria). It is remarkable just how few feathers are actually needed to cover a bird completely. Among more commonly available taxa, this may be best appreciated in herons (Ardeidae), in which two rows of two feathers serve to cover most of the dorsal and the ventral surfaces of the body.

Study of the shape and distribution of feather tracts has occupied the attention of numerous ornithologists, but that such tracts exist at all generally escapes comment. Gadow (1896, p. 744) articulated the commonly held belief that "presumably the first birdlike creatures had their skin uniformly clothed." Such an assumption receives no support from ordinary experience, however. All birds have the feathers arranged in distinct pterylae; those that seem to have the plumage uniformly distributed either have vestigial apteria or have apteria in the embryonic stages (Clench, 1970). Thus, to have the feathers distributed in discrete tracts is as much an avian characteristic as the possession of feathers itself. There is no reason to regard this as being anything other than the primitive state in the class Aves. This could be viewed as contrary to Regal's (1975) hypothesis of evolution of feathers from elongate scales that functioned as heat shielding devices. Such scales would presumably have been originally distributed over most of the body, as in the lizards that provided Regal's model. If contour feathers first evolved in disjunct rows, it is still not certain what their original function may have been, although the fact that contour feathers in flightless birds quickly degenerate into less complicated, more hairlike structures, through the loss of hooklets and barbules, seems to indicate that the structure, even of body feathers, has an aerodynamic function (Feduccia, 1980b).

The specimens of *Archaeopteryx* are as yet the only certain birds known from the Jurassic. Rautian (1978) described a new genus and species, *Praeornis sharovi*, from an impression of a single feather from Upper Jurassic lake deposits in Kazakhstan. Because the specimen differed so greatly from feathers of *Archaeopteryx* or living birds, he placed the species in a new family, order, and subclass. The significance of this fossil will depend heavily on whether it was correctly identified as a feather. Jensen (1981), in a popular magazine in Japanese, first proposed the name *Palaeopteryx thompsoni* for a sacrum and a few fragments of long bones that he regarded as avian from the late Jurassic of Colorado, and he later postulated on the significance of these finds to the position of *Archaeopteryx* (Jensen, 1983). A convincing case that these are in fact bird bones has not yet been made.

III. Early Cretaceous Birds

The morphological and temporal gaps between *Archaeopteryx* and other known birds were for many years essentially a great void. The morphological gap is still as great, but the temporal one is beginning to close. The most important discovery bridging this gap is a partial associated skeleton of a true carinate bird from Lower Cretaceous (Neocomian) lacustrine deposits at Khurilt-Ulan-Bulak in central Mongolia (Kurochkin, 1982a). This consists of the pectoral girdle and wing, including the sternum, coracoid, scapula, furcula, vertebrae, proximal end of humerus, and partial carpometacarpus with carpals and digits, as well as feather impressions. Kurochkin named the specimen *Ambiortus dementjevi*, placing it in its own family and order (Ambiortidae, Ambiortiformes).

I have had the advantage of examining and comparing a cast and photographs of *Ambiortus* and of discussing its morphology with E. N. Kurochkin and P. Houde. *Ambiortus* was unquestionably a true, volant bird, as it has a typically avian coracoid, scapula, and furcula, in addition to a keeled sternum. Although it cannot be referred to any modern or fossil order of birds, as Kurochkin (1985) points out, it shows some decided similarities to the volant Tertiary paleognathous birds called to attention by Houde and Olson (1981). It may also share some similarities with *Ichthyornis*, particularly in the humerus. *Ambiortus* definitely has none of the primitive features of the pectoral girdle that characterize *Archaeopteryx*, although it did have a third phalanx on the major digit of the wing, a primitive character.

In addition to the holotype of *Ambiortus*, abundant feather impressions were recovered from the same site, from five other early Cretaceous localities in Mongolia, and from one at Bajsa in Transbaikalia (Kurochkin, 1985). Feather impressions have also been obtained from lowermost Cretaceous ambers in Lebanon (Schlee, 1973) and Lower Cretaceous ambers from the Khatanga River in northern Siberia (Kurochkin, 1985). Feather impressions from Lower Cretaceous claystones in Victoria, Australia (Talent *et al.*, 1966; Waldman, 1970; Rich, 1976), establish that birds were in the Southern Hemisphere by the beginning (Neocomian) of the Cretaceous (Brodkorb, 1971c, p. 37). Footprints attributed to birds have also been described from later in the early Cretaceous (Aptian) of British Columbia (Currie, 1982).

Gallornis straeleni from the early Cretaceous (Neocomian) of France had once been termed the oldest Cretaceous bird. It is based on the proximal end of a femur that was assigned to the Anseriformes by Lambrecht (1931b), but was placed near flamingos by Brodkorb (1963c). So old a specimen is much too incomplete for confident assignment (Howard, 1964; Olson and Feduccia, 1980a), and even its status as a bird probably deserves scrutiny. At this point, *Gallornis* tells us nothing about avian evolution. Nor does the worn humerus of *Wyleyia valdensis* Harrison and Walker, 1973, described as a bird from the early Cretaceous (Wealdan) of England. Brodkorb (1978, p. 228) considered this as "almost certainly a reptilian humerus." Although Elżanowski (1983) was once of the opinion that *Wyleyia* was avian, he has now reconsidered in favor of reptilian relationships (A. Elżanowski, personal communication).

Thus, other than *Ambiortus,* the only early Cretaceous bird based on reasonably diagnostic specimens is *Enaliornis*, from the Albian of England. This was a very specialized diving bird, probably flightless, of the order Hesperornithiformes, subclass Odontoholcae.

The picture that now emerges alters some prevalent ideas concerning the early evolution of birds. The feathers, tracks, and few osseous remains mentioned above indicate that birds were already widespread in early Cretaceous faunas. *Ambiortus* proves that typical flying birds were in existence some 15 to 20 million years after *Archaeopteryx*, whereas *Enaliornis* shows that birds of an apparently different subclass had by then already evolved into highly specialized diving forms.

In the course of avian evolution there evidently were several major radiations, each of which probably gave rise to a variety of forms with diverse morphological and ecological adaptations. The Hesperornithiformes appear to be the only group yet known of one of the earliest of these radiations. Inasmuch as they were already highly specialized for foot-propelled diving by the early Cretaceous, they serve to remind us that there must once have been other members of this radiation, probably with very different adaptations, that remain to be discovered.

It is increasingly evident that *Archaeopteryx* is indeed likely to be on a side branch of avian evolution, as postulated by some authors (e.g., Martin, 1983b). It appears to have been a late-surviving relict of an even earlier stage of avian development and was very likely contemporaneous with birds of more typically avian construction. With future fossil discoveries we may find that much more of the evolution of birds took place in the Jurassic than has previously been believed.

IV. Hesperornithiformes

The order Hesperornithiformes consists of medium to large flightless birds that were highly specialized for foot-propelled diving. Most specimens have come from marine deposits. *Hesperornis* possessed teeth on the dentary and maxilla, which has occasioned much admiration and discussion since the group was monographed by Marsh (1880); it has been assumed that the other genera in this order were toothed as well, although this is not certainly known. Much new and original information on the Hesperornithiformes has been gathered by L. D. Martin, who has published certain portions of it (Martin, 1980, 1983a), from which I have attempted, perhaps not altogether successfully, to extract the more important points.

The earliest Hesperornithiformes are two nominal species of *Enaliornis* from the early Cretaceous (Albian) of England. Until the discovery of *Ambiortus*, these were the earliest known birds, other than *Archaeopteryx*, to be founded on diagnostic material. Although placed with the loons in the order Gaviiformes by Brodkorb (1963b; 1971b), the Enaliornithidae has been suggested as being the most primitive family of Hesperornithiformes (Martin and Tate, 1976; Martin, 1983a). An "*Enaliornis*-like" tarsometatarsus from the Cenomanian Greenhorn formation of Kansas is alluded to by Martin (1983a).

The order next appears in the late Cretaceous (Coniacian or later) of Kansas, where two families and supposedly four genera and six species are represented (Martin, 1983a). The more primitive of these is the Baptornithidae, the best-known species of which, *Baptornis advenus* Marsh, has been treated in detail by Martin and Tate (1976), who established that the members of the Baptornithidae belong in the Hesperornithiformes and not with the grebes (Podicipediformes), where they had been placed by Brodkorb (1963b, 1971b). Thus, neither loons nor grebes are known from the Mesozoic. Although contemporaneous with *Hesperornis*, *Baptornis* was somewhat less specialized for diving. Martin and Bonner (1977) have discussed the possible significance of juvenile specimens of *Baptornis*.

Martin and Tate (1976) assigned *Neogaeornis wetzeli* Lambrecht to the Baptornithidae. This species is known from a tarsometatarsus from the late

Cretaceous (Maastrichtian) of Chile and shows that the order was also present in the Southern Hemisphere. If the age of the Chilean deposits is truly Maastrichtian, this would be the latest occurrence of the order, as no other Hesperornithiformes have been reported from rocks younger than Campanian.

The best known family of the order is the Hesperornithidae. Marsh (1880) recognized three species of *Hesperornis* from the late Cretaceous of Kansas in deposits often attributed to the Coniacian but that are possibly younger (Bryant, 1983). All three species, however, may be referable to *H. regalis* Marsh (Martin, 1980). There are apparently several undescribed forms of Hesperornithidae now known from the same deposits (Martin, 1980; 1983a). One of these was introduced in a general, nonsystematic publication (Martin, 1983a) under the name *Parahesperornis alexi*, along with illustrations of the reconstructed skeleton and skull, a precise designation of the holotype, and statements in the text concerning osteological characters. The name *Parahesperornis alexi* is therefore clearly available from this point, notwithstanding that its description does not conform with the best modern nomenclatural practices. Other fossils of *Hesperornis* are known from marine deposits in Alaska, the Northwest Territories, Manitoba, South Dakota, Montana, and Wyoming, and from a brackish or estuarine deposit in the Campanian of Alberta (see Fox, 1974; Elżanowski, 1983; Bryant, 1983). It has not yet been established whether the hesperornithiform from the Campanian of Montana originally described as *Coniornis altus* Shufeldt, is really referable to a separate genus or is but a form of *Hesperornis*, although Martin (1980) has tentatively maintained it as distinct.

Considerable new material of *Hesperornis* is now known from the Upper Cretaceous (Campanian) Pierre Shale of South Dakota, supposedly including two genera and five species, some of which are much smaller than any hesperornithiforms yet described (Martin, 1980, 1983a). There was thus a much more extensive radiation of Hesperornithiformes than has hitherto been apparent. This order is not known in the Cenozoic and almost certainly did not cross the Cretaceous–Tertiary boundary, although the virtual absence of hesperornithiform fossils in Maastrichtian deposits makes it unlikely that the disappearance of these birds can be attributed to the same cause as other terminal Cretaceous extinctions. Elżanowski (1983, p. 75) has speculated that the demise of the Hesperornithiformes "may have been caused by the explosive radiation of acanthopterygian fishes."

I concur with Martin (1980) that the Hesperornithiformes probably branched off at a very early stage in avian evolution, but not necessarily from an ancestor incapable of sustained powered flight, as he has proposed. Some of the features of the hesperornithiform coracoid may well have resulted secondarily from flightlessness alone. The loss of the acrocoracoid, for example, also occurs in flightless carinates such as some of the extinct gooselike birds of the Hawaiian Islands (Olson and Wetmore, 1976).

Although the physical constraints of extreme specialization for foot-propelled diving has produced similarities in morphology between Hesperornithiformes and loons and grebes, there are many important points in which the Mesozoic divers differ greatly, not only from loons and grebes, but in some respects from all other birds as well (Martin and Tate, 1976). Gingerich (1973, 1976) has interpreted the palate of *Hesperornis* as being paleognathous, although McDowell (1978) identifies some of the palatal components differently. A. Elżanowski (personal communication) has quite another interpretation of the palate but notes that some aspects of it are indeed similar to the paleognathous condition. The important point here, however, and the cause of the controversy, is the fact that the palate of *Hesperornis* is utterly different from that of other known birds. Recognition of a separate subclass, Odontoholcae, for the Hesperornithiformes, is still justified. Martin (1983a) ranked them only as an infraorder, but his reasons for grouping the Hesperornithiformes, Ichthyornithiformes, and all modern birds in a subclass Ornithurae are not acceptable (Steadman, 1983).

Cracraft (1982) has resurrected the hypothesis that the Hesperornithiformes, loons, and grebes form a monophyletic group. The evidence for this was derived almost entirely from the same convergent specializations of the hindlimb and pelvis that led earlier workers to the same erroneous conclusion. Cracraft's phylogeny requires, among other things, that the Hesperornithiformes re-evolved teeth from an edentulous ancestor. I can only hope to distance myself from those who would accept the likelihood of such nonsense.

V. Ichthyornithiformes

These notorious but poorly understood fossil birds were discovered along with *Hesperornis* in the late Cretaceous of Kansas and were eventually recognized as having teeth. Much later this was challenged by Gregory (1952), who concluded that the jaws attributed to *Ichthyornis* belonged to a small species of mosasaur. That this mosasaur was smaller than any ever discovered (Russell, 1967, p. 121, footnote), and that more than one of the specimens of *Ichthyornis* happened to die next to such anomalous mosasaur jaws, were later to bode ill for Gregory's hypothesis, although this hypothesis was accepted, often exuberantly (e.g., Brodkorb, 1971c), for 20 years. It has now been established beyond doubt that *Ichthyornis* had teeth (Gingerich, 1972; Martin and Stewart, 1977).

Unlike *Hesperornis*, the species of *Ichthyornis* were obviously flying birds. They were the size of gulls or terns and may have had somewhat similar habits, as Marsh (1880) suggested long ago. It was probably this allusion that prompted many authors (see those cited by Lambrecht, 1933, p. 581) to place *Ichthyornis* near the Charadriiformes. This is certainly unjustified, as it is likely that *Ichthyornis* is a relict of an earlier radiation on a line quite apart from modern birds. The enormous deltoid crest in *Ichthyornis* is unique among birds in size, shape, and orientation, as noted by the original describer and later redundantly by Harrison (1973). The palate is unknown in *Ichthyornis* and there is no reason to suppose that these birds were even neognathous.

Several species of *Ichthyornis* have been proposed, principally on size (see Marsh, 1880). Most of these came from the Niobrara Chalk (Coniacian or later) in Kansas, with one species being named from the Upper Cretaceous Austin Chalk in Texas. The supposed ibislike bird *Plegadornis antecessor* from the Upper Cretaceous Selma Group (Santonian) in Alabama is also a species of *Ichthyornis* (Olson, 1975a). Much new material of *Ichthyornis* has been collected recently in Alabama (D. Womochel, personal communication). On the basis of a single vertebral centrum that they identified as *Ichthyornis* sp., Martin and Stewart (1982) extended the range of the family northward to southern Manitoba (late Cretaceous, Campanian), and Lucas and Sullivan (1982) extended it westward on the basis of a humerus of *Ichthyornis* sp. from Upper Cretaceous (late Turonian) deposits in northwestern New Mexico. An even earlier record, stated to be the "oldest Cretaceous skeletal fossil of a bird from the Western Hemisphere," is a humerus of *Ichthyornis* sp. from the early Turonian of Alberta (Fox, 1984, p. 258).

There has been no modern revision of *Ichthyornis* and until such a study is undertaken it would be unsafe to venture a guess as to how many of the nominal species are valid or what the relationships of *Ichthyornis* to other birds may be. The affinities of the genus *Apatornis*, formerly considered to be related to *Ichthyornis*, are uncertain but are probably not with the Ichthyornithiformes (see Howard, 1955, and Section X,D,1,c). For the present, *Ichthyornis* should be retained in its own order, Ichthyornithiformes, and should be removed far from the vicinity of the Charadriiformes.

VI. Other Mesozoic Birds

In describing supposed Mesozoic birds, many authors have not troubled to establish that the bones they were studying were in fact avian. Consequently the literature of fossil birds has been intruded upon by a number of reptilian taxa.

A supposed pelecaniform, *Elopteryx nopcsai*, from the late Cretaceous (Maastrichtian) of Romania, was described by Andrews (1913) on the basis of the proximal end of a femur and two referred distal ends of tibiotarsi. Harrison and Walker (1975b) decided that the tibiotarsi had been incorrectly referred and described them as two new genera in a new family of owls. Their illustrations, however, clearly show that these are not from birds and are instead the tibiae of small dinosaurs (Brodkorb, 1978, pp. 223–224; Elżanowski, 1983; Martin, 1983a). An error of such magnitude does not inspire confidence in other identifications by these authors. It is likely that the holotypical femur of *Elopteryx nopcsai* is also nonavian. Grigorescu and Kessler (1980) identified a fossil from the same deposits as the distal end of a femur of *Elopteryx*, but their illustrations of it show no particular likeness to femora in general or to those of birds in particular.

Sternberg (1940) described *Caenagnathus collinsi* as a new order of birds based on a mandible from the late Cretaceous (Campanian) of Alberta. This was done against the advice of A. Wetmore (personal communication), who later transferred the genus to the theropod dinosaurs (Wetmore, 1960). Cracraft (1971b) nevertheless attempted to prove that *Caenagnathus* was avian and even named another species on a fragment of jaw. This was to no avail, however, as these bones actually come from an ornithomimid dinosaur related to *Oviraptor* (Brodkorb, 1976; Osmolska, 1976).

Walker (1981) introduced a collection of bones from the late Cretaceous (probable Maastrichtian) of Argentina as a new subclass, Enantiornithes. The only named genus and species, *Enantiornis leali*, appeared solely in the legend of a table, and the subclass was proposed with no named orders or families. Martin (1983a) erroneously credits Walker with naming an order Enantiornithiformes, but the first use of that term appears to be attributable to Martin (1983a) himself. The name Enantiornithidae would seem to date from its use by Nesov and Borkin (1983). No one has ever stated whether there may be more than one order or family within the Subclass Enantiornithes, or what taxa are to be included in the Enantiornithiformes or the Enantiornithidae. One can only lament the casual and unprofessional manner in which the nomenclature of this new group of birds has been introduced.

Regardless, there is evidently a great deal of material of these birds now available from Argentina, representing a fair diversity of genera and species. Whereas the Enantiornthes had a birdlike wing skeleton, with a true carpometacarpus, their metatarsal morphology is so different from that in modern birds, and so reptilian in aspect, that the preliminary reaction of many workers, myself included, was that they were not correctly identified as birds. P. Houde (personal communication), who has examined the Argentinian fossils while at the British Museum, informs me that the material is so extensive that there can hardly be any doubt about the association of the various elements, at least at the level of subclass. The precise significance of the Enantiornithes is difficult to ascertain from the meager amount that has yet been published concerning them, but it is certain that they are far removed from all living birds.

Another enigmatic Mesozoic bird is *Gobipteryx minuta* (Gobipterygidae, Gobipterygiformes) known from two crushed and incomplete skulls and mandibles from the late Cretaceous (Santonian–Campanian) of Mongolia (Elżanowski, 1974, 1976, 1977). These skulls were considered to be paleognathous and they have a reptile-like quadrate similar to that of *Archaeopteryx*. Elżanowski (1981) later described embryonic skeletons from the same formation that probably belong to *Gobipteryx*. He refrained from referring them to that genus, however, a fact that other authors have tended to overlook. The Mongolian embryos belong to a decidedly volant bird and the coracoid is suggestive of that in the Enantiornithes (Martin, 1983a; Elżanowski, personal communication). As far as the skulls of *Gobipteryx* are concerned, Elżanowski (personal communication) would reemphasize the paleognathous morphology of the preserved parts of the palate, while rejecting the possibility of any close relationship between *Gobipteryx* and the living paleognaths.

Another enigmatic Cretaceous bird is *Alexornis antecedens*, described from several different skeletal elements from Upper Cretaceous (Campanian–Maastrichtian boundary) deposits in Baja California (Brodkorb, 1976). Brodkorb erected a new order and family for this species and regarded its similarities as being most like the living families Momotidae and Bucconidae. For this reason, he considered that the Alexornithiformes were ancestral to the Coraciiformes and the Piciformes, a conclusion that would have to be modified, however, if the Bucconidae properly belong in the Coraciiformes rather than the Piciformes (Olson, 1983a). Regardless, it now appears that *Alexornis* has no close relationship to any living birds. Elżanowski (1983) pointed out that the transverse orientation of the external condyle of the humerus is unlike that of living birds but similar to that in the Enantiornithes. Martin (1983a) suggested that Brodkorb had confused the scapula with the coracoid in *Alexornis*, the configuration of these bones being so different from that in modern birds. With this realization, these elements of *Alexornis* are then seen to be similar to those in the Enantiornithes, an interpretation with which Elżanowski (personal communication) concurs.

Martin (1983a) combined the Alexornithiformes, Gobipteryigiformes, and "Enantiornithiformes" in an "infraclass Enantiornithes," which he then grouped with *Archaeopteryx* in the subclass Sauriurae. The characters he used to justify this classification either cannot be shown to exist (the supposed "sauriurine" scapulo-vertebral articulation, for example, is entirely imaginary) or are not known for more than one of the included taxa (see

Steadman, 1983). The similarities in the coracoid and scapula in *Alexornis*, the Enantiornithes, and the Mongolian embryos, suggest the possibility that these may eventually prove referable to some higher level taxon distinct from all other known birds, but there is certainly no reason to group these birds with *Archaeopteryx* at any level other than the class Aves.

Several Cretaceous birds have been named from the Soviet Union on relatively undiagnostic fragments (see Nesov and Borkin, 1983, and references therein). Certain vertebrae appear to have been amphicoelous, as in *Ichthyornis*, and a coracoid was illustrated that shows similarities to that in the Enantiornithes, but beyond this little can be said of these fossils. Nesov (1984), in a publication received too late for translation and evaluation, reports additional Cretaceous bird remains from Asia, including a sacrum described as *Zhyraornis kashkarovi* and referred to a new family, Zhyraornithidae, in the Ichthyornithiformes, and the distal end of a humerus described as *Kizylkumavis cretacea*, considered to be of uncertain affinities but showing similarities to *Alexornis* and the Enantiornithes.

Most other Mesozoic birds come from Upper Cretaceous (Maastrichtian) deposits in New Jersey and Wyoming. Apart from two bones that may represent primitive members of the Procellariiformes (neither referable to living families), all other taxa from these deposits appear to be primitive charadriiforms that share similarities with the living Burhinidae and the early Tertiary genus *Presbyornis* (see Graculavidae in Charadriiformes).

In summary, the Mesozoic fossil record of birds is as follows. In the late Jurassic only the Archaeopterygiformes are known. True flying birds of the order Ambiortiformes existed by the later part of the early Cretaceous. The Hesperornithiformes are known from both Lower and Upper Cretaceous deposits, whereas the Ichthyornithiformes are known in the late Cretaceous only. By late Cretaceous time, these two orders of toothed birds were probably oceanic relicts, much as the Phaethontidae and Fregatidae are today. From the Cretaceous of South America, North America, and Asia there is evidence of what appears to be another distinct radiation of birds that may have included the Enantiornithes, *Alexornis*, *Gobipteryx*, and the Mongolian embryos. Our knowledge of these birds is so incomplete at this stage that it is quite uncertain how many orders and families should be recognized in this apparent radiation.

Only two modern orders have been discerned in the Cretaceous, the Charadriiformes and possible Procellariiformes, but *none* of the Mesozoic fossils can be referred to modern families, whereas by the Paleocene, and certainly by the early Eocene, there was a great diversity of both paleognathous and neognathous birds, with many different modern families and orders being represented. Thus the fossil record of birds actually closely parallels that of mammals: the Mesozoic is characterized by several radiations of strange, extinct higher level taxa, followed by an explosive radiation of modern forms in the early Tertiary. This pattern will doubtless be interpreted in light of the possibility of terminal Cretaceous catastrophic extinctions being of extraterrestrial origin.

VII. Paleognathous Birds

A. THE PROBLEM OF THE ORIGINS OF PALEOGNATHOUS BIRDS

The origin and relationships of the paleognathus ratites and tinamous is the most contentious issue in avian systematics. The difficulty in finding a satisfactory answer to the ratite problem arises in part from a failure to ask the right questions and a failure to ascertain whether the data being applied to the problem are sufficient to resolve those questions. Ever since it has generally been agreed that the ratites descended from a flying ancestor (following de Beer, 1956), the ratite issue has usually been thought of in an oversimplified manner: "Do the ratites and tinamous constitute a monophyletic or a polyphyletic assemblage?" Yet there are several possible patterns of origin for each of the contending viewpoints. Central to the argument of a polyphyletic origin is the phenomenon of neoteny, the retention into adulthood of characters from earlier developmental stages, which de Beer (1956) suggested was responsible for many of the characteristics of ratites. Although there is little doubt that the characteristics associated with flightlessness can be derived through neoteny (Olson, 1973), it still remains to be determined whether the characters that distinguish the ratites and tinamous from other birds, particularly those of the palate and rhamphotheca, can in fact be derived through neoteny.

Cracraft (1974) undertook a morphological analysis of the ratites in order to determine that they were monophyletic, as required by his zoogeographical hypotheses (Cracraft, 1972b; 1973b). He listed three characters, all of which he considered to be derived within birds, that he used to define the ratites and tinamous as a natural group. Chief among these, of course, was the paleognathous palate, first pointed out by Huxley (1867), augmented by the open ilioischiatic fenestra of the pelvis noted by Pycraft (1900), and the conformation of the rhamphotheca described by Parkes and Clark (1966).

To interpret the paleognathous palate correctly it is necessary to establish the proper homologies of the bones of the avian palate with those in reptiles, in order to determine what is primitive and what is derived. McDowell (1978) has challenged the traditional view concerning these homologies and his interpretation would require that many of the characters that define the paleognathous palate, if not the entire complex of characters, be primitive. The association of paleognathous characters with birds that retain teeth (*Hesperornis*) or a very reptile-like quadrate (*Gobipteryx*) is further evidence of the primitiveness of this condition. At least some of the characters of the paleognathous palate appear in earlier developmental stages of neognathous birds (Jollie, 1958; A. Feduccia, personal communication) and it remains to be determined through continuing embryological studies whether all of the characters by which Bock (1963) defined the paleognathous palate are in fact present in the early stages of development of at least some neognathous birds. It should be recognized that even if components of the paleognathous palate are primitive, this does not necessarily indicate the paleognathous palate to represent the ancestral condition in birds, although it would still be primitive relative to the neognathous configuration.

The unfused condition of the pelvis (i.e., three separate bones forming the innominate) is obviously primitive for vertebrates as a whole and occurs during the embryonic development of all birds (e.g., Rallidae, see Olson, 1973). The closed ilioischiatic fenestra of the pelvis in most neognathous birds results simply from the ossification of the sheet of connective tissue between the ilium and ischium. Furthermore, the open ilioischiatic fenestra occurs in the archaic Mesozoic birds *Hesperornis* and *Ichthyornis.* Any thoughtful zoologist would regard this as a primitive character, and because it is present in the embryonic state it could presumably arise through neoteny in any group of birds. Pycraft (1900, p. 225) considered that "the Struthious [and] Neognathine pelvis . . . cannot apparently be defined in mutually exclusive terms." That neognathous birds can give rise to species with an open ilioischiatic fenestra is shown in the Hawaiian Goose or Nene (*Branta sandvicensis*), in which the usual condition is to have the ilium and ischium unfused (Fig. 1; see also A. H. Miller, 1937). Clearly, the open ilioischiatic fenestra of ratites and tinamous has not been shown to be a uniquely derived character that supports monophyly.

The final character that has been cited as uniting the ratites and tinamous is the configuration of the rhamphotheca, which in these groups appears to be partitioned into segments, with a median nail-like section separated by longitudinal grooves from two lateral pieces. Lönnberg (1904) interpreted this kind of rhamphotheca as being composed of separate plates, which he even attempted to homologize with particular reptilian scales. In describing this condition, Parkes and Clark (1966, p. 462) originally state cautiously that the ratite rhamphotheca "appears tripartite," although through oversight they lapsed once into referring to the grooves as "sutures" and to the rhamphotheca as being "segmented." The point is not just a semantic one, as the degree of complexity implied by this terminology is somewhat greater

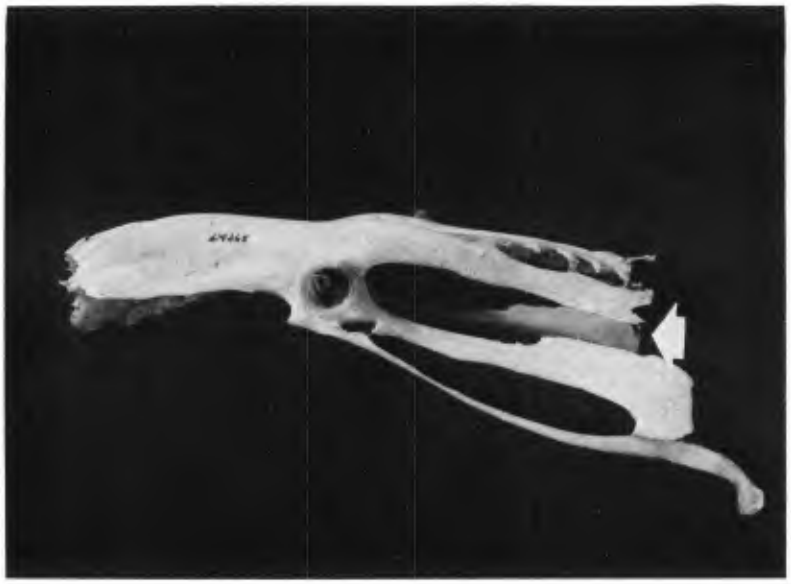

FIG. 1. Lateral view of the pelvis of the Nene or Hawaiian Goose (*Branta sandvicensis*) showing the open ilioischiatic fenestra (arrow), a supposedly ratite character. This condition is individually variable in the Nene, and the fenestra may sometimes be closed by a narrow ossified strip, but usually it is open.

than a matter of grooves. Their observation that the *pattern* of the rhamphotheca in paleognathous birds is unique is not compromised, however, regardless of its structure. Furthermore, it should be noted that the grooves in the rhamphotheca are reflected by grooves in the underlying bone, so that this condition can be detected in fossils in which the appropriate skull parts are preserved.

As there had been no histological study of the nature of the ratite rhamphotheca, I examined cross-sections of mandibles in an ostrich (*Struthio*), emu (*Dromaius*), rhea (*Rhea*), and a tinamou (*Nothoprocta pentlandii*). In all of these the epidermis is continuous, although usually thinned, through the "sutures" (Fig. 2a). Thus the grooves in the ratite rhamphotheca represent invaginations in a continuous epidermis rather than sutures between separate plates. The configuration of these grooves is undeniably characteristic of the ratites and tinamous and no such condition has been recognized in neognathous birds. But what is the origin of these grooves? Why should they be there at all?

Some evidence exists, although it is as yet only suggestive, that this character, too, could result from the retention of an embryonic condition. Parkes and Clark (1966) have already indicated that these grooves are more distinct

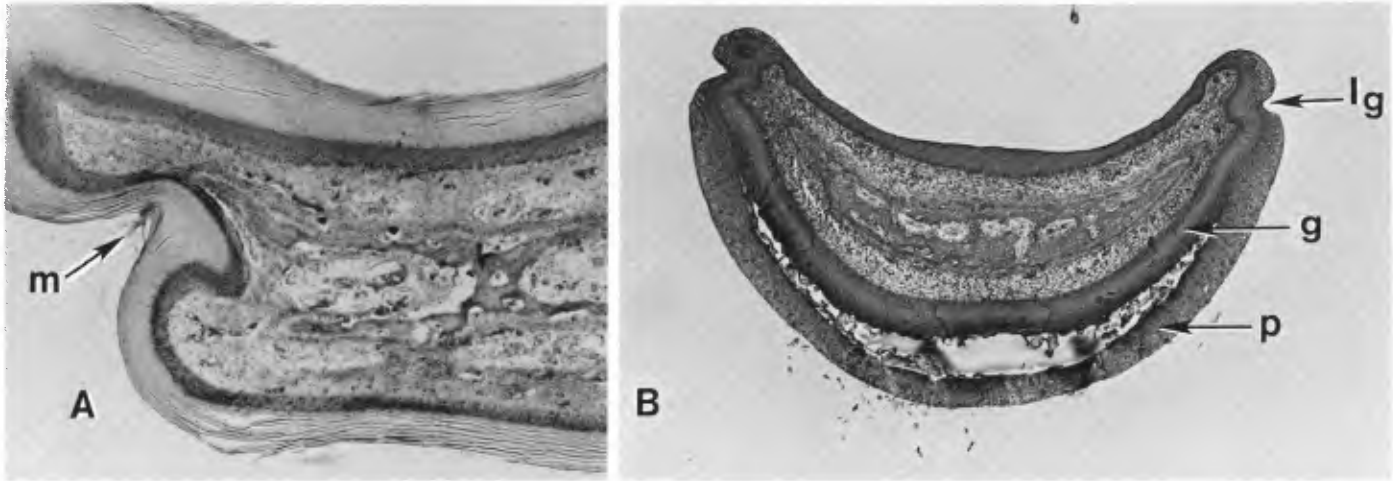

FIG. 2. Photomicrographs of cross sections of mandibles stained with hematoxylin and eosin. (A) Downy chick of an Emu (*Dromaius novaehollandiae*) cut ~65 mm from the tip showing the deep indentation of the mandibular groove (m); note that the epithelium is continuous around this groove. (B) Embryo of *Gallus gallus* at day 13, cut ~0.2 mm from the tip. At this stage the periderm (p), is largely free from the germinativum (g) and stops at a distinct labial groove (lg) that may be homologous with the mandibular grooves seen in ratites. (Photographs by Margaret Melville Barber.)

in downy young than in adults, and that in the adults of two genera of tinamous the grooves on the mandible may be obsolete or absent. In the embryogenesis of the avian rhamphotheca, the epidermis is originally covered with a layer of cells that, along with the stratum corneum and the egg tooth, is secreted by the stratum germinativum (Kingsbury *et al.*, 1953). This covering layer is known as the periderm, or in some of earlier literature as the "epitrichium" (Rosenstadt, 1897; Lüdicke, 1933). Kingsbury *et al.* (1953, p. 99) note that: "At first [the] newly formed peridermal cells are added along the extent of the germinativum, but later only at the anterior, lateral, and posterior margins of the cornifying beak, where the periderm does not form a distinct layer but is contiguous with the rapidly proliferating cells of the germinativum." This pattern may thus possibly conform with that observed in paleognathous birds. In examining embryos of *Gallus* one finds that in the later stages the periderm seems to be largely free from the surface of the epidermis, and in cross section its lateral connection with the germinativum is marked by a distinct indentation, both in the mandible (Fig. 2b) and in the rostrum (fig. 9 in Kingsbury *et al.*, 1953). This indentation is almost certainly the origin of the so-called "labial grooves" that appear on the rostrum and mandible in the embryos of *Gallus* between day 10 and day 12 (stages 36–38) and that are lost at about day 17 (stage 43), immediately prior to the sloughing off of the periderm (Hamburger and Hamilton, 1951).

There is a good possibility then, that the grooves in the rhamphotheca in ratites and tinamous may represent the site of attachment of the generative portions of the embryonic periderm during the later stages of development and may thus be homologous with the labial grooves described in the embryos of *Gallus*. No alternative explanation has been suggested, but it must be noted that practically all that is known of the embryogenesis of the periderm has been derived from studies of *Gallus* (Galliformes), so that virtually nothing can as yet be said about the positioning, relative development, or the length of retention of this structure and the "labial grooves" in other orders of birds, including ratites.

As far as can be determined from available evidence, the characters used by Cracraft (1974) to define the ratite–tinamou assemblage as monophyletic cannot be demonstrated to be derived within birds. Furthermore, we have established at least a reasonable possibility that each could evolve through neoteny from neognathous birds, just as flightlessness itself has been repeatedly evolved in the same manner (Olson, 1973). Showing that a character *could* have arisen neotenically, however, is not the same as showing that it *did*, so this has been established only as a possibility and nothing more.

Now, let us examine the various possible origins for the ratites and tinamous:

Origin 1. The characters by which the ratites and tinamous may be recognized as a group are derived within birds so that this group is strictly monophyletic in a cladistic sense, with the paleognathous palate being a specialized condition that was derived from the neognathous palate. This is the view adopted by Bock (1963) and Cracraft (1974). A corollary of this is that flightlessness arose only once in the paleognathous lineage, so that all the ratites evolved from a common flightless ancestor (Cracraft, 1974). The validity of Origin 1 is not dependent on the truth of this corollary, however.

Origin 2. The paleognathous birds arose through neoteny from a neognathous ancestor but this happened only once, with all living paleognathous birds being traceable to a single neognathous ancestor. This is hardly different from Origin 1 except that the characters defining the group are derived by a different mechanism. It is this origin to which Cracraft resorted (1980, 1981b) when confronted with the likelihood that his ratite "synapomorphies" were in fact primitive. The difficulty with it is in showing that these characters were derived only once, as the mechanism for their derivation is potentially available in most birds.

Origin 3. The living paleognathous birds are the only surviving descendents of some early group of birds, all of which had paleognathous palates, that represent a separate lineage from the neognathous birds. Within this group the various types of ratites may have originated independently from what Parkes and Clark (1966) envisioned as a family of "proto-tinamous." This is the view propounded by Parkes and Clark (1966).

Origin 4. Some of the living paleognathous birds are primarily paleognathous descendents of the archaic group postulated in Origin 3, whereas others have arisen independently from neognathous birds through neoteny and are secondarily paleognathous.

Origin 5. The living paleognathous birds all arose through neoteny from neognathous ancestors on more than one occasion, potentially as many times as there are distinct families, so that the various ratite groups might each be more closely related to some neognathous taxon than to another paleognathous one.

The available morphological and paleontological evidence strongly suggests that the characters defining the ratites and tinamous are *not* derived, making Origin 1 the least likely on presently available data. The case for either Origin 3 or 4 has been greatly strengthened by the recent discovery in the Northern Hemisphere of a previously unrecognized order of birds for which there is as yet no name. These were medium-sized volant birds with a perfectly well developed wing and pectoral girdle and a definitely paleognathous palate (Houde and Olson, 1981). Nearly all the elements of the skeleton, including skulls and mandibles, are known, and the distinct grooves in the latter show that the configuration of the rhamphotheca was as in the living paleognathous birds (P. Houde, personal communication). These birds occur in Paleocene and Lower Eocene deposits in the western United States. In addition, P. Houde (in preparation) has also recognized many individual specimens and several species among the extensive collections of fossil birds from the Paleogene of Europe. Many of these have already been described in a number of different modern families and orders. These birds answer very well for the family of "proto-tinamous" postulated by Parkes and Clark (1966). Thus this requirement of Origins 3 and 4 has been removed from the realm of speculation.

If the living paleognaths came about as postulated in Origin 4, the Tinamidae would be the most likely group to be primarily paleognathous, whereas the fossil record suggests that we should consider the possibility that ostriches may have descended from a neognathous ancestor (Section X,A,2) and are secondarily paleognathous. The parallelisms between the flightless geese and ibises of the Hawaiian Islands and the moas and kiwis of New Zealand (James and Olson, 1983) are at least suggestive of the descent of the last two from neognathous ancestors. The great divergence from the original ancestral stock of the Hawaiian birds took place in a very brief span of geological time (considerably less than 2 million years in the case of the ibises), so we must ask what geese and ibises would look like if they had 5 to 20 million years or more to evolve in an insular situation. Furthermore, the species diversity of moas is very difficult to explain with the assumption of only a single ancestral colonization of New Zealand, considering that speciation events within New Zealand have not produced comparable radiations in any other group of terrestrial vertebrates (S. L. Olson, manuscript).

The great diversity in palatal types (McDowell, 1948) and pelvis morphology (Feduccia, 1980b) within the large ratites would favor their having evolved their ratite grade of morphology independently of one another. Yet this would not necessarily preclude a close genetic similarity between the large living ratites. If, for example, a single genus of wide-ranging volant birds, belonging to an extinct family, gave rise independently to each of the families of large ratites on different continents, these birds might still be genetically more similar to one another as a group than to any other living taxon. Biochemical analyses would be incapable of determining whether the ancestral genus was paleognathous or neognathous, with the latter still being possible if the paleognathous palate can evolve secondarily through neoteny.

If any of the various ratites did evolve from a neognathous ancestor, it would be useful, to say the least, to establish from which neognathous group it descended. The fact that no such relationships have been postulated has been used as a criticism of those who have argued for a possible polyphyletic origin of ratites. The practical difficulties inherent in determining such relationships should be recognized, however. After all, imagine the problems one would encounter in attempting to determine the relationships of various taxa of birds by comparing only the characters seen in embryos or very young chicks. It is doubtful that the familial or even ordinal relationships of most taxa could be ascertained using only this information. The difficulties would be magnified if the taxa being compared were at different stages of development, which may well be true of ratites. When uniquely derived characters, such as the olfactory apparatus of kiwis, are superimposed on an otherwise ambiguous morphology, the difficulties of determining relationships would be compounded even further.

At this point there is no real proof for any of the various origins proposed above and it is well to ask just how far some of the data that have been applied to the ratite question actually go toward resolving the problem. Although the validity of electrophoretic studies of egg-white proteins for systematic purposes has been vitiated, it is nevertheless instructive to examine the conclusions that Sibley and Frelin (1972) derived from these data. They considered the large ratites to be "more closely related to one another than any one of them is to any other group of living birds" and that the patterns in the tinamous and kiwis were not similar to those of the ratites although they bore some resemblance to each other. However, a phylogeny in which the large ratites are more closely related to one another than to other paleognathous or neognathous birds could be constructed within each of the possible origins listed above, with the exception of the most extreme version of Origin 5, so even if these data were completely reliable they would tell us little about ratite origins.

A more recent biochemical analysis, based on DNA–DNA hybridization (Sibley and Ahlquist, 1981), starts out with the assumption that the paleognathous birds are monophyletic, so that all the hybrid combinations discussed are between the different groups of paleognathous birds. Thus the data presented have no bearing at all on resolving ratite origins. Furthermore, Sibley and Ahlqnist (1981, 1983) assumed that the ancestral ratites originated in Gondwanaland and could have dispersed between continents only when they were joined in the Mesozoic, this being one of their major points for calibrating the supposed DNA "molecular clock." But we now know that not only were volant paleognathous birds abundant and widespread in the Paleogene of North America and Europe, but also that at least one, *Palaeotis*, had achieved a ratite grade of morphology by the middle Eocene (Section VII,B). Therefore, the ratites certainly cannot be regarded as having originated in Gondwanaland and no calibration of a "molecular clock" can reliably be based on such an assumption.

B. THE FOSSIL RECORD OF PALEOGNATHOUS BIRDS

In dealing with fossils it must be remembered that large size and flightlessness do not a ratite make. Several fossil taxa of very large flightless birds were not paleognathous, for example, the Phorusrhacidae and Diatrymidae. The three characters used to define a true ratite (Cracraft, 1974) are all in the skull or pelvis, which are rarely preserved intact as fossils. Such taxa as the purported aepyornithids *Eremopezus eocaenus* Andrews or *Stromeria fajumensis* Lambrecht from the Paleogene of Egypt (Brodkorb, 1963b), which are based on very fragmentary limb elements, cannot be positively diagnosed as ratites, much less as aepyornithids.

Rich (1979) has monographed the Dromornithidae, a family of five named genera and seven named species of very large flightless Australian birds that range in age from middle Miocene to late Pleistocene. She considered the Dromornithidae to be paleognathous ratites most closely related to the Casuariidae, but avoided assigning the family to an order (Rich, 1979; 1980b).

Although Rich (1979, p. 3) cites the fact that Stirling (1913) reported "a partial skull and parts of a second with a lower jaw" of *Genyornis newtoni*, she did not mention the two quadrates he described. There is neither description nor discussion of cranial material in her lengthy "diagnoses" of the Dromornithidae (pp. 8–23) and of *Genyornis* (pp. 41–44), nor is this material mentioned among the referred specimens of *Genyornis newtoni* or in the description of bones of that species (pp. 45–49). Although specimens of pelvis are listed among the referred material (p. 45), these are never described or discussed. Thus, she ignored the only specimens by which one could establish whether the dromornithids were in fact ratites.

If we turn to the descriptions and illustrations of Stirling (1913), augmented by a specimen of mandible in the Smithsonian collections (Fig. 3), we find that the mandible of *Genyornis* was very deep and troughlike, being utterly different from that in any known ratite. Furthermore, it lacks any trace of the rhamphothecal grooves that are evident in the mandibles of paleognathous birds. The descriptions of the quadrates in Stirling (1913), which were made in comparison with true ratites and are quite detailed, show that *Genyornis* lacked the characteristic features of the quadrate that are found in paleognathous birds. In addition, as illustrated by Stirling (1913), and also in the reconstructed skeleton of *Genyornis* in Rich (1979; fig. 1), the ilioischiatic fenestra of the pelvis is not open.

Therefore, *Genyornis* lacks all of the characters that identify a true ratite and it almost certainly was not paleognathous. Hence, if *Genyornis* may be taken as representative of the Dromornithidae as a whole, then this family must have been derived from some group altogether different from ratites. Despite the praise that Rich (1980b) received for her "rigorous analytical

FIG. 3. Dorsolateral (top) and dorsal (bottom) views of a mandible of the late Pleistocene dromornithid *Genyornis newtoni*, from the collections of the Smithsonian Institution. Although rather poorly preserved, and lacking the articulations, this specimen shows *Genyornis* to have had a bill structure very different from that of any known ratite. (Photograph by Victor E. Krantz.)

methods" (Raikow, 1981, p. 410), it would seem that her phylogenetic hypotheses of possible interrelationships between the genera of dromornithids have been entirely compromised by the choice of an inappropriate outgroup for the determination of "character polarity."

A new genus and species of supposed ratite, *Sylviornis neocaledoniae*, from the late Quaternary of New Caledonia, was proposed in a wretched paper by Poplin (1980), the holotype being a fragmentary toe bone still embedded in matrix and the referred material being only some very worn shafts of leg bones. The genus was not referred to any family or order.

Despite the fact that such material could not possibly be identified as being from a ratite, *Sylviornis* was almost instantly incorporated into a fantastic reconstruction of ratite dispersal from Gondwanaland (Sibley and Ahlquist, 1981). It has now been determined that *Sylviornis* was not paleognathous (Poplin *et al.*, 1983), although I regard its true relationships as still being uncertain (see Section VIII,J, Megapodiidae).

Of the truly paleognathous birds, the earliest records are of the volant extinct family reported by Houde and Olson (1981) from the Paleocene and early Eocene of North America and now known from the early Eocene of England. P. Houde (personal communication) has examined parts of the holotype and much additional new material of the putative bustard *Palaeotis weigelti* Lambrecht, 1928, from the middle Eocene of Geiseltal and Messel, in Germany, and found that it was definitely a paleognathous bird, with the rhamphothecal grooves being clearly preserved. Furthermore, this bird, which was roughly crane-sized but smaller than the large living ratites, was flightless, with a reduced wing and a fused scapulo-coracoid, just as in modern ratites. Its overall similarities appear at this time to be most like cassowaries.

Alvarenga (1983) has described a flightless ratite from the late Paleocene of Itaboraí, Brazil, as *Diogenornis fragilis*, based on leg and wing bones, vertebrae, and a premaxilla. These also indicate a bird smaller than the large living ratites. The premaxilla in this bird was slender and very similar in form to that in *Casuarius*. Alvarenga tentatively referred *Diogenornis* to the Opisthodactylidae (see below) and noted that if it were involved in the ancestry of the Rheidae, then the similarity in the broad, flat bills of *Rhea* and *Struthio* is probably due to convergence. This extremely interesting fossil establishes that birds with a ratite grade of morphology were present in South America by the late Paleocene.

A presumed rhea, *Opisthodactylus patagonicus* Ameghino, was described on a fragmentary rostrum and the distal portions of a tibiotarsus and tarsometatarsus from Tertiary deposits in southern Argentina that are now known to be only Lower Miocene (Santacrucian) in age (Tonni, 1980a), rather than Lower Eocene as listed in Brodkorb (1963b). *Opisthodactylus* was originally described as forming a new family of phorusracoids (Ameghino, 1895), but was later stated by B. Patterson and Kraglievich (1960) to belong near the rheas (Rheidae), although documentation of this was never forthcoming. The validity of the Opisthodactylidae, which was maintained by Brodkorb (1963b), remains to be confirmed. The only Tertiary species presently assigned to the Rheidae is *Heterorhea dabbenei* Rovereto, 1914, from the late Pliocene (Montehermosan) of Argentina, founded on the distal portion of a tarsometatarsus. The validity of the genus should be reevaluated.

The only fossil tinamous yet described are late Pliocene (Montehermosan) or younger (Brodkorb, 1963b). Certain of these were revised by Tonni (1977), who synonymized the fossil genus *Cayetornis* Brodkorb with the living genus *Nothura* and the fossil genus *Tinamisornis* Rovereto with the living genus *Eudromia*. He overlooked the fact, however, that the combination *Eudromia intermedia* (Rovereto, 1914) that arose in the process, is preoccupied by the name of a living subspecies, *Eudromia elegans intermedia* (Dabbene and Lillo, 1913), and a new name is therefore required for the fossil.

There is no confirmable Tertiary record for the moas (Dinornithidae, Anomalopterygidae) (see Fordyce, 1982), kiwis (Apterygidae), or elephantbirds (Aepyornithidae). Apparently the only Tertiary records of the Casuariiformes are of the fossil emu *Dromaius ocypus* A. H. Miller (1963b), from presumed Lower Pliocene deposits of South Australia, another species of emu known from the Miocene of South Australia, and some toe bones referred to *Casuarius* from the Pliocene of New Guinea (Rich and van Tets, 1982). I have discussed the fossil history of ostriches (Struthionidae) under the Gruiformes, where they may or may not belong.

VIII. The "Basal" Land Bird Assemblage

The constituents of what I call the "basal" land bird assemblage are grouped to some extent by default, as they belong neither among the waterbirds nor among the "higher" land birds. I include here the Opisthocomidae, Cuculiformes, the Falconiformes (except the Vulturidae), Galliformes, Columbiformes, and Psittaciformes. The Turnicidae may belong here as well.

The Opisthocomidae have been shifted back and forth between the Galliformes and Cuculiformes, which in itself speaks for a possible connection between these two orders. There is some evidence for an association between the Columbiformes and Psittaciformes (see Sibley and Ahlquist, 1972), but the evidence cited for a relationship between the Columbiformes (to which the Pteroclidae unquestionably belong) and the Charadriiformes (Fjeldså, 1976), I believe will prove spurious. Further inquiry into the belief of earlier systematists for a relationship between the Columbiformes and the Galliformes is warranted. Likewise, the true position of the Turnicidae, which have many similarities to Galliformes and which are almost certainly out of place in the Gruiformes (Olson and Steadman, 1981), should be sought.

The order Falconiformes is for the most part a demonstrably unnatural assemblage. The extensive treatment of Jollie (1976–1977) has helped to establish that the diurnal raptors probably arose from several different sources, although his treatise is so prolix and idiosyncratic that extracting information from it becomes something of a labor of love. The New World vultures, Vulturidae (Cathartidae, *auct.*), are almost certainly derived from a group of waterbirds that includes storks and pelecaniforms (Olson, 1979). I have placed them in the Ciconiiformes, as have Ligon (1967), König (1982), and Rea (1983). The Falconidae, as Jollie (1976–1977) concludes, are not closely related to the Accipitridae, but in contrast to the Vulturidae are from some "arboreal" stock of land birds. There are osteological similarities between the primitive falconid caracaras and the Opisthocomidae. Very likely the Falconidae are a raptorially adapted group that is part of the radiation of primitive birds that includes the Opisthocomidae and Cariamidae, which are at present restricted to South America, as are the majority of genera of falconids.

What the closest relatives of the Accipitridae may be is one of the more difficult questions in systematic ornithology. Skull structure suggests a possible affinity between the Sagittariidae and Accipitridae, but these families are widely divergent in other respects. I have pondered at length on other possible relatives of the Accipitridae and the only suggestive similarities I find are with the Musophagidae, with such elements as the humerus and femur being somewhat similar in these two groups. An excellent complete skeleton newly available from the early Eocene Green River Formation of Wyoming may eventually shed light on this possibility, as it is most similar to the Musophagidae but differs utterly in proportions from any of the living members of the family and is in some ways suggestive of a raptor. *Pandion* differs so strikingly from the true hawks in almost all aspects of its anatomy that its presumed close relationship with the Accipitridae must be seriously questioned.

It is probably from birds belonging to the "basal" land bird assemblage that the "higher" land birds arose. Likewise, the water bird group appears to have originated here in birds similar to the Cariamidae. Were it not for the probable link between the Cariamidae and some of the Gruiformes, the seriemas could be included with the basal land birds, as they share many similarities with the Opisthocomidae. I have arbitrarily placed the Cariamidae at the base of the waterbird lineage instead.

Obviously, ordinal limits need to be redefined in the basal land bird assemblage, and for this reason I have not attempted to place all of the families treated here in a ordinal taxon; no inferences should be drawn from the sequence in which they are presented.

A. OPISTHOCOMIDAE

The young of the living Hoatzin (*Opisthocomus hoazin*) are renowned for having well developed, functional claws on the alular and major digits of the wing, an obviously primitive, reptilian character. The systematic position of *Opisthocomus* has been much debated but it usually has been considered to be related either to the Galliformes or the Cuculiformes. On the basis of analyses of egg-white proteins and the superficial resemblances in plumage between *Opisthocomus* and the cuckoo *Guira guira*, Sibley and Ahlquist (1973) placed the hoatzin in the subfamily Crotophaginae of the Cuculidae. The egg-white evidence was later negated, however (Brush, 1979). *Opisthocomus* lacks any of the derived osteological characters of either the Cuculidae or the Galliformes, but shows decided similarities, although probably primitive ones, to the Cariamidae (Section X,A,1). If, as it appears to be, *Opisthocomus* is a very primitive bird, it may prove impossible to place it in any higher taxon that is clearly defined by "synapomorphies."

Only one Tertiary fossil has been referred to the Opisthocomidae, this being the holotype of *Hoazinoides magdalenae* A. H. Miller, 1953, which consists of much of a cranium from the late Miocene La Venta Formation of the Magdalena Valley in Colombia. No living hoatzins occur west of the Andes, but it is not unexpected that some member of the group existed there in the Tertiary before the Andes were uplifted. There is no reason to doubt that the cranium of *Hoazinoides* is in fact similar to that of *Opisthocomus*, but considering that *Opisthocomus* is evidently but part of a more diverse and primitive radiation of South American birds, it could well be that *Hoazinoides* differed greatly in habits and postcranial osteology from *Opisthocomus*.

B. MUSOPHAGIDAE

A recent examination by P. Houde (personal communication) of the bird described by Harrison and Walker (1977) as *Promusophaga magnifica* from the Lower Eocene (Ypresian) London Clay, reveals not only that it is not a musophagid, it is not even a neognathous bird, being referable instead to an extinct order of volant paleognathous birds (Houde and Olson, 1981).

The genus *Dynamopterus*, from the Eo–Oligocene Phosphorites du Quercy, France, was placed in the Musophagidae by Brodkorb (1971b). The type species, *D. velox*, was named by Milne-Edwards (1892), and illustrated by Gaillard (1908), who later (Gaillard, 1939) described a second species, *D. boulei*, from the same deposits. Milne-Edwards, Gaillard, and Lambrecht (1933) referred *Dynamopterus* to the Cuculidae. Gaillard (1939) intimated that *D. boulei* should probably be referred to a genus different from *D.*

velox. Both species were based on humeri that, as illustrated, appear to differ significantly from the Musophagidae. Ballmann (1972) states definitely that *Dynamopterus* is not a musophagid. Mourer-Chauviré (personal communication) would refer *D. velox* to the Cuculidae and *D. boulei* to the genus *Aquilavus* in the Accipitridae.

T. Rasmussen (personal communication) has identified bones from the Oligocene Jebel Qatrani Formation in the Fayum of Egypt as belonging to the Musophagidae, these being practically indistiguishable from the modern genus *Crinifer*. The next earliest record of the family is of a humerus of an unidentified genus that Ballmann (1970) reported from late Oligocene (lower Chattian) deposits in Bavaria. Ballmann (1972) also assigned the distal end of a tarsometatarsus from the early Miocene of Vieux Collonges, France, to the Musophagidae. A carpometacarpus from the late Miocene of La-Grive-St.-Alban, France, was described by Ballmann (1969a) as *Musophaga meini* and he listed a few other musophagid fragments from the same locality that could not be identified to genus. Brodkorb (1971b) created a new genus, *Apopempsis*, for *M. meini*, but in a sketchy diagnosis given in a footnote. P. Ballmann (personal communication) considers the genus to be poorly defined and would retain the species in *Musophaga*. Harrison (1980a) described the distal end of a humerus from Lower Miocene deposits at Songhor, Kenya as *Apopempsis africanus*. It was tentatively referred to *Apopempsis* because of the specimen's greater similarity to *Musophaga* than to other genera in the family, but if the species *meini* is not separable from *Musophaga*, then the generic status of *A. africanus* should be reevaluated.

The appearance of what is now a purely African family in the Tertiary of Europe is a pattern that we will see repeated in several other groups of birds.

C. CUCULIDAE

From their structure and distribution, the Cuculidae appear to be a relatively ancient family, yet their fossil record is exceedingly poor. Two purported cuckoos from the early Eocene of England (Harrison and Walker, 1977) were shown to be misidentified to order (Olson and Feduccia, 1979b; Steadman, 1981). Although Brodkorb (1971b) placed the middle Eocene (Bridgerian) species *Uintornis lucaris* in the Cuculidae, this species was later referred to the "piciform" family Primobucconidae (Feduccia and Martin, 1976).

The earliest apparent cuculid is the species *Dynamopteryx velox* from the Eo–Oligocene of France (see Musophagidae). Another Tertiary paleospecies of cuckoo is *Neococcyx mccorquodalei* Weigel, 1963, based only on the distal end of a humerus from the early Oligocene (Chadronian) of Saskatchewan.

Martin and Mengel (1984) have described a new genus and species of cuckoo from the early Miocene of Colorado as *Cursoricoccyx geraldinae*. In addition, I have identified the distal end of a tibiotarsus in the Smithsonian collections from lower Pliocene (late Hemphillian) marine deposits at Lee Creek, North Carolina, as belonging to a large cuckoo of uncertain affinities. That fossils of the Cuculidae are known so far only from very few localities, and only in the Northern Hemisphere, is probably not representative of their actual distribution in the Tertiary.

D. FALCONIDAE

This family is now concentrated in South America (Olson, 1976b), with only the genus *Falco* and the falconets (*Microhierax* and *Polihierax*) occurring much beyond the Neotropics. Mourer-Chauviré (1982) lists the Falconidae among the taxa recognized from Eo–Oligocene deposits at Quercy, France. In South America the family is known as far back as the early Miocene (Santacrucian) of Argentina through the species *Badiostes patagonicus* Ameghino, 1895. The holotype is the proximal end of a tarsometatarsus that Ameghino (1895) originally described as an owl. Wetmore (1922), however, recognized its affinities with the Falconidae, where it was placed by Lambrecht (1933) and Brodkorb (1964). Ameghino's illustrations are sufficient to show that *Badiostes* had the short, truncate hypotarsus characteristic of the caracaras and *Spiziapteryx* (Olson, 1976b).

Falconids roughly contemporaneous with *Badiostes* were in North America as well. *Falco ramenta* Wetmore, 1936, was based on the distal end of a tarsometatarsus from the Miocene (probably Hemingfordian) of Nebraska. In the American Museum of Natural History, I have examined a coracoid and a humerus of the same or a similar-sized falcon from Lower Miocene (Hemingfordian and early Barstovian) deposits in Nebraska. *Falco ramenta* was a rather small species, about the size of modern *F. columbarius*.

I examined a cast of the holotype of *Falco pisanus* Portis (the distal end of ulna from the Pliocene of Italy) and found that it is not from a falconid; Mourer-Chauviré (personal communication) considers it to belong to the Columbidae. The only other named Tertiary falconid is *Sushkinia pliocaenica* Tugarinov, based on the distal end of a tibiotarsus from the early Pliocene of Kazakhstan. This needs restudy before its status as a falcon can be accepted. The presumed extinct genus and species *Plioaetus furcillatus* (De Vis), from the late Pleistocene of Australia, at times also referred to the Accipitridae, has been synonymized with the living species *Falco berigora* (P. V. Rich *et al.*, 1982).

E. SAGITTARIIDAE

The secretarybird (*Sagittarius serpentarius*) is the only living member of this family and is confined to Africa, whereas the two fossil species known are both from the Tertiary of France. These have been treated by Mourer-Chauviré and Cheneval (1983) in an fine paper that others could well consult as a model for paleontological revisions. Several of the specimens that these authors referred to the Sagittariidae had previously been assigned to the Ciconiidae or Vulturidae and the "ciconiid" name *Pelargopappus* has priority over other generic names used for these forms. Two species are recognized, *P. schlosseri* (Gaillard) from the Phosphorites du Quercy, with specimens of known stratigraphic provenance coming from the Medial and Upper Oligocene. The second species, *P. magnus* (Milne-Edwards), the type of the genus, from the early Miocene (Aquitanian) at St. Gérand-le-Puy, is larger, with a straighter femur than *P. schlosseri* and was the size of the living secretarybird. *Pelargopappus* had the tarsometatarsus less elongated than *Sagittarius* but in other respects appears too specialized to have been ancestral to that genus.

F. ACCIPITRIDAE

Although extensive fossil material exists for the Accipitridae, divining its significance in our present state of systematic ignorance proves nearly impossible. The greatest handicap to understanding the fossil record is the lack of a modern anatomical revision of the genera and subgroups of the Accipitridae. The taxonomic changes that have been proposed in recent years have been based for the most part on superficial examination of study skins and on field impressions. We can hardly hope to fit fossil hawks and eagles into a classification with such a poor foundation and at the same time hope to learn something of the evolutionary history of the family.

Brodkorb (1964) lists 62 paleospecies of Accipitridae. More have been described subsequently and much unstudied fossil material of the family exists. The Frick Collection in the American Museum of Natural History, for example, contains a wealth of Tertiary accipitrids from North America.

Two nonaccipitrids may be removed from Brodkorb's listing of the family. Tonni (1970) has shown that *Foetopterus ambiguus* Moreno and Mercerat, from the Pleistocene of Argentina, is based on the humerus of the living goose *Chloephaga picta*. I agree with Tonni (1980a) that the illustrations of the holotypical humerus of the supposed accipitrid *Lagopterus minutus* Moreno and Mercerat, 1891, also from the Pleistocene of Argentina, indicate that it belongs with the falconid genus *Polyborus*. It equals in size individuals of *Polyborus plancus* from southern South America and should be synonymized with that living species.

The earliest accipitrids are two species from late Eocene to early Oligocene deposits in France that are listed in Brodkorb (1964) under the genus *Aquilavus*, the type species of which, however, is from Lower Miocene (Aquitanian) deposits. Three species from the middle Oligocene and one from the late Oligocene have been attributed to the modern genus *Buteo* (Brodkorb, 1964; Kurochkin, 1968), one of which, *Buteo grangeri* Wetmore and Case, was based on a skull. The generic assignment of these fossils needs confirmation, as buteonine hawks of modern aspect do not appear in European deposits until the middle Miocene (e.g., La-Grive-St.-Alban) (P. Ballmann, personal communication). Those from the early Miocene (Aquitanian) of France do not belong with the great modern radiation of Buteoninae and Accipitrinae and include such forms as *Palaeohierax gervaisii* (Milne-Edwards), which is most similar to the aberrant living Palm-nut Vulture, *Gypohierax angolensis* (Milne-Edwards, 1867–1871; Rich, 1980a; P. Ballmann, personal communication).

A number of Tertiary species have been identified as kites and are listed in Brodkorb (1964) in the subfamily Milvinae. However, a good many of the modern genera usually placed in the Milvinae probably do not belong with the group that includes *Milvus* (Olson, 1982b), and the relationships of the fossils bear reinvestigation.

The so-called Old World vultures, subfamily Gypaetinae (Aegypiinae *auct.*), are of particular interest as they occur in Tertiary and Quaternary deposits of North America. The living and fossil forms of this group are treated by Rich (1980a) in a work in which the text and even the two sections of discussion consist almost entirely of unrelieved osteological descriptions, with the most readily comprehended summary being the publisher's announcement on the back cover. Whereas Rich (1980a, pp. 111–112) says ultimately of the Gypaetinae that "The New World genera could have been (1) derived entirely from New World stock, once or several times or (2) derived from Old World stock once or several times and vice versa [I have no idea how to interpret the "vice versa" here]," the back cover states rather more lucidly that "the New World fossils may represent one or more separate derivations from eagles and hawks and are unique to the New World." On the other hand, Howard (1966b, p. 3), after studying the extensive material of the extinct New World form *Neophrontops americanus*, concluded that "the skeleton of *Neophrontops* is markedly like that of the Recent Old World vulture, *Neophron*" and that such differences as exist between these genera "are of less note than those which exist between *Neophron* and its contemporaries among the vultures today [Howard, 1932, p. 70]."

A major part of Rich's monograph is concerned with the description of a new species, *Neophrontops ricardoensis*, based on most of a skeleton including the skull, from the middle Miocene (Clarendonian) of California. Sixty pages of text, tables, and illustrations are devoted to the description and comparison of this fine specimen and the other species of *Neophrontops*, after which the author finally concludes that the "phylogenetic position [of *Neophrontops*] within the Accipitridae is yet unresolved [Rich 1980a, p. 112]," leaving one unenlightened and with a deep sense of frustration.

G. PANDIONIDAE

Few Tertiary fossils of ospreys have been found. The earliest are from the Oligocene Jebel Qatrani Formation in the Fayum of Egypt (T. Rasmussen, personal communication). *Pandion homalopteron* Warter, 1976, is known from associated right and left humeri and right and left ulnae and the distal end of a tibiotarsus referred later by Becker (1985) from middle Miocene (Barstovian) marine deposits in southern California. This was the size of the living species *P. haliaetus* and differed from it only in minor details. In contrast, a second paleospecies, *Pandion lovensis* Becker, 1985, based on several hindlimb elements from the late Miocene (latest Clarendonian) of Florida, is thought to represent a lineage different from *P. homalopteron* and *P. haliaetus*. Individual claws of *Pandion* have been found in Pliocene marine deposits in Florida and North Carolina (Warter, 1976). Brunet's (1970) assignment of the late Eocene species *Palaeocircus cuvieri* Milne-Edwards to the Pandionidae is probably incorrect (Warter, 1976). Formerly placed in the Accipitridae, *Palaeocircus* is known only from a fragmentary carpometacarpus and is best relegated to Incertae Sedis.

H. GALLIFORMES

Although many fossils have been described in the Galliformes, these are in such dire need of revision that comparatively little can reliably be said about the evolutionary history of the order at present. Of the taxa listed in Brodkorb (1964), the following species have been removed from the Galliformes: *Palaeortyx hoffmanni* (Gervais) and *Ludiortyx blanchardi* (Milne-Edwards) (said to be rallid—see references in Olson, 1977a); the three species of *Filholornis* Milne-Edwards (referable to the gruiform family Idiornithidae, see Section X,A,1,c) *Palaeophasianus meleagroides* Shufeldt (a gruiform, see Cracraft, 1969); *Paracrax antiqua* (Marsh) (removed to the Bathornithidae, Gruiformes, see Cracraft, 1968); *Anisolornis excavatus* (also probably a gruiform, see Cracraft, 1973a, and Section X,A,3,c).

Several genera and species of Galliformes have been recognized in the late Eocene to early Oligocene Phosphorites du Quercy, France. All were placed in the Cracidae by Brodkorb (1964). These, while most similar to the Cracidae, are now believed to be an archaic group meriting its own separate family (Mourer-Chauviré, 1982). Brodkorb (1964) also referred the four Oligocene and Miocene European species that he included in *Taoperdix* Milne-Edwards to the Cracidae. The three Miocene forms he later (Brodkorb, 1967, p. 112) removed to the Phasianidae, genus *Palaeortyx*, leaving only the late Oligocene (Chattian) *Taoperdix pessieti* in the Cracidae. Ballmann (1969b) described a new species, *Taoperdix miocaena*, from the early Miocene (early Burdigalian) of Germany, and referred it to the Gallinuloididae, superfamily Cracoidea. It is clear that primitive galliforms were present in Europe up to the Neogene and some of these may well have been related to cracids, though not necessarily belonging to the same family.

1. Cracidae

The earliest known galliform is *Gallinuloides wyomingensis* Eastman, based on a skeleton from the Lower Eocene (Wasatchian) deposits of the Green River Formation in Wyoming. Lucas (1900) proposed a separate family for it, the Gallinuloididae. Tordoff and Macdonald (1957) reanalyzed the characters set forth by Lucas and concluded that *Gallinuloides* belonged in the Cracidae. Cracraft (1973b, p. 507) asserted that *Gallinuloides* was closer to phasianids than cracids, but never presented evidence to substantiate his claim. At least one other specimen of *Gallinuloides* has been found in the Green River Formation, but it is not available for scientific examination. New specimens of *Gallinuloides* and additional preparation of the holotype of *G. wyomingensis* would doubtless tell us quite a bit more about the early history of the Galliformes.

The next oldest occurrence of a cracid is *Procrax brevipes* Tordoff and Macdonald, 1957, based on a postcranial skeleton from the early Oligocene (Chadronian) of South Dakota. The specimen, which I have examined briefly, is still largely encased in matrix and needs further preparation. Tordoff and Macdonald regarded *Procrax* as being somewhat intermediate between *Gallinuloides* and modern cracids, but included it with *Gallinuloides* in a separate subfamily, Gallinuloidinae.

Six other species of cracids, or probable cracids, have been named from Lower Miocene to Lower Pliocene deposits from Florida, Kansas, Nebraska, South Dakota, and California (Brodkorb, 1964; Feduccia and Wilson, 1967). Three of these species were originally described in the modern genus *Ortalis*, but Brodkorb (1964) placed them in his genus *Boreortalis*, an action that appears to have been purely arbitrary. More than one species of cracid is indicated in the early Miocene (Hemingfordian) Thomas Farm local fauna in Florida (Olson and Farrand, 1974), the type locality of *Boreortalis laesslei* Brodkorb.

Because cracids are unlikely to cross substantial water barriers (one species is found on Cozumel Island, Mexico, but no member of the family is known certainly to have reached the West Indies unaided by man) and because the North American fossil cracids are older than the late Pliocene isthmian connection between North and South America, it may be concluded that the Cracidae are unlikely to have originated in South America (Olson, 1980a).

2. *Megapodiidae*

The mound-builders, or megapodes, are confined to Australasia and have a distribution nearly perfectly complementary to that of the Asian Phasianidae (Olson, 1980a). In contrast to most other Galliformes, at least some of the megapodes are capable of crossing water barriers. As there is no galliform group known from South America with which the Megapodiidae could have shared a common ancestor before Gondwanaland was fragmented, it seems more likely that the megapodes arrived in Australasia from the north. This is now supported by Mourer-Chauviré's (1982) discovery of a small megapode in the late Eocene deposits at Quercy, France.

Megapodes are otherwise unknown in the Tertiary, but some of the Quaternary forms from Australia are divergent enough to merit mentioning here. Van Tets (1974) showed that the supposed giant pigeon *Progura gallinacea* De Vis is actually a giant megapode. The megapode *Chosornis praeteritus* De Vis and the supposed stork *Palaeopelargus nobilis* De Vis are both synonyms of this species, which was estimated to weigh two to three times more than the largest living megapode. It is known from Quaternary deposits in southern Queensland and New South Wales.

Van Tets (1974) described an additional species of giant megapode, *Progura naracoortensis*, from Quaternary cave deposits in southeastern South Australia. This was somewhat smaller than *P. gallinacea* but was nevertheless much larger than any living megapode. My very brief examination of some material of these two species in the Queensland Museum suggested that they may belong to different genera. The relationships of either species of *Progura* to living genera of megapodes have not as yet been determined.

The large, flightless bird *Sylviornis neocaledoniae*, originally described as a ratite from late Quaternary cave deposits in New Caledonia, has lately been referred to the Megapodiidae (Poplin, *et al.*, 1983). Much newly collected material of this species should permit a more detailed evaluation of its relationships (J.-C. Balouet, personal communication). If *Sylviornis* is indeed a megapode, it is a highly peculiar one.

3. *Numididae*

The only intimation of the Numididae in the Tertiary came from my assignment of *Telecrex grangeri* Wetmore to this family (Olson, 1974c). Based on a femur from the late Eocene of Inner Mongolia in China, this species was originally described as a member of the Rallidae. It is definitely from one of the more advanced Galliformes, however, and the greatest similarity of the holotype was to the modern guineafowl *Phasidus niger* (Olson, 1974c). Additional material would be desirable before stating definitely that the Numididae existed in the late Eocene of Asia. Nevertheless, it does seem quite probable that the Ethiopian distribution of this family is a relictual one and that the group once ranged outside of Africa, as did the Struthionidae, Musophagidae, Coliidae, Phoeniculidae, Sagittariidae, and other families.

4. *Phasianidae*

a. Odontophorinae. Brodkorb (1964) lists five Tertiary species of New World quails from North America, ranging in age from early Oligocene to late Pliocene, to which may be added *Miortyx aldeni* Howard, 1966b, from the early Miocene (Arikareean) of South Dakota. Almost all are based on single ends of bones. It is best at present to regard the postulated relationships of the four pre-Pliocene taxa (*Nanortyx inexpectatus* Weigel, *Miortyx teres* A. Miller, *M. aldeni*, and *Cyrtonyx cooki* Wetmore) with caution, as there were evidently nonphasianid Galliformes in the North American Tertiary that were quite small (e.g., "*Cyrtonyx*" [= "*Boreortalis*"] *tedfordi* L. Miller). The holotypical proximal end of a humerus of *Miortyx aldeni*, on the other hand, is considerably larger than in any living odontophorine quail. Tordoff (1951) assigned to the Odontophorinae the distal end of a tarsometatarsus from the "middle" Oligocene (Orellan) of Colorado. The Odontophorinae may well have been present in North America from the Oligocene onward, but better material would be desirable to establish this with certainty.

b. Tetraoninae. Brodkorb (1964) lists two early Miocene and two late Miocene species of grouse for North America in addition to Quaternary taxa. I would not accept these as grouse without careful comparison of the types with the Cracidae, Phasianinae, and Meleagridinae. Grouse have not been found in European deposits older than early Pleistocene.

c. Phasianinae. Pheasant- and partridgelike birds are abundant in the Tertiary of Europe (Brodkorb, 1964). All of the pre-Pliocene species have been assigned to extinct genera. There is bound to be much of evolutionary and zoogeographic interest in a study of the European fossil Phasianinae, but before order can be made of this extensive record, the modern genera of the family will have to be revised and diagnosed osteologically. It will then remain to be determined to which modern genera the various fossil species are most closely related. In this connection, the rather obscure publications of Villalta and Crusafont (1950) and Villalta (1963) should not be overlooked, as a number of Galliformes from the Tertiary of Spain are reported therein. Also, more recent papers by Yeh (1977, 1980) describe two new genera and species of Phasianidae from nearly complete skeletal impressions from Medial Miocene diatomite deposits in Shandong Province, China. One of these, *Linquornis gigantis*, was of very large size, approximating the living peacocks (*Pavo*).

The difficulties mentioned above notwithstanding, there are nevertheless a few generalizations that can be made at this time about the Tertiary history of the Phasianinae in Europe (Ballmann, 1969a,b, 1973, personal communication). The primitive and distinctive genus *Palaeortyx* (type species *P. gallica* Milne-Edwards—see Brodkorb, 1967, p. 112, for revised classification) has been reported from the early Miocene (Aquitanian) through the middle to late Miocene (La-Grive-St.-Alban) of Europe. Mourer-Chauviré (personal communication) has found that *Palaeortyx* first appears in the Upper Oligocene portions of the deposits at Quercy. *Palaeortyx* differs from other Phasianidae in having a nonpneumatized humerus. The genus *Palaeocryptonyx*, which appears in the deposits at La-Grive-St.-Alban, is generally similar to the living Old World partridges that lack spurs on the tarsometatarsus, such as *Arborophila*. At the same time, the larger species of the genus *Miophasianus* appear. These are related to the modern *Argusianus* group, but also need comparison with *Afropavo*.

d. Meleagridinae. The only group of Galliformes for which there is now a comprehensive modern revision is the turkeys, Meleagridinae, thanks to Steadman's (1980) excellent review, from which the following is extracted. The earliest probable turkey is *Rhegminornis calobates* Wetmore, from the early Miocene (Hemingfordian) of Florida, which was originally identified as a charadriiform. It was later shown to be a galliform and was referred to the Meleagrididae by Olson and Farrand (1974). *Rhegminornis* was very much smaller than any other fossil or modern turkey. Steadman (1980) considered the known specimens to be too few and fragmentary to determine with certainty that *Rhegminornis* was meleagridine as opposed to phasianine, and he stressed its possibly intermediate nature.

Proagriocharis kimballensis Martin and Tate, from the late Miocene (early Hemphillian, see Breyer, 1981) of Nebraska, was smaller than any other known turkeys except *Rhegminornis* and was probably part of a lineage separate from that giving rise to *Meleagris*.

Of similar age is a tibiotarsus referred tentatively to *Meleagris* from the early late Miocene of Virginia. This was from a rather large bird, about in the lowest size range of living *M. gallopavo.* All other turkeys, living and fossil, were assigned by Steadman (1980) to the genus *Meleagris*, with *Agriocharis* and *Parapavo* becoming synonyms. The fossil species *M. progenes* (Brodkorb), *M. leopoldi* A. Miller and Bowman, and *M. anza* (Howard), along with the living *M. gallopavo*, appear to represent a temporal sequence in a single lineage extending from late Pliocene (Blancan) to the present. The famous *Meleagris* ("*Parapavo*") *californica* (L. Miller), known mainly from the late Pleistocene Rancho La Brea tar pits, is merely a small geographical representative of this same lineage that was isolated in California. Steadman (1980) has shown that the late Pliocene (Blancan) and early Pleistocene (early Irvingtonian) members of this lineage (*M. progenes, M.* cf. *leopoldi* or *anza* from Inglis 1A in Florida) lack a pneumatic foramen in the scapula, whereas turkeys from the late Irvingtonian onward possess this foramen. Because *M. gallopavo, M. ocellata,* and *M. californica* all possess this foramen, it was hypothesized that they descended from a common ancestor in the middle Irvingtonian.

An enigmatic and distinctive form is *M. crassipes* (L. Miller), which was described from the late Pleistocene San Josecito Cave deposit in Nuevo Leon, Mexico, and from Quaternary cave deposits in Arizona and New Mexico that antedate the Indian agricultural period, after which *M. gallopavo* is believed to have been introduced into the same areas (Rea, 1980).

In summary, a group of Phasianidae appears to have arrived in North America from the Old World by the early Miocene and to have given rise to the Meleagridinae. The earliest known member of this group was rather small, but the large size that characterizes the *Meleagris* radiation in the Plio–Pleistocene arose at least by the late Miocene. The extent to which these New World phasianids may have radiated into forms other than the *Meleagris* lineage is not yet known.

I. FAMILY INCERTAE SEDIS TURNICIDAE

There is no published Tertiary record of the buttonquails, or hemipodes, although in the collections of the South African Museum I found a few specimens of *Turnix* among the extensive early Pliocene material from Langebaanweg, South Africa.

J. COLUMBIFORMES

1. Pteroclidae

The sandgrouse are strictly an Old World group, confined to Africa and Eurasia. Milne-Edwards (1892) named two species of *Pterocles* (*P. validus* and *P. larvatus*), differing in size, from the late Eocene to Oligocene Phosphorites du Quercy, France. As illustrated by Gaillard (1908), there seems to be little doubt of their familial allocation, and the same is true of the tarsometatarsus from the early Miocene (Aquitanian) of France that Milne-Edwards (1867–1871) described as *Pterocles sepultus*. The generic status, particularly of the two older species, is in need of further inquiry, however. A coracoid from the middle Pliocene of Mongolia was referred to the genus *Syrrhaptes* by Kurochkin (1982b).

2. *Columbidae*

Despite the fact that many pigeons are largely terrestrial and the modern species are frequently taken as prey by owls, which are responsible for the accumulation of bones in many fossil deposits, the Columbidae have a very meager record in the Tertiary. The earliest dove yet known, from the early Miocene (Aquitanian) of France, was a small species named *Columba calcaria* by Milne-Edwards (1867–1871) from a single humerus, for which Lambrecht (1933) later created the genus *Gerandia*. Although its small size would appear to exclude it from the genus *Columba*, its relationships to existing genera of Columbidae otherwise have not been determined.

Fossils of very small doves, the size of the modern species of *Columbina*, are fairly abundant in the Thomas Farm Local Fauna from the early Miocene (Hemingfordian) of north-central Florida (P. Brodkorb, personal communication), but these have not yet been described. The only other columbid yet reported from deposits earlier than latest Pliocene is *Columba omnisanctorum* Ballmann, 1976a, known from three elements from the late Miocene of the Gargano Peninsula of Italy, an area that consisted of an island or islands at the time of deposition. *Falco pisanus*, from the Pliocene of Italy, may also be a columbid (see Section VIII,D, Falconidae).

Because they are now known almost exclusively from osseous remains, the dodos and solitaires of the Mascarene Islands deserve mention. These were very large flightless birds that do not differ from pigeons except in the characters that mark most flightless insular birds. I do not consider the family Raphidae to be valid and I would include both *Raphus* and *Pezophaps* in the Columbidae, although it remains to be determined what their closest relatives are within the family.

K. PSITTACIFORMES

As with the Columbidae, parrots (Psittacidae) are poorly represented in the fossil record. The earliest fossils that have been referred to the family make up the type material of *Palaeopsittacus georgei* Harrison, 1982, from the Lower Eocene (Ypresian) London Clay of England. This consists of 11 apparently associated bones and fragments, including the coracoid, scapula, ulna, tibiotarsus, and carpometacarpus. Harrison (1982) also assigned to this species a fragmentary distal end of tarsometatarsus from Medial Eocene deposits at Kempsport, Hampshire. *Palaeopsittacus* lacks most of the salient features that distinguish modern parrots, such as the unossified tendinal bridge of the tibiotarsus, and its referral to the Psittacidae needs confirmation.

Otherwise, the earliest reported parrot fossils are from the late Eocene of La Bouffie, France (Mourer-Chauviré, 1982). *Psittacus verreauxi* Milne-Edwards, 1867–1871, is a small species of parrot based on a tarsometatarsus, tibiotarsus, and humerus from the early Miocene (Aquitanian) of France. Lambrecht (1933) erected the genus *Archaeopsittacus* for *P. verreauxi*, but his diagnosis was quite inadequate. P. Ballmann (personal communication) feels that the species is closely related to the modern genus *Psittacus*, as stated by Milne-Edwards. Fossils of parrots have also been recovered from the Middle Miocene Nördlinger Ries in southern Germany and at Sansan, France (P. Ballmann, personal communication).

The only parrot reported from the Tertiary of North America is *Conuropsis fratercula* Wetmore, 1926a, from the early Miocene (late Hemingfordian) of Nebraska. This was based on a humerus of a medium-small parrot, although I would not regard its generic affinities as having been positively established.

L. Family Incertae Sedis Zygodactylidae

Ballmann (1969b) described a new genus and species of bird of uncertain affinity, *Zygodactylus ignotus*, known from the tarsometatarsus and tibiotarsus, from the early Miocene (early Burdigalian) of Bavaria. The tarsometatarsus shows clearly that this bird had a highly developed zygodactyl foot, with the fourth toe reversed. The structure is unlike that in either the Cuculidae or Galbulae, and is comparable only to that in the Pici and the Psittacidae. Although *Zygodactylus* was compared to members of all living groups of birds with zygodactyl feet, it could not be placed in any living order of birds, its differences from the both Pici and Psittacidae being trenchant. Ballmann (1969a) described another tarsometatarsus from the middle to late Miocene deposits at La-Grive-St.-Alban, France, as a second species, *Z. grivensis*, and indicated that *Zygodactylus* was a perching bird rather than a climbing bird like a woodpecker.

Brodkorb (1971b) created a new family, Zygodactylidae, for *Zygodactylus*, placing it between the Galbulae and the Pici in the Piciformes. Simpson and Cracraft (1981, p. 492) suggested "placing the Zygodactylidae as a basal member of the Pici," but this was unjustified (see Olson, 1983a). P. Ballmann (personal communication) denies that *Zygodactylus* belongs with the Pici, and he considers that if anything it might be closer to parrots, although the tarsometatarsus is more slender than in parrots and shows a well developed scar for the short extensor muscle of the fourth toe, this muscle being reduced in parrots. On the other hand, *Zygodactylus* may indicate that the zygodactyl foot evolved completely independently in some other group of birds. For the present, the family Zygodactylidae seems valid enough but its relationships remain a mystery.

Brunet (1961) described a few bones from the middle Miocene of Beni Mellal, Morocco, inexplicably referring all of them to living species. Included was the distal end of a tarsometatarsus that he identified as "*Jynx* cf. *torquilla*." His illustrations clearly show that this was a zygodactyl bird but it could hardly belong to the genus *Jynx* or even in the suborder Pici. Nor is it a cuckoo or a parrot. It does seem to have some similarities to the Zygodactylidae and should be restudied.

IX. The "Higher" Land Bird Assemblage

The orders included here may actually constitute a monophyletic taxon, as they are very nearly the "Anomalogonatae" as originally defined by Garrod (1874), and are exactly the equivalent of the term as used by Beddard (1898), who included the Strigiformes and Coliiformes omitted by Garrod. This group is characterized by the absence of the ambiens muscle. Although the ambiens has been lost in certain other taxa, in no instance does the loss occur in an entire order, and only in two other families (Pelecanidae and Ardeidae), other than a few monotypic ones, is the ambiens apparently absent in all species (see Berger, 1966, p. 421). As Garrod (1874, p. 115) noted, "there are some families of birds, such as the *Columbae* and *Psittaci*, in which different genera vary in possessing or not having the ambiens muscle developed. Those in which it is absent must, from previous considerations, have lost it since the families differentiated off; and therefore those families may be classed with the others in which the ambiens is present." As any particular order in the "Anomalogonatae" is now usually considered to be more closely related to some other order in that group than to one of the "Homologonatae," the idea that the "Anomalogonatae" may represent a natural group deserves modern consideration.

The inclusion of the Coliiformes with the "higher" land birds is at this point somewhat arbitrary, as the order consists only of two genera, so the loss of the ambiens here may carry less significance. The colies are anomalous and cannot clearly be associated with any one particular family among the "higher" land birds. Possibly they represent a link with the "basal" land bird assemblage.

Recent studies of myology have maintained that both the Coraciiformes and the Piciformes are monophyletic (Swierczewski and Raikow, 1981; Maurer and Raikow, 1981), but in each case the only evidence for this lies in the configuration of the deep plantar tendons traditionally used to define these orders. The new studies did not reveal any additional characters not related to the flexor tendons that corroborates the monophyly of these groups. I believe that both of these orders are unnatural. Their polyphyletic nature has obscured perception of what may be two major lineages within the "higher" land birds—a coraciiform lineage and a "pico–passerine" lineage.

In the true coraciiform lineage the rollers (suborder Coracii) appear to be the most primitive. I have argued elsewhere (Olson, 1983a) that the suborder Galbulae of the Piciformes is in fact closely related to the rollers and ground-rollers (Coraciidae and Atelornithidae = Brachypteraciidae) of the Coraciiformes; this is corroborated by studies of cranial anatomy (Burton, 1985). The roller group also may have given rise to the Strigiformes and Caprimulgiformes, probably through forms like *Leptosomus* (Leptosomidae), the postcranial osteology of which is very divergent from that of typical rollers and is quite owl-like. As discussed beyond, the Caprimulgiformes are in turn probably closely related to the swifts.

There is as yet little evidence directly linking the Halcyones (= Alcedini *auct.*), including the Trogonidae, to the roller group and its derivatives, but neither is there any evidence contrary to this association. On the other hand, I regard it as highly unlikely that hornbills, hoopoes, and woodhoopoes (Bucerotidae, Upupidae, and Phoeniculidae) belong in the Coraciiformes, and it is more likely that they belong instead to the radiation that includes the four families of the suborder Pici and the Passeriformes. Their removal from the Coraciiformes is also supported by studies of cranial anatomy (Burton, 1985).

Although much reanalysis of characters is still needed, it should be noted that when the Piciformes and Coraciiformes are split apart and realigned into the two lineages I have proposed here, then a number of morphological characters that were used by early systematists, but that were later largely abandoned, become much more consistent. For example, all of the taxa in the "pico–passerine" lineage, including the Bucerotiformeses, have a nude oil gland and vestigial or absent intestinal ceca, whereas in the "coraciiform lineage" the oil gland is tufted and the ceca are usually well developed. In the arrangement I have used here I have placed the Trochilidae and "Bucerotiformes" at a point between the two major lineages outlined above, to reflect the present uncertainty about their placement.

A. COLIIFORMES

The modern species of the enigmatic family Coliidae occur only in Africa. The earliest fossil record is from the Upper Eocene deposits at Quercy, France, where fossils very similar to living colies occur (Mourer-Chauviré, 1982). Our knowledge that these birds have a fossil record at all began with Ballmann's (1969a) discovery that three genera and species described by Milne-Edwards from the Miocene of France, and variously identified as woodpeckers, hoopoes, swifts, or cuckoos, were in reality colies. Ballmann referred these taxa to the genus *Colius*. There are two species, *C. paludicola* and *C. archiaci*, in the early Miocene (Aquitanian), and one, *C. palustris*, from the middle Miocene at Sansan, France. Ballmann (1969a) also reported *Colius* cf. *palustris* from the mid to late Miocene of La-Grive-St.-Alban. Brodkorb (1971b), resurrected the genus *Limnatornis* for the earlier forms, and *Necrornis* for the later ones. The early Miocene species definitely belong in the Coliidae but their generic affinities are uncertain, particularly as the modern colies are separable into more than one genus, the species *indicus* and *macrourus* being quite distinctive enough to merit separation in the genus *Urocolius* Bonaparte. I have examined a humerus of *Colius* cf. *palustris* from La-Grive-St.-Alban in the Smithsonian collections and would agree with Ballmann that it is not generically distinct from modern *Colius*; thus *Necrornis* should be synonymized. Ballmann (personal communication) has also identified bones of *Colius* from the middle Miocene Nördlinger Ries of Germany. Thus we see that the restriction of the Coliidae to Africa is a post-Miocene event and we may therefore expect to find fossils of colylike birds elsewhere in the Tertiary outside of Africa.

B. CORACIIFORMES (INCLUDING TROGONIDAE AND GALBULAE)

As outlined above, the order Coraciiformes confronts us with several problems of higher-level systematics that are as yet imperfectly resolved. The morphology of the stapes (Feduccia, 1975) and appendicular myology (Maurer and Raikow, 1982) suggest that the Trogonidae are most closely related to the coraciiform suborder Halcyones (= Alcedines), for which reason I have included them here, although they are very divergent from the Halcyones in many respects.

Although the late Cretaceous bird *Alexornis* was originally considered to be ancestral to both the Coraciiformes and Piciformes, it is now believed to belong in another subclass altogether (see Section VI). Despite its removal from the vicinity of the Coraciiformes, there is still much good evidence to show that by the early Tertiary, members of the Coraciiformes, in the sense used here, were the dominant arboreal "perching" birds in North America and Europe.

There are a number of undescribed fossils of Coraciiformes from Eocene and Oligocene deposits, many of which are either in private hands or are scattered in various smaller museums, mainly in Europe. The majority come from the early Eocene (Wasatchian) Green River Formation in the western United States and from the roughly contemporaneous London Clay (Ypresian) in England. An introduction to the geology and paleontology of these deposits may be found in Grande (1980), for the Green River Formation, and in Sherlock (1960) and various papers in *Tertiary Research*, for the London Clay. I also know of fossils of coraciiform birds from the younger middle Eocene (Lutetian) Messel oil shales in Germany (see Hoch, 1980, for the history of this site). When these specimens are studied and described scientifically, our knowledge of the early history of the Coraciiformes will be greatly enhanced.

Halcyornis toliapicus Koenig, known only from a cranium from the Lower Eocene London Clay in England, had previously been referred to the Laridae or to the Alcedinidae. Harrison and Walker (1972) considered that its affinities were with the Coraciiformes but that it required its own family, Halcyornithidae. *Halcyornis* could well be a coraciiform, but without finding another cranium in association with postcranial skeletal elements, it would be impossible to determine its precise relationships.

1. *Suborder Coracii*

The Madagascan families Atelornithidae (Brachypteraciidae *auct.*) and Leptosomidae (Leptosomatidae *auct.*) have no fossil record. Likewise, no fossil record exists for either of the two living families Galbulidae and Bucconidae, both of which are now strictly Neotropical in distribution. The only fossil as yet recognized in the Coracii is *Geranopterus alatus* Milne-Edwards, 1892, from the late Eocene to Oligocene Phosphorites du Quercy, France. Milne-Edwards (1892) did not illustrate this species but Mourer-Chauviré (personal communication) assures me not only that *Geranopterus* is a roller, but that it is very close to the living genus *Coracias*. This is in accord with a beautifully preserved specimen of a bird from the early Eocene Green River Formation in Wyoming that can hardly be distinguished from the living genus *Eurystomus*, at least on the basis of its photograph (Fig. 4). The Coracii were definitely present in North America in the Tertiary and

FIG. 4. A particularly excellent fossil from the Lower Eocene Green River Formation in Wyoming. This bird appears to be very similar to the living rollers of the genus *Eurystomus* (Coraciiformes: Coraciidae). (Photograph by H. Heckel, courtesy of S. Rietschel, Landessammlungen für Naturkunde, Karlsruhe, Germany, where the specimen is deposited.)

their appearance in essentially "modern" form by the early Eocene suggests that the history of the order Coraciiformes may well extend farther back in time.

Many new specimens, some of them complete, from the early Eocene of the western United States, necessitate a complete revision of the species that have been assigned to the family Primobucconidae. Brodkorb (1970b) described an incomplete wing from the early Eocene Green River Formation of Wyoming as *Primobucco mcgrewi*, which he assigned to the Bucconidae. Feduccia (1973a) then described another species, *P. kistneri*, based on a small incomplete skeleton with zygodactyl feet. He later (Feduccia, 1976) considered that *Neanis schucherti* (Shufeldt), also from the Green River, was related to *Primobucco*, although he maintained *Neanis* as distinct and assigned *P. kistneri* to that genus. Feduccia and Martin (1976) erected a new family, Primobucconidae, for these species and described another supposedly zygodactyl skeleton as *Primobucco olsoni*. They referred the middle Eocene (Bridgerian) taxa *Uintornis lucaris* Marsh and *Botauroides parvus* Shufeldt to this family and described two contemporaneous new species as *Uintornis marionae* and *Eobucco brodkorbi*. All of the middle Eocene taxa were known only from tarsometatarsi. *Uintornis lucaris* had previously been thought to be a woodpecker or cuckoo, whereas *B. parvus* was originally described as a heron.

With the new and better preserved specimens available now, I have come to the following very tentative conclusions. One of the more abundant taxa, known from complete skeletons, is an anisodactyl coraciiform similar to the Atelornithidae but with proportionately shorter tarsometatarsi. As far as can be determined from size and such few details as remain in the poorly preserved holotype, this appears to be *Primobucco mcgrewi*, which carries with it the family name Primobucconidae.

"Neanis" kistneri is the smallest of the "primobucconids" and appears to be truly zygodactyl, therefore probably belonging to a different family from *P. mcgrewi*. Determining the relationships of this species, even at the ordinal level, will depend on further preparation of the holotype.

All of the other species of "primobucconids," including *"Primobucco" olsoni*, belong to yet another very interesting family having decidedly raptorial feet, with very shortened, owl-like phalanges, and possibly having been at least facultatively zygodactyl, as are owls. In the holotype of *"P." olsoni*, it is actually the second toe that is reversed, possibly as an accident of preservation, rather than the fourth, so it cannot be said to have been zygodactyl on this basis. The skull in these birds is not raptorlike. It is too early to determine the phylogenetic significance of these birds but at least they show that the evolution of a raptorlike foot is not linked to the simultaneous development of a raptorlike skull.

2. *Suborder Halcyones (Alcedini* auct.)

This group of Coraciiformes is defined by a derived morphology of the stapes (Feduccia, 1975) and several derived myological characters (Maurer and Raikow, 1982) that also argue for the inclusion of the Trogonidae in the same taxon. The Halcyonidae (= Alcedinidae) and Meropidae have no named Tertiary forms, although I have examined specimens from the Lower Eocene Green River Formation of Wyoming and from the Medial Eocene Messel oil shales of Germany that appear to be close to these two families, and Mourer-Chauviré (1982) lists both the Alcedinidae and the Meropidae in the Eo–Oligocene avifauna of Quercy, France.

The living members of the Momotidae and Todidae are now strictly Neotropical and Antillean, respectively, in distribution. That todies probably originated outside the Greater Antilles was shown by the discovery of *Palaeotodus emryi* Olson, 1976a, in "middle" Oligocene (Orellan) deposits of Wyoming. This was based on a skull, mandible, and humerus from an owl-pellet assemblage. *Palaeotodus* was larger than the modern genus *Todus*, with a proportionately longer wing.

The species *Protornis glarniensis* von Meyer, from the early Oligocene of Switzerland, was thought to be a kingfisher by Peyer (1957) but was removed to the Momotidae by Olson (1976a), thus showing that this family may have originated in the Old World. Cracraft (1980, pp. 13–14), with no supporting facts, hypothesized that *Protornis* might be the sister-group of the Todidae and Momotidae, stating that this "would make more sense zoogeographically by restricting the todid–momotid lineage to the New World." This would imply that *Protornis* is something other than a motmot, for which there is no evidence. Also, the subsequent discovery of a tody in the Eo–Oligocene Phosphorites du Quercy, France (Mourer-Chauviré, 1982), would appear to vitiate any preconceptions about restricting the tody–motmot lineage to the New World.

a. Trogonidae. With the removal of the species of *Archaeotrogon* to their own family, Archaeotrogonidae (Mourer-Chauviré, 1980), only two Tertiary records exist for the Trogonidae. The earliest of these is an unnamed specimen from the early Oligocene of Switzerland that had previously been referred to *Protornis glarniensis*. This is too large for that species and has the heterodactyl foot diagnostic of the Trogonidae (Olson, 1976a). The only other fossil trogon is *Paratrogon gallicus* (Milne-Edwards), known from two humeri from the early Miocene (Aquitanian) of France. Lambrecht's (1933) creation of the genus *Paratrogon* for this species reflects his predilection for placing fossil species in extinct genera, whereas the relationships of *Paratrogon* within the Trogonidae remain to be determined.

b. Archaeotrogonidae. Even with the extensive review by Mourer-Chauviré (1980), this group remains enigmatic. Mourer-Chauviré recognizes four species, all in the genus *Archaeotrogon* Milne-Edwards, and all from the Phosphorites du Quercy, France. One of these, *A. venustus* Milne-

Edwards, is found in late Eocene to late Oligocene deposits at Quercy and thus has an incredible temporal range of about 14 million years. The other three species, *A. zitteli* Gaillard, *A. cayluxensis* Gaillard, and *A. hoffstetteri* Mourer-Chauviré, are known solely from the Oligocene deposits at Quercy that formed subsequent to the extinctions of the *grand coupure* at the end of the Eocene. Bones of *Archaeotrogon* are abundant in the Quercy deposits and most of the major limb and girdle elements are known. *Archaeotrogon* lacks the heterodactyl foot of the Trogonidae and otherwise differs so substantially that Mourer-Chauviré (1980) created a new family for the genus. The humeri and tarsometatarsi are short and stout, and the carpometacarpus is distinctive in having a spurlike first metacarpal.

The differences between the Archaeotrogonidae and the Trogonidae are so profound that one wonders whether they may not be more significant than their apparent similarities. Mourer-Chauviré (1980, 1982) noted similarities between *Archaeotrogon* and the Caprimulgiformes, particularly the Caprimulgidae. This has some interesting possible ramifications. If the Aegialornithidae, Hemiprocnidae, and Apodidae are derived from members of the Caprimulgiformes, as suggested in Section IX,E, then perhaps *Archaeotrogon* was derived from an ancestor that was intermediate between the more typical Caprimulgiformes and the more swiftlike Aegialornithidae. *Archaeotrogon* itself, at least as presently known, cannot be ancestral to the Aegialornithidae, as the latter do not occur after the *grand coupure*, whereas most of the species of *Archaeotrogon* do. More work needs to be done to determine the significance of the caprimulgidlike characters of *Archaeotrogon* and to ascertain whether the genus actually has any close relationship with the Trogonidae.

C. STRIGIFORMES

Owls are abundantly represented in the fossil record and numerous taxa have been described. There has been no comprehensive revision of these taxa, or even a significant portion of them, and until such is undertaken, only some rather vague generalities can be made about the evolutionary history of owls.

Certainly one of the most egregious errors ever made in avian paleontology was the description of two distal ends of tibiae of dinosaurs as a new family of Cretaceous owls (Harrison and Walker, 1975b). Discounting this, the earliest known owl that actually belongs in the class Aves is *Ogygoptynx wetmorei* Rich and Bohaska, 1976, based on a tarsometatarsus from the Paleocene (Tiffanian) of Colorado. At first considered to be of uncertain affinities, *Ogygoptynx* was later separated as a distinct family, Ogygoptyngidae, said to be intermediate between the Tytonidae and Strigidae and different from the Protostrigidae and all Paleogene owls of Europe (Rich and Bohaska, 1981).

Several species of owls have been described from the Eocene of North America (Brodkorb, 1971b; Martin and Black, 1972), all of which have been referred to the extinct family Protostrigidae. Two genera have been recognized: *Protostrix*, from the middle Eocene (Bridgerian) of Wyoming and late Eocene (Uintan) of California; and *Eostrix*, hitherto known only from the early Eocene (Wasatchian) of Wyoming. Mourer-Chauviré (1983a) has shown that the phalanges constituting the type of *Minerva antiqua* (Shufeldt) are in fact those of an owl and not an edentate mammal as once proposed. *Aquila ferox* Shufeldt and *A.* ("*Protostrix*") *lydekkeri* Shufeldt are synonyms of *Minerva antiqua;* the genus *Minerva* Shufeldt, 1915, now replaces *Protostrix* Wetmore, 1933a, and becomes the type of the Protostrigidae, the family name being retained in accordance with article 40 of the International Code of Zoological Nomenclature.

Rich (1982) has described the distal end of the tarsometatarsus in *Protostrix* (= *Minerva*) and given characters by which it may be separated from *Eostrix*. A number of undescribed specimens in the Smithsonian collections provide additional information on the Protostrigidae. Associated material of *Eostrix* from the middle Eocene (Bridgerian) of Wyoming extends the temporal range of that genus. From this it appears that *Eostrix* is so different from *Minerva* that it quite possibly should be referred to a different family. Regardless, these Eocene owls are so different from either the Tytonidae or Strigidae that they definitely cannot be placed with either family. The only other early Eocene owl as yet described is *Eostrix vincenti* Harrison, 1980b, known from a tarsometatarsus, lacking the distal end, and a pedal phalanx (the holotype!) from the London Clay (Ypresian) of England. Comparable elements have not yet been described for the Protostrigidae, so the assignment of these specimens, particularly the phalanx, to the genus *Eostrix* is at best only speculative.

Seven species of owls in four genera have been named from the late Eocene to Oligocene Phosphorites du Quercy in France, and three species in three genera (including the tytonid *Prosybris*) from the early Miocene (Aquitanian) of France (Brodkorb, 1971b). It is virtually certain that those species from Quercy that were referred to modern genera are incorrectly assigned (e.g., "*Asio*" *henrici*—see Rich and Bohaska, 1981), and the same is perhaps true of the early Miocene taxa assigned to modern genera. Mourer-Chauviré (1981) has shown that the holotypical humerus of the supposed owl *Strigogyps minor* Gaillard, 1939, from Quercy, is in fact from a phorusrhacidlike bird. The characters that led Brodkorb (1971b) to place the Aquitanian species *Paratyto arvernensis* in the "Phodilidae" (stout tarsometatarsus lacking an ossified tendinal loop) occur in many of the supposedly strigid taxa from Quercy, as well as in certain modern species of Strigidae (Rich and Bohaska, 1981). The determination of the relationships of the various Tertiary owls from France awaits a comprehensive revision.

As yet, no owls have been described from the Oligocene of North America, but there are nevertheless a fair number of specimens from the early Oligocene (Chadronian) of Wyoming in the Smithsonian and other collections. In addition, there are also several complete and perfectly preserved skeletons of a small species of owl collected by R. J. Emry from the "middle" Oligocene (Orellan) of Wyoming (see Olson, 1976a) that should eventually provide us with much new information on the morphology of Paleogene owls. These also have the stout tarsometatarsus without an ossified tendinal loop of the "phodiline" owls.

It is not certain just when modern genera of strigid owls first appear. The generic placement of the species *Strix dakota* A. H. Miller, 1944, described from a tarsometatarsus from the early Miocene (Hemingfordian) of South Dakota, was questioned by Ford (1967). Two owls, *Strix brevis* and *Otus wintershofensis,* were described by Ballmann, 1969b, from the early Miocene at Wintershof West, Bavaria. Ballmann made these generic assignments mainly on size, and he now considers these two species to be more closely related to each other than either is to *Strix* or *Otus.* Both may actually be more similar to the living genus *Ninox* (P. Ballmann, personal communication).

Ballmann (1972) named *Strix collongensis* from the early Miocene at Vieux-Collonges, France. This was based on a coracoid that does not differ substantially from that of the modern genus *Strix.* Ballmann (1976a) also provisionally named an owl from the late Miocene of the Gargano Peninsula as *Strix? perpasta,* but believed it actually to represent an extinct genus. This species was the size of the modern Snowy Owl, *Nyctea scandiaca.* The species described as *Ardea perplexa* by Milne-Edwards (1868) from the distal end of a humerus from the middle Miocene at Sansan, France appears to be an owl rather than a heron (see Section X,B, Ardeidae), but its affinities cannot be determined without reference to the type.

The Pleistocene owls of the genus *Ornimegalonyx* Arredondo, from cave deposits in Cuba, deserve mention here, as they are the largest owls known (see Arredondo, 1976). *Ornimegalonyx* was a typical strigid owl, probably not far removed from such genera as *Strix* and *Ciccaba,* but it had a proportionately small wing and a reduced sternum. That *Ornimegalonyx* was flightless, as has sometimes been proposed, may be doubted, although it cannot have been a strong flier. It has been known for some time that more than one species of *Ornimegalonyx* formerly occurred in Cuba (Kurochkin and Mayo, 1973). Arredondo (1982) has subsequently named three new species, for a total of four, although if such factors as sexual and geographic size variation were to be taken into account, it would seem unlikely that so many species could be recognized.

P. Ballmann (personal communication) considers *Prosybris antiqua* (Milne-Edwards) from the early Miocene (Aquitanian) of France, to have been correctly assigned to the Tytonidae (Brodkorb, 1971b). This species was smaller than any modern tytonid and was clearly generically distinct from *Tyto*.

Three species of barn owls of the genus *Tyto* have been named from middle to late Miocene deposits in France (Brodkorb, 1971b) and one of these, *T. sanctialbani*, has also been identified from the late Miocene of the Gargano Peninsula in Italy, where two additional species of *Tyto* also occur (Ballmann, 1973, 1976a). One of these, *T. robusta*, is very much larger than modern barn owls, while the other, *T. gigantea*, is quite simply gigantic. These three species of barn owls have a remarkable parallel in the three species known from Quaternary deposits in Cuba (*T. alba*, *T. noeli*, and *T. riveroi*), which fall into the same size classes (see Arredondo, 1976). In the Miocene, the Gargano Peninsula was an island, or possibly an archipelago, where, in the absence of carnivorous mammals, a considerable increase in size took place in rodents and insectivores that was matched by an increase in size in strigid and tytonid owls and in accipitrids (Freudenthal, 1976; Ballmann, 1973; 1976). The similarity to the Quaternary faunas of the Antilles, particularly that of Cuba (Arredondo, 1976), is quite striking.

Fossil barn owls of the very large but not gigantic size are known also from the Quaternary of Hispaniola (*T. ostologa*), the Bahamas (*T. pollens*), and the Plio–Pleistocene of Majorca and Minorca (*T. balearica*) in the Mediterranean (see Wetmore, 1922; Olson and Hilgartner, 1982; and Mourer-Chauviré *et al.*, 1980). Thus gigantism in *Tyto* has evolved repeatedly in different insular environments.

Lechusa stirtoni L. Miller, a supposed new genus and species of tytonid from the late Pliocene San Diego Formation of southern California, has been shown to have been based on a recent coracoid of *Tyto alba* that was mistaken for a fossil (see Chandler, 1982).

D. Caprimulgiformes

The published fossil record of the Caprimulgiformes is very scanty, with significant specimens having thus far been described only for the Aegialornithidae. Undescribed material of all the other families except the Nyctibiidae now exists in collections, however, and this completely alters our concepts of the biogeography of the order.

1. *Podargidae*

The frogmouths are found today in southern Asia through Australia, but that they were once more widely distributed is attested to by fossils reported from late Eocene deposits at Quercy, France (Mourer-Chauviré, 1982).

2. *Steatornithidae*

This monotypic family, consisting of the Guácharo, or Oilbird, *Steatornis caripensis*, is restricted to South America. Mourer-Chauviré (1982) tentatively referred a fragmentary sternum from the late Oligocene at Quercy, France, to the Steatornithidae, and the occurrence of the family outside of South America is confirmed by a nearly complete skeleton of a primitive steatornithid from the early Eocene Green River Formation of Wyoming now in the Smithsonian collections (S. L. Olson, unpublished).

3. *Aegothelidae*

The earliest possible specimen of owlet-nightjar is a fragment of a sternum from the Eo–Oligocene deposits at Quercy, France, that Mourer-Chauviré (1982) tentatively referred to the Aegothelidae. This family is now restricted to Australasia. A most interesting specimen, consisting of a partial skeleton including the skull, from early to middle Miocene deposits in New South Wales, Australia, also has been referred to the Aegothelidae. This was described as a new genus and species, *Quipollornis koniberi* Rich and McEvey, 1977, that differs from modern aegothelids in several respects but perhaps most notably in having the humerus about twice the length of the femur, rather than "nearly subequal." Thus this ratio in *Quipollornis* is more like that in the Podargidae and other Caprimulgiformes, suggesting that "the marked emphasis placed on hind limbs in the Owlet-nightjar group had not as yet begun to develop significantly" (Rich and McEvey, 1977, p. 251).

The fossil record also indicates that the Aegothelidae inhabited New Zealand well into the Holocene. Remains of a quite large endemic genus and species, *Megaegotheles novaezealandiae* Scarlett, 1968, have been recovered from Pleistocene to "subrecent" deposits in various parts of both the North and South Islands (Rich and Scarlett, 1977). Compared to *Aegotheles*, this form had larger legs but proportionately smaller wings, although I doubt that it was completely flightless—a possibility raised by Rich and Scarlett (1977). A number of birds, as among the Rallidae, appear from their morphology to be "flightless" and yet can still fly short distances.

4. *Caprimulgidae*

The only mention of nightjars in the Tertiary is Mourer-Chauviré's (1982) listing of the family as occurring in the Eo–Oligocene deposits at Quercy, France.

E. APODIFORMES

1. *Aegialornithidae*

The earliest of the primitive swiftlike birds of the fossil family Aegialornithidae is *Primapus lacki* Harrison and Walker, 1975a, a very small species known from several humeri from the early Eocene (Ypresian) of England. Four much larger species are now recognized in the genus *Aegialornis* (see Collins, 1976a) from the late Eocene to Oligocene Phosphorites du Quercy, France, the smallest of which has also been identified in deposits of equivalent age at Sainte Néboule (Mourer-Chauviré, 1978b). A third genus, *Cypselavus*, whose single species, *C. gallicus*, is considerably smaller than any of the species of *Aegialornis*, occurs in the same two deposits. With more refined stratigraphic information it is now known that *Aegialornis* apparently died out with the *grand coupure* at the end of the Eocene, whereas *Cypselavus* persisted into the Oligocene (Mourer-Chauviré, 1978b).

Lydekker (1891) originally referred the genus *Aegialornis* and the family Aegialornithidae to the vicinity of the Lari. I assume this decision was based on the bifenestrate proximal phalanx of the major digit of the wing, a condition found not only in the Lari, but also in certain Caprimulgiformes. Milne-Edwards (1892), Gaillard (1908), Lambrecht (1933), and Harrison (1975a), all regarded *Aegialornis* as being related to the swifts (Apodi). Collins (1976a), however, placed *Aegialornis* in the Caprimulgiformes, where Brodkorb (1971b) likewise had placed the Aegialornithidae, on Collins' advice. Collins considered only the humeri to be certainly assignable to *Aegialornis*, whereas the other elements of the skeleton that had been referred to the genus he thought belonged to the Charadriiformes and Coraciiformes. Within the Caprimulgiformes, Collins regarded the Chordeilinae as most closely related to *Aegialornis*.

Mourer-Chauviré (1978b) studied additional material of *Aegialornis* and *Cypselavus* and concluded: (1) that the referred elements of *Aegialornis* had been correctly assigned and did not belong to charadriiforms or coraciiforms, and (2) that the Aegialornithidae are most similar to swifts, particularly the Hemiprocnidae, and consequently belong in the Apodiformes. Similarities in the humeri of *Aegialornis* and the modern genus *Chordeiles*, along with other characters considered below, may indicate a derivation of the Aegialornithidae, Hemiprocnidae, and Apodidae from the Caprimulgiformes. The osteology of the Aegialornithidae deserves more scrutiny in this regard, as these birds are in many respects obviously more primitive than modern genera of swifts. As mentioned above, the bifenestrate proximal phalanx of the major digit of *Aegialornis* is a character shared with certain Caprimulgiformes and that presumably has been lost secondarily in modern swifts, in which these fenestrae are closed by a very thin layer of bone.

I have examined a skeleton from the early Eocene (Wasatchian) Green River Formation of Wyoming, of a very small bird the same size as *Primapus lacki* of the early Eocene of England and possibly congeneric with it. This has a large caprimulgiformlike skull and a longer hindlimb than in modern swifts but decidedly swiftlike coracoids and wing elements. The phalangeal formula of the pes is complete, so this bird branched off before the Caprimulgidae, in which the fourth toe has only four phalanges. The tarsometatarsus in this specimen is the same size as that of the supposed cuckoo *Procuculus minutus* (Harrison and Walker, 1977), which has a tarsal morphology that would not be out of line for a relative of swifts and caprimulgiforms. *Procuculus* cannot be a cuckoo in any case (Olson and Feduccia, 1979b), and I suspect that it may prove to be a synonym of *Primapus*.

2. *Apodidae*

The fossil record of true swifts begins in the early Miocene (Aquitanian) of France. The three nominal species from these deposits that are listed by Brodkorb (1971b) in the genera *Cypselavus*, *Apus*, and *Collocalia*, were shown by Collins (1976b) to constitute but a single species, now known as *Cypseloides ignotus* (Milne-Edwards). The Cypseloidinae appear to be the most primitive group of modern swifts, all the extant species of which are confined to the New World. The French record is thus of particular interest in showing the modern pattern of distribution to be relictual.

The only other Tertiary species of swifts are both from the middle to late Miocene and both are referred to the modern genus *Apus*. These are *Apus gaillardi* (Ennouchi, 1930) from La-Grive-St.-Alban, France, and *A. wetmorei* Ballmann, 1976a, from the Gargano Peninsula of Italy.

F. FAMILY INCERTAE SEDIS TROCHILIDAE

It is possible that the similarities between swifts (Apodidae) and hummingbirds (Trochilidae) are due to convergence, so until their proper affinities have been determined, I have placed the Trochilidae between the coraciiform and "pico–passerine" lineages. There is no fossil record of the

Trochilidae other than of modern species from a few Quaternary cave deposits, mostly in the West Indies (summarized in Olson and Hilgartner, (1982).

G. Order Incertae Sedis Bucerotiformes (Including Upupae)

There is good evidence from the stapes (Feduccia, 1975) and from myology (Maurer and Raikow, 1981) for a close relationship between the Upupidae and Phoeniculidae. These derived characters are absent in the Bucerotidae, which in turn have many unique derived features of their own. Maurer and Raikow (1981) did not consider the hoopoes to be particularly closely related to hornbills, but maintained both in the Coraciiformes. The myological evidence for including either of these groups with the remainder of the Coraciiformes is nevertheless very scanty. I am in agreement with Fürbringer (1888, 1902), Kemp (1979), and Burton (1985), that the hornbills are most closely related to the hoopoes and woodhoopoes. Following Fürbringer (1888) and Burton (1985), I have combined these three families in a single taxon and separated it from the Coraciiformes. The Bucerotiformes are probably more closely related to the Pici and the Passeriformes than to the true Coraciiformes.

1. Bucerotidae

Brodkorb (1971b) lists three paleospecies of hornbills, none of which, however, can be confirmed as belonging to this highly distinctive family. The earliest, *Geiseloceros robustus* Lambrecht, 1935, is based on a right wing and shoulder girdle from the middle Eocene (Lutetian) Geisel Valley brown coal in Germany. Lambrecht's (1935) illustrations of the specimens are very indistinct, but, along with the measurements, they show *Geiseloceros* to have had an extremely short wing, with the humerus (117 mm) exceeding the ulna (90 mm) in length. In the Bucerotidae the ulna is considerably longer than the humerus and thus it is highly unlikely that *Geiseloceros* is a hornbill. It may, however, belong to the same species as the putative vulturid *Eocathartes robustus* (P. Houde, personal communication), although the true relationships of that form are likewise uncertain (see Section X,F,5).

Cryptornis antiquus (Gervais), based on a partial skeletal impression from the late Eocene (Ludian) of the Paris Basin in France, was originally described very tentatively as a cuckoo. Milne-Edwards (1867–1871) established that it definitely was not a cockoo but only hinted at a possible relationship with the Bucerotidae. Lambrecht (1933) listed *Cryptornis* as

Incertae Sedis after the Piciformes. Brunet (1970) considered its relationships to be uncertain, although he listed it under the Picidae. Brodkorb (1971b) nevertheless placed *Cryptornis* in the Bucerotidae without comment. Harrison (1979b) provisionally placed it with the Coraciidae, but it is not evident that he actually examined the specimen. No evidence for a bucerotid relationship for *Cryptornis* has ever been presented and its affinities can be regarded only as undetermined.

Homalopus picoides Milne-Edwards, from the middle Miocene at Sansan, France, was founded on the distal end of a tarsometatarsus, with tibiotarsi and a humerus being referred to the same species. Milne-Edwards (1867–1871) compared it to a variety of nonpasserine land birds, including hornbills, but made no clear disposition of the genus. Lambrecht (1933) considered its relationships uncertain, stating only that Milne-Edwards had compared it with hornbills. Evidently for this reason, Brodkorb (1971b) placed *Homalopus* in the Bucerotidae.

Homalopus was smaller than modern hornbills and Milne-Edwards' (1867–1871) illustrations show the tarsometatarsus to differ greatly from that in the Bucerotidae. In particular, the middle trochlea is very deeply incised, so as in effect to make two trochleae of it, in the manner seen in many tree-creeping birds such as Dendrocolaptidae, Certhiidae, and Sittidae (see Feduccia, 1973b). This is also true in the Phoeniculidae, with which *Homalopus* appears to share some similarities. *Homalopus* is almost certainly not a hornbill.

The hornbills do have a valid fossil record, however, as Brunet (1971) has described the distal end of a tarsometatarsus from the middle Miocene of Beni-Mellal, north of the Atlas Mountains in Morocco, as *Bucorvus brailloni*. The ground-hornbills of the genus *Bucorvus* are so distinctive osteologically that Brunet's illustrations are sufficient to corroborate his assessment of this fossil as a somewhat more primitive species of that genus. The record is far north of the modern range of *Bucorvus* in sub-Saharan Africa, and indicates that bucerotids should be looked for in Tertiary deposits of the modern Palearctic region.

2. *Upupidae*

The only mention of hoopoes in the Tertiary is Mourer-Chauviré's listing of the Upupidae in the Eo–Oligocene Phosphorites du Quercy, France, although it is not clear whether her concept of the family includes the Phoeniculidae. The only paleospecies named so far is *Upupa antaios* Olson, 1975c, from the Quaternary of St. Helena Island in the South Atlantic. This was a large species with reduced wings.

3. *Phoeniculidae*

Wood-hoopoes are now restricted to sub-Saharan Africa, but are known from fossils from the Tertiary of Europe. Ballmann (1969b) referred bones from the early Miocene (early Burdigalian) of Bavaria to the Phoeniculidae, genus and species undetermined. A somewhat older humerus from the early Miocene (Aquitanian) of France that Milne-Edwards (1867–1871) thought related to *Limnatornis* (see Coliidae) was also referred to the Phoeniculidae by Ballmann (1969b).

H. PICIFORMES

As I restrict it (Olson, 1983a), this "order" now consists only of the four families of the former suborder Pici. Of these, the Ramphastidae, which should probably be ranked only as a subfamily of the Capitonidae, have no significant fossil record. At the South African Museum I have examined specimens of Indicatoridae from the early Pliocene at Langebaanweg, South Africa; these are the only fossils yet known of the family.

The modern barbets, Capitonidae, occur in both the New World and Old World tropics. All the fossil occurrences of the family, however, are from more northern areas. Ballmann (1969b) described a new genus, *Capitonides*, with two species, *C. europeus* and *Capitonides* sp., from the early Miocene (early Burdigalian) of Bavaria. He also referred a carpometacarpus from the mid to late Miocene deposits at La-Grive-St.-Alban, France, to the Capitonidae (Ballmann, 1969a). In describing another species, *Capitonides protractus*, from the middle Miocene Nördlinger Ries in Southern Germany, Ballmann (1983) determined that *Capitonides* is very closely related to the living genus *Trachyphonus* and confirmed Swierczewski and Raikow's (1981) observation that *Trachyphonus* is the most primitive of the extant barbets. Additional fossils of Capitonidae have been recovered from the early Miocene (Hemingfordian) Thomas Farm Local Fauna in central Florida (P. Brodkorb, personal communication).

The woodpeckers, Picidae, have a poor fossil record. I have examined a few fossils of a medium-sized woodpecker from the middle Miocene (late Barstovian) of New Mexico; this seems to be the earliest known occurrence of the family. Ballmann (1976a) assigned the proximal end of an ulna from the late Miocene of the Gargano Peninsula, Italy, to the Picidae. *Pliopicus brodkorbi* Feduccia and Wilson, 1967, and *Palaeonerpes shorti* Cracraft and Morony, 1969, both from the early Pliocene Ogallala Group in Kansas and Nebraska, respectively, are each known from a single end of a hindlimb element. Because of the relative homogeneity of postcranial elements in modern North American woodpeckers, it may be doubted that either of these represents an extinct genus. From the late Pliocene (Blancan) of Texas, Brodkorb (1971a) has described a woodpecker of the ivory-billed group as *Campephilus dalquesti.*

I. PASSERIFORMES

Although passerines are the dominant land birds in almost all modern faunas, their fossil record is as yet very sketchy. Because of the difficulty in identifying passerine bones to family, paleontologists often devote little attention to them. Some of the most significant paleontological information about passerines concerns their absence. All of the supposed passerines so far named from Eocene and Oligocene beds that have been reexamined have proven to be referable to some other order. One of the best known of these is *Palaeospiza bella* Allen, 1878, based on most of a skeleton in two slabs from the "middle" Oligocene (Orellan) Florissant shales in Colorado (not Upper Miocene as given in Brodkorb, 1978). Allen (1878), and also Wetmore (1925), who restudied the specimen and erected a new family for it, considered *P. bella* to be an oscine passerine. Brodkorb (1978, p. 216) placed it in Incertae Sedis, stating that "even the ordinal assignment may be incorrect." I reexamined the holotype and found that, although it could benefit greatly from further preparation, several characters can nevertheless be discerned that absolutely preclude *Palaeospiza* from being a passerine. Because it is anisodactyl it is most likely some sort of coraciiform.

An increasing amount of new evidence has not altered the view (Feduccia, 1977a; Olson and Feduccia, 1979b) that passerines did not become prevalent in the Northern Hemisphere until the Miocene, whereas before that the dominant group of arboreal birds there was the Coraciiformes. A good many small land birds are now known from the early Eocene (Wasatchian) Green River Formation of the western United States, the early Eocene (Ypresian) London Clay, and the middle Eocene (Lutetian) Messel oil shales in Germany. Not one is a passerine. Nor has a single passerine been identified in Oligocene deposits from North America. In the very extensive collections of fossil birds from the Tertiary of France, the earliest passerine occurs in deposits from Gannat, Département Alliers, that correspond to the Coderet mammalian biozone, so C. Mourer-Chauviré (personal communication) would place the appearance of passerines in France just before the end of the late Oligocene. Because the Passeriformes must have existed before then, Feduccia and Olson (1982) hypothesized that the order may have originated in the Southern Hemisphere and did not spread from there until the mid-Tertiary.

The earliest passerines hitherto named are *Lanius miocaenus, Motacilla humata*, and *M. major*, all described by Milne-Edwards (1867–1871) from the Lower Miocene (Aquitanian) deposits near Langy, France. Brodkorb (1978) listed the last two as Aves Incertae Sedis but carried *Lanius miocaenus* in the Laniidae. All three do appear to be passerines, but nothing further can be said about their relationships without extensive comparisons, if then. There are also several passerines among the material from the early Miocene (Hemingfordian) Thomas Farm local fauna in central Florida (P. Brodkorb, personal communication). In the early Miocene (early Burdigalian) deposits at Wintershof West, Bavaria (Ballmann, 1969b), passerine fossils outnumber all other birds combined.

Howard (1957b) described a medium-sized passerine skeletal impression from the middle to late Miocene (Mohnian) of California as *Palaeoscinis turdirostris*, creating for it a new family Palaeoscinidae. The affinities of this bird lie with some of the more generalized oscines such as the Pycnonotidae, Bombycillidae, and Corvidae. In the Smithsonian collections are a few bones of passerines of similar size and relationships from the middle Miocene (Barstovian) Calvert Formation of Chesapeake Bay.

From the early Miocene of Vieux-Collonges, France, Ballmann (1972) has identified the proximal end of a humerus as that of a lark (Alaudidae), and he mentions the occurrence of other oscines in the same deposits. By the middle to late Miocene, passerines are common and diverse in deposits from France, Germany, and Italy, but the majority have not been named or even identified to family (Milne-Edwards, 1867–1871; Ballmann, 1969a,b, 1973). Most appear to be oscines, and none of these passerines, or those mentioned above, appears to be referable to the New World nine-primaried oscine group.

Corvus larteti Milne-Edwards, from the middle Miocene of Sansan, France, was listed in the Corvidae by Brodkorb (1978), although it would be desirable to check its generic and familial affinities. Brodkorb (1972) named a new corvid (*Miocitta galbreathi*), based only the the distal end of a humerus, however, from the late Miocene of Colorado. Several late Pliocene corvids have also been named (see Brodkorb, 1978).

Although from a passerine, the material from the middle Miocene of Beni Mellal, Morocco, identified as *Luscinia* cf. *megarhyncha* by Brunet (1961), is unlikely to be correctly identified even to family. Ballmann (1973) tentatively identified a tarsometatarsus from the late Miocene of the Gargano Peninsula in Italy as belonging to the Sylviidae. Specimens indistinguishable from the distinctive tarsometatarsi of *Sitta* have been recovered from La-Grive-St.-Alban in France (Ballmann, 1973; personal communication), thus suggesting the probable existence of nuthatches in the mid to late Miocene.

There are only two published records of any of the New World nine-primaried oscine group in the Tertiary, other than latest Pliocene. The earliest is a rostrum of a sparrow from the late Miocene (late Clarendonian or early Hemphillian) of Kansas. This was originally described as *Palaeospiza hatcheri* by Shufeldt (1913), but was later made the type of a new genus, *Palaeostruthus*, by Wetmore (1925). Subsequently, Steadman (1982) showed that this rostrum could not be distinguished from rostra of the modern genus *Ammodramus* (Emberizinae) and in fact was barely separable from the modern Grasshopper Sparrow (*A. savannarum*). As Steadman (1982, p. 172) points out, "many living genera of nonpasserines have been recorded from Miocene deposits and an improved fossil record may well prove the widespread existence in the Miocene of modern genera of passerines as well." Steadman and McKitrick (1982) identified three fragments of humeri from the Pliocene (late Hemphillian) of Mexico as belonging to the emberizine genus *Passerina*, establishing the possibility of the presence of these buntings in Mexico approximately 4 million years ago.

The only Tertiary record of a suboscine is Ballmann's (1969b) interesting report of an indeterminate species of Eurylaimidae from the early Miocene of Wintershof West, Bavaria. Modern eurylaimids are restricted to Africa and Asia, mainly in tropical areas.

X. The Waterbird Assemblage

The "waterbird assemblage" probably arose from the "basal" land birds through forms similar to the the Cariamidae and their relatives, with the most primitive remaining members of the "waterbird assemblage" surely to be found among the Gruiformes. Another possible link with the land birds might be through the Mesitornithidae, which have some features in common with herons and certain Gruiformes but are otherwise so anomalous that they defy convenient placement.

It has long been recognized that the Gruiformes and the Charadriiformes are intimately related, to the extent that it is at times difficult to separate one from the other (take, for example, the debate over the affinities of the Jacanidae). Bridging the differences are certain birds that make up what I have called the "transitional" Charadriiformes, as opposed to the "higher" Charadriiformes. The ibises (Plataleidae) belong with the transitional forms, as they are mosaics of gruiform and charadriiform characters (Olson, 1979). The Burhinidae, too, I would put here, along with a variety of late Cretaceous and early Tertiary birds in the families Graculavidae and Presbyornithidae. The latter shows the Anseriformes to have their origins in the "transitional" Charadriiformes.

The gruiform–charadriiform assemblage is to the remaining waterbirds what the "basal" land bird assemblage is to the "higher" land birds. Among the "higher" waterbirds, the Pelecaniformes, Procellariiformes, Gaviiformes, and Sphenisciformes each seem too specialized to be particularly close to the ancestry of the assemblage, so we should probably look among the Ciconiiformes, as I redraw the order, for primitive taxa close to the base of the "higher" waterbirds. I would suggest a careful investigation into the characters and affinities of *Scopus*, in particular, in this connection. Gadow (1893, p. 189), for example, found reasons to make comparisons between *Scopus* and the gruiform *Rhynochetus*. A link between the Ciconiiformes and Gruiformes would not be unexpected, inasmuch as it is likely that the "higher" waterbirds had their origin in the basal gruiform–charadriiform group.

The Ciconiiformes in turn share striking similarities with the Pelecaniformes. This is especially evident in *Balaeniceps* (Cottam, 1957) but is also seen in *Scopus* and in the Teratornithidae and Vulturidae. The Pelecaniformes in turn have been recognized as sharing similarities with the Procellariiformes. The birds in the extinct family Pelagornithidae, for example, had mainly pelecaniform characters but evidently had tarsometatarsi similar to the Procellariiformes (Section X,G,2). Several anatomical studies have linked the Phaethontidae and Fregatidae with the Procellariiformes. There is additional evidence, though as yet scanty, that the Procellariiformes, Gaviiformes, and Sphenisciformes may be each other's closest relatives (Section X,I). The phylogeny and branching pattern within this "higher" waterbird assemblage remains to be determined.

A. GRUIFORMES

If we remove the Pedionomidae to the Charadriiformes (Olson and Steadman, 1981), regard the affinities of the Turnicidae as uncertain but unlikely to be gruiform (see Olson and Steadman, 1981, pp. 21–22), and place the Otididae in the Charadriiformes after the coursers (Glareolidae), then the remaining living families of the order Gruiformes possibly constitute a fairly natural group.

There is an extensive paleontological record associated with the Gruiformes, but not all of the fossil taxa named as gruiform necessarily belong in this order. It would be tedious and probably unrewarding to discuss each of these here, although many of the species that are included in Brodkorb's (1967) and Cracraft's (1973a) treatments of the Gruiformes are mentioned in my discussions of the Cariamae and of the evolution of ostriches.

I have not attempted to treat the Diatrymidae, gigantic Paleocene and Eocene birds known from North America and Europe. This family will probably have to be included in the Gastornithidae, which is the earlier name and includes similarly gigantic birds from the Paleocene of France. A new species, *Zhongyuanus xichuanensis*, has been described in the Gastornithidae on the distal end of a tibiotarsus from the early Eocene of Honan Province, China (Hou, 1980). *Diatryma* is treated in most paleontological textbooks, but much of what has been written about it is subject to reinterpretation. I doubt that any convincing evidence has been presented that these birds belong in the Gruiformes, although this remains a possibility. Much new unpublished information exists concerning these birds, but I have only a few details of this, and I shall therefore say no more about *Diatryma*.

1. Suborder Cariamae

Before getting on with the complicated fossil history of this suborder, it is necessary to mention the only taxa that have survived as living forms, the monotypic genera *Cariama* and *Chunga* of the family Cariamidae (seriemas). These are large, long-legged, mainly terrestrial birds confined to forest and savanna, largely in Brazil and Argentina. It is certain that the phylogenetic and evolutionary significance of the seriemas, a family unfamiliar to most ornithologists, is totally unappreciated.

The association of the Cariamidae with the Gruiformes has been largely by default, as they do not clearly seem to belong in any other order. Even within the Gruiformes, however, there is no family that is obviously closely related to the Cariamidae, although the bustards, Otididae, have often been mentioned. The bustards, however, definitely belong in the Charadriiformes (Section X,D,2,h).

In their anatomy and life history, the seriemas differ vastly from bustards. To begin with, bustards are entirely terrestrial, lay their eggs in a scrape in the ground, and have highly precocial downy young, as in most Charadriiformes. Seriemas, on the other hand, are at least partly arboreal, build a nest of sticks in a tree or bush, and have completely altricial young with long, fluffy down. Osteologically, the seriemas bear no resemblance to bustards and show scarcely any similarities to the Gruiformes. Apart from its obvious terrestrial adaptations, the skeleton of seriemas is actually much more similar to that of the Hoatzin (Opisthocomidae). This is especially evident in the carpometacarpus, which, except for size, is very similar to that of *Opisthocomus* (Fig. 5). If the seriemas have any reasonably close affinity with a living family of Gruiformes, it would have to be the trumpeters (Psophiidae), as noted by Stegmann (1978). The seriemas and hoatzins appear to be part of an early radiation of primitive land birds, members of which have persisted in South America, perhaps as a result of its isolation

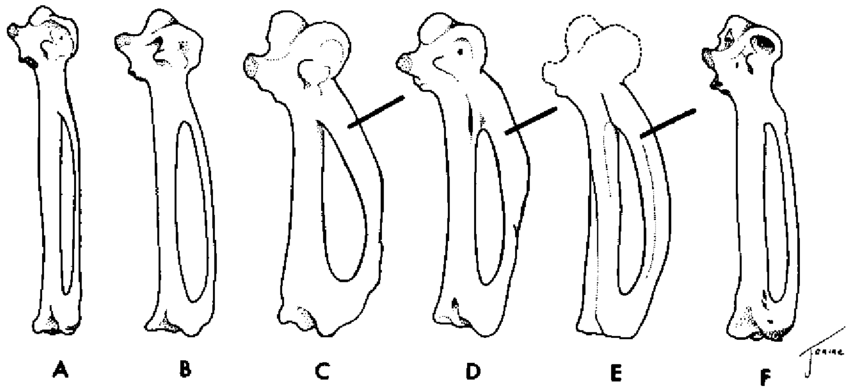

FIG. 5. Right carpometacarpi in ventral view: A, crane, *Grus canadensis* (Gruidae); B, bustard, *Tetrax tetrax* (Otididae); C, hoatzin, *Opisthocomus hoazin* (Opisthocomidae); D, seriema, *Cariama cristata* (Cariamidae); E, the late Eocene fossil *Bathornis* ("*Neocathartes*") *grallator* (Bathornithidae); F, "New World" vulture, *Coragyps atratus* (Vulturidae). Not to scale. The strongly bowed and very broad minor metacarpal (indicated by arrows) is characteristic of seriemas, hoatzins, and *Bathornis*, in which respect these three groups differ markedly from the typical Gruiformes, bustards, or vultures. Not to scale. (Drawing by Janine Higgins.)

from other continents through most of the Tertiary. The Falconidae probably represent a raptorial branch of this radiation.

Although Brodkorb (1967) placed a number of different fossil groups in the Cariamidae, some of these have been removed to the Phorusrhacidae, and the Bathornithidae can perhaps be separated as a distinct family. The relationships of *Riacama caliginea* (Ameghino) from the early Oligocene (Deseadan) of Argentina are uncertain (Mourer-Chauviré, 1981), leaving the extinct species *Chunga incerta* from the late Pliocene (Montehermosan) of Argentina (Tonni, 1974) as the only named fossil form definitely referable to the same family and subfamily as the modern species of Cariamidae.

The Cunampaiidae, from the Eocene (Divisadean) of Argentina, consists of a single species based on inadequately illustrated material. Brodkorb (1967) tentatively included the family in the suborder Cariamae, but B. Patterson and Kraglievich (1960) and Mourer-Chauviré (1981) consider its position to be uncertain. It will have no instructive value until it is restudied.

a. Phorusrhacidae and Relatives. Included the suborder Cariamae are the giant flightless predatory birds of South America known as the Phorusrhacidae (Phororhacidae of many works), as well as several other possibly related groups. I have no firsthand experience with the South American taxa and will not pretend to be knowledgeable about them. Most were described in the last century and have never been adequately reviewed or monographed. Brodkorb's "Catalogue" (1967) will lead one to most of the previous literature. Hardly anything of note has been published on the South American Cariamae since then, apart from Tonni's (1980a) compendium summarizing the geologic ages of the Cenozoic birds of Argentina.

That the Phorusrhacidae are associated with the Cariamae is the result of comparisons made by Andrews (1899b). Andrews' papers on fossil birds were usually outstandingly perceptive (with the exception of the supposed Cretaceous birds from Romania), particularly for his time, and his conclusion that the closest living relatives of *Phorusrhacos* are the seriemas has as much validity today as it did when first published (see also Mourer-Chauviré, 1981).

The Phorusrhacidae and their relatives were very large flightless predatory birds that are discussed in most general paleontological treatises or textbooks and are therefore reasonably familiar. Marshall (1978) presents a useful popular account of the discovery and radiation of some of these birds. Tonni (1980a) summarizes the temporal distribution of the "phorusrhacoids" in South America. These include the nominal taxa Brontornithinae, Paleociconiinae, Phorusrhacidae, Psilopterinae, and Prophorusrhacinae. The last two were included as subfamilies of Cariamidae by Brodkorb (1967), but all of these taxa were placed in the Phorhusrhacidae by Mourer-Chauviré (1981). An important and well illustrated recent contribution to the morphology of the Phorusrhacidae is the description of a new species, *Physornis brasiliensis*, based on much of an associated skeleton from the early Oligocene of Brazil (Alvarenga, 1982). Also in the phorusrhacoids, an additional species of *Psilopterus* was mentioned by Tonni from the early Pliocene of Buenos Aires Province, Argentina (Bondesio *et al.*, 1980).

The large phorusrhacoids in South America range in age from early Oligocene (Deseadan) to late Pliocene (Montehermosan). The most recent paper that attempts a revision of part of the South American phorusrhacoids is B. Patterson and Kraglievich's (1960) treatment of the Pliocene taxa of Argentina, which contains valuable information but is not sufficiently illustrated and is a nightmare of typographical errors. It was to have been preliminary to a proposed revision of the entire group by the late Bryan Patterson, but this was never forthcoming and is still sorely needed.

The Phorusrhacidae apparently died out by the end of the Pliocene in Argentina. Consequently, the discovery of fossils of one of these giant birds in Florida (Brodkorb, 1963a) was nothing short of phenomenal. This bird, named *Titanis walleri*, was originally known only from fluviatile deposits without stratigraphic control. Since then it has been determined that these bones of *Titanis* are late Pliocene (Blancan) in age and additional material, as yet unpublished, has been discovered in central Florida in association with mammals that are latest Blancan or earliest Irvingtonian in age. This indicates that the phorusrhacids survived in South America at least until the isthmian gap was closed in the late Pliocene, whereupon at least one species spread up through Middle America and along the Gulf Coast as far as Florida.

Perhaps even more surprising, however, was the discovery of a phorusrhacid in the Eo–Oligocene Phosphorites du Quercy in France. Mourer-Chauviré (1981) determined that the holotypical humerus of the supposed owl *Strigogyps minor* Gaillard was actually from a phorusrhacid, to which she applied the new generic name *Ameghinornis*. She also assigned some carpometacarpi and coracoids from the same deposits to *A. minor*. There is a possibility that these elements of the wing and shoulder girdle of *Ameghinornis* evolved their similarities to South American phorusrhacids in parallel, and that their similarities are due in part to degenerative reduction. Nevertheless, *Ameghinornis* was a large flightless derivative of the Cariamae, which is what phorusrhacids are, so as yet there would seem to be no grounds for denying *Ameghinornis* a place in the Phorusrhacidae.

Other members of the suborder Cariamae are also known from the Tertiary of the Northern Hemisphere—another probable indication of the antiquity of the group. The complex and still poorly comprehended history of these birds follows.

b. The Tangle of the Bathornithidae. The story of the Bathornithdae begins with Wetmore's (1927) description of four new genera and species of early Oligocene (Chadronian) birds from the famed *Trigonias* rhinoceros quarry in Weld County, Colorado. These were promulgated as two vultures (Vulturidae: *Phasmagyps patritus, Palaeogyps prodromus*), a rail (Rallidae: *Palaeocrex fax*), and a thick-knee (Burhinidae: *Bathornis veredus*). All of these were large birds represented by the ends of tarsometatarsi and tibiotarsi.

Wetmore (1927) originally considered his genus *Bathornis* to consitute a new subfamily, Bathornithinae, in the charadriiform family Oedicnemidae (= Burhinidae). Later, Wetmore (1933b) described two additional new species, *B. celeripes* and *B. cursor*, from what were said subsequently to be Lower Oligocene (Chadronian) deposits (Cracraft, 1968) in South Dakota. *B. celeripes* was abundant at the type locality, and, because Wetmore (1933b) mentions 65 distal ends of tibiotarsi, we may assume that no fewer than 33 individuals were represented. At this time, Wetmore elevated the Bathornithidae to family rank and transferred it to the vicinity of the Cariamidae in the Gruiformes. He subsequently named another species, *B. geographicus*, from the late Oligocene of South Dakota (Wetmore, 1942).

Cracraft (1968) studied the Bathornithidae and described a new species, *B. fricki*, from the early Miocene of Wyoming, thus extending the temporal

FIG. 6. Fossil tarsometatarsi of the early Oligocene genus *Bathornis* (Gruiformes: Bathornithidae): A, associated proximal and distal ends referred to *Bathornis veredus;* B, proximal end associated with the holotype of the putative vulture *Palaeogyps prodromus;* C, holotype of *Bathornis veredus;* D, holotype of the putative rail *Palaeocrex fax*. These specimens definitely belong to a single genus, and perhaps to a single species. (Photograph by Victor E. Krantz.)

When properly restored, I found that this specimen is also clearly referable to *Bathornis*, although it is slightly smaller than the type of *B. veredus*. Thus, of the four new genera proposed by Wetmore (1927) from the *Trigonias* quarry, three are actually congeneric. As first revisor, to preserve the names that are the types of higher level taxa, I designate *Palaeogyps* and *Palaeocrex* as synonyms of *Bathornis*, and the species *Palaeogyps prodromus* as a synonym of *Bathornis veredus*. It will remain for further revisionary work to establish whether the size differences between *B. veredus* and *B. fax*

Fig. 7. Proximal ends of tarsometatarsi in posterior view (top) and proximal view (bottom): A, *Bathornis veredus;* B, "*Bathornis*" *celeripes*. The simple, blocklike hypotarsus of *B. veredus* is utterly unlike that of *celeripes,* indicating that more than one genus is probably included under the name *Bathornis.* (Photographs by Victor E. Krantz.)

are due to sexual or individual variation or whether *B. fax* is a valid smaller species, in which case it may prove to be an earlier name for *B. cursor.*

We now see that the simple blocklike hypotarsus of *B. veredus* is completely unlike the hypotarsus of *B. celeripes* or *B. geographicus,* which is elongate and complex, with grooves and canals (Fig. 7). The distal end of the tarsometatarsus in these species is very similar to that in *B. veredus,* but the hypotarsal differences are much greater than one finds within genera, or even within most families of modern birds. A new genus may thus be warranted for the species with complex hypotarsi. The blocklike hypotarsus of *B. veredus* may be partly what led Wetmore to identify this portion of the skeleton as belonging to a "cathartid" vulture. A similar hypotarsus is found in the seriemas, however.

The intricacies of the *Bathornis* story do not stop here—far from it. For now we are led into the saga of one of the best publicized of Tertiary birds, the renowned "terrestrial vulture" described by Wetmore (1944) as *Eocathartes grallator* (later emended to *Neocathartes* because the name *Eocathartes* was preoccupied by a European fossil). *Neocathartes grallator* was based on an associated incomplete skeleton, including the skull and elements of both the wing and leg, from the late Eocene (Uintan) of Wyoming. The somewhat raptorial beak and the furrowed cranium of *Neocathartes* indicated to Wetmore (1944) that the bird was vulturelike. He noted that the wing and pectoral girdle were greatly reduced as compared with the Vulturidae, and this, along with the very long legs and other characters, led him to place *Neocathartes* in its own family and superfamily (Neocathartidae and Neocathartoidea). The reconstruction published with the original description of *Neocathartes* has often been reprinted and has now made the "terrestrial vulture" an integral part of the lore of avian paleontology. Well, forget it.

Neocathartes is just our old friend *Bathornis* in another guise. When I borrowed the specimen in 1980, it was somewhat the worse for wear, so that certain parts, such as the mandibular articulations, are now missing. In their proportions, and in such details as remain on them, the tibiotarsus, tarsometatarsus, and toes of *Neocathartes* not only closely resemble those of *Bathornis*, but are very close in size and structure to the species *B. veredus*, from which *Neocathartes* is separated by relatively little geological time. The wing elements, particularly the carpometacarpus, of *Neocathartes* (Fig. 5), are completely unlike those of vulturids, as Wetmore (1944) had noted, and bear a close resemblance to those of the Cariamidae. The reduced coracoid of *Neocathartes* indicates that it had lesser powers of flight, even as compared to seriemas. From my examination of the type of *Neocathartes grallator*, I conclude that *Neocathartes* and Noecathartidae are synonyms of *Bathornis* and Bathornithidae, respectively. *Bathornis grallator*, as it should now be known, provides us with further evidence that the Bathornithidae belong in the Cariamae.

c. The Idiornithidae, European Relatives of the Bathornithidae. A group of genera from the late Eocene and early Oligocene of France contribute further to our knowledge of the Cariamae. This is the Idiornithidae, consisting of the genus *Idiornis*, with four nominal species, and *Elaphrocnemus*, with three nominal species. The family was considered to be of uncertain affinity by Brodkorb (1967), who placed it after the Rallidae. Cracraft (1973a) regarded the Idiornithidae as having their closest affinities with the Bathornithidae. He referred the late Eocene species *Gypsornis cuvieri* Milne-Edwards, formerly in the Rallidae, to the Idiornithidae, but there is some doubt about this assignment (Olson, 1974d). Mourer-Chauviré (1981) reduces the Idiornithidae and Bathornithidae to subfamilies of the Cariamidae. Regardless of whether these are kept as distinct families, they are certainly most closely related to the Cariamidae and belong in the suborder Cariamae, contrary to Cracraft (1973a).

Idiornis itself has a simple hypotarsus like that in the Cariamidae and *Bathornis veredus*. Idiornithids were evidently relatively long-legged terrestrial birds like the bathornithids, but have so far been known only from the elements of the hindlimb. This seems odd in view of their comparative abundance in the Phosphorites du Quercy, and it would be strange if other elements of the skeleton had not already been collected. Indeed, I believe that certain wing bones from the same deposits that have been referred to completely different groups probably belong to members of the Idiornithidae.

The genus *Filholornis* was erected by Milne-Edwards (1892) for three species of birds from Quercy that are collectively known from the major bones of the wing. These three species differ in size. Milne-Edwards stated repeatedly that the bones of *Filholornis* bore an extraordinarily close resemblance to those of the Hoatzin (*Opisthocomus*). Gaillard (1908) illustrated the humerus (but not the other elements) of *Filholornis paradoxa*, and, while he considered the genus to be of uncertain affinities, he suggested that it also showed some resemblance to the Cracidae (Galliformes). This is probably what led Brodkorb (1964) to erect a new subfamily, Filholornithinae, which he put in the Cracidae.

Milne-Edwards, the father of avian paleontology, should have been heeded more carefully. Gaillard's (1908) illustration of the humerus of *Filholornis* shows that it does indeed bear a striking resemblance to that of *Opisthocomus*. But Milne-Edwards did not realize that this humerus, apart from its relatively shorter shaft, is equally similar to that in the Cariamidae. In fact, it is almost perfectly intermediate between seriemas and hoatzins. Now, if the Idiornithidae are related to the Cariamidae, then it follows that the cariamidlike wing bones of *Filholornis* probably belong to one of the genera of Idiornithidae. The similarity of these wing bones to those of *Opisthocomus* also supports my view that the Cariamae and the Opisthocomidae are related.

[Because this chapter was so long in manuscript, numerous portions of it were superseded by recent publications while the manuscript was still in preparation. These sections I have generally rewritten, but rather than recasting all of the above in light of Mourer-Chauviré's (1983b) excellent revision of the Idiornithidae, which I did not receive until May 1984, I have left it as it was, partly out of laziness and frustration but more to show that we arrived independently at the same basic conclusions. Mourer-Chauviré

(1983b) includes the Idiornithinae as a subfamily of the Cariamidae, although she notes that the idiornithids "are equally close to the genus *Opisthocomus* [p. 139]," and she presents extensive comparisons between the Idiornithidae and the Bathornithidae, Opisthocomidae, and Psophiidae. *Elaphrocnemus* is considered to consist of four species, with *E. brodkorbi* being described as new, and *Idiornis* to consist of five species, with *I. itardiensis* described as new. These were not all contemporaneous and some species appear to be later derivatives of earlier taxa. The wing elements of *Filholornis* belong mainly to *Elaphrocnemus*, with the former now being relegated to a junior synonym of the latter, and partly to *Idiornis*. The putative stork *Propelargus cayluxensis* Lydekker is reassigned, under that name, to the Idiornithinae, and the putative crane *Geranopsis elatus* Milne-Edwards is likewise removed to the Idiornithinae under the new generic name *Occitaniavis*. The remaining taxon in the Idiornithinae is the new genus and species *Oblitavis insolitus*, known from two humeri and a coracoid from Quercy.]

Having led the reader through a mire of nomenclature, probable misidentifications, and original observations, a brief summary is needed. The Cariamae were an important and diverse element in the Cenozoic avifaunas of North and South America and Europe. The suborder Cariamae appears to have been derived from "basal" land birds related to *Opisthocomus*. The suborder is represented in North America by the Bathornithidae (late Eocene to early Miocene) and in Europe by the Idiornithidae (late Eocene and early Oligocene). These include taxa that have hitherto been referred to families as diverse as the Vulturidae, Ciconiidae, Rallidae, Gruidae, Cracidae, and Cuculidae. The Bathornithidae and Idiornithidae were long-legged, terrestrial predators or scavengers that were closely related to, and possibly confamilial with, the South American Cariamidae. Some, such as the bathornithid *Paracrax gigantea*, were of very large size. The large predatory phorusrhacoids also belong in the Cariamae and are known principally from the early Oligocene through Pliocene of southern South America. One genus, *Titanis*, spread into North America after the isthmian connection and is known from the Plio–Pleistocene of Florida. Another, *Ameghinornis*, from the early Oligocene of France, indicates either that the Phorusrhacidae had differentiated before the breakup of Gondwanaland, or that large size and flightlessness evolved more than once within the Cariamae.

Much revisionary work remains to be done before our knowledge of the Cariamae approaches a truly satisfactory state. As mentioned, the phorusrhacoids need a thorough modern revision. It is not at all clear how many species, or even genera, are currently encompassed in *Bathornis*. The anatomy and relationships of the living seriemas should be investigated in detail. Also, in order to understand more of the habits and ecology of the fossil forms, we need detailed information on the life history of these living remnants of an ancient group of birds. Another object of research should be to determine if the Gruiformes, or a portion of them, were in fact derived from the Cariamae, perhaps through taxa resembling, or related to, the South American trumpeters, Psophiidae.

2. *The Fossil Record of Ostriches and Their Possible Relatives*

The evolution of ostriches (Struthionidae) I believe may be intimately involved with the nominal fossil families Geranoididae, Eogruidae, and Ergilornithidae. Although our knowledge of these birds is still quite imperfect and much remains to be documented about them before positive taxonomic conclusions can be drawn, the story of the ostrich may ultimately prove to be one of the most interesting in the fossil record of birds. It is conceivable that the three fossil families treated here will perhaps later be combined under the Struthionidae, much as *Hyracotherium* ("*Eohippus*") and later horses are all placed in the Equidae. The evolutionary story of ostriches might then gain as much notoriety as that of horses.

The Geranoididae consists of several large, poorly known, but superficially cranelike birds known mainly from scanty hindlimb material from the early and middle Eocene of North America. The Eogruidae are large, seemingly cranelike birds known from a fair number of better preserved specimens from the late Eocene and early Oligocene of central Asia. The Ergilornithidae consists of several species of large running birds from the early Oligocene of Asia and the late Miocene and Pliocene of Asia and Europe. In these birds the hind and inner toes are lost, making them didactylous, as are ostriches.

Most of the fossil record of the Eogruidae and Ergilornithidae has recently been summarized by Kurochkin (1981; 1982c), who has also described several new species. A partial translation of the 1981 paper was dictated to me by Kurochkin, and I have relied extensively on these notes for the following brief review of the taxa, occurrence, and material of these families. The history of the classification of these birds follows this overview.

The Geranoididae were studied by Cracraft (1969, 1973a), who recognized the following nominal taxa: *Geranoides jepseni* Wetmore, *Paragrus prentici* (Loomis), *P. shufeldti* Cracraft, *Palaeophasianus meleagroides* Shufeldt, *P. incompletus* Cracraft, *Eogeranoides campivagus* Cracraft, and *Geranodornis aenigma* Cracraft. These were all based on very fragmentary or poorly preserved specimens of tibiotarsi and tarsometatarsi and it is far from certain at this point how many genera or species can really be admitted, or whether all belong to the same family. *Geranodornis aenigma* is particularly dubious; it is also the only geranoidid described from the middle Eocene (Bridgerian), whereas all the rest are from the early Eocene (Wasatchian) of Wyoming. I have had access to a few additional specimens that are mentioned below in considering the adaptations and relationships of this family.

In the Eogruidae, *Eogrus aeola* Wetmore, 1934, was originally based on several specimens of tarsometatarsi and tibiotarsi from the late Eocene of Irdin Manha in Inner Mongolia, China. Only a single wing element was referred, a phalanx of the major digit, although I believe that a coracoid from the same site identified as that of an accipitrid (Wetmore, 1934) also belongs here (see below). *Eogrus aeola* is known from the type locality and one other late Eocene site in the southern Gobi. *Eogrus crudus* Kurochkin, 1981, is known from a single proximal end of a tarsometatarsus from Choloboldzhi Nuur in Mongolia, and was contemporaneous with *Eogrus aeola*. *Progrus turanicus* Bendukidze, 1971, was originally described in the Geranoididae, but Kurochkin (1981) places it in the Eogruidae as *Eogrus turanicus*. It is based on the distal end of a tibiotarsus from Kalmakpai, in eastern Kazakhstan, and is also from the middle Upper Eocene. Wetmore (1934) tentatively referred the distal end of a tibiotarsus from the late Miocene Tung Gur Formation in Inner Mongolia to *Eogrus;* Brodkorb (1967) later named this *Eogrus wetmorei*. Because the genus *Eogrus* is not otherwise known in deposits younger than Eocene, the identity of this fragment requires confirmation.

Abundant eogruid bones from Lower Oligocene deposits at Khoer Dzan in Outer Mongolia were originally referred to *Eogrus* (Kurochkin, 1976a), but were later described as a new genus and species of Eogruidae, *Sonogrus gregalis* Kurochkin, 1981. This is represented by proximal and distal ends of tarsometatarsi, distal ends of tibiotarsi, and pedal phalanges. There are two size classes, suggesting sexual dimorphism, whereas this is not true of *Eogrus aeloa*.

The Oligocene specimens of Eogruidae proved to be very difficult to separate from bones of Ergilornithidae in the same deposits (Kurochkin, 1976a). Two species of Ergilornithidae are recognized in the early Oligocene deposits at Ergilyeen Dzo and Khoer Dzan. *Ergilornis rapidus* Kozlova, 1960, is as yet known only from two distal ends of tarsometatarsi marked by the almost complete absence of the trochlea for digit II. *Ergilornis minor* (Kozlova, 1960), was originally described in a separate genus, *Proergilornis*, that Kurochkin (1981) now considers synonymous with *Ergilornis*. Only tarsometatarsi have positively been assigned to this species. Distal ends of tibiotarsi, phalanges, and the proximal end of a humerus from Khoer Dzan were referred only to the genus *Ergilornis*, although most of these almost certainly belong to *E. minor* (Kurochkin, 1981). In *E. minor*, the trochlea for digit II is present, although it is vestigial.

Another genus of Ergilornithidae, *Urmiornis* Mecquenem, 1925, has been found in Upper Miocene and Pliocene deposits. Harrison (1981), however, has shown that the supposed stork *Amphipelargus majori* Lydekker, 1891, known from the distal end of a tibiotarsus from the late Miocene of the Grecian island of Samos, is in fact congeneric with *Urmiornis*. Unfortunately, *Amphipelargus* has priority over *Urmiornis* and must now be used for the five nominal species that have been proposed in this genus.

Amphipelargus maraghanus (Mecquenem, 1925) was described on a tarsometatarsus and a tibiotarsus from the Maragheh region in northwestern Iran, collected in deposits now known to be late Miocene (Turolian) in age and probably contemporaneous with the deposits on Samos from which *A. majori* was described (B. G. Campbell *et al.*, 1980). It is quite possible, therefore, that *A. majori* and *A. maraghanus* are synonymous. *Amphipelargus ukrainus* (Kurochkin, 1981) is based on two tarsometatarsi, the distal end of a tibiotarsus, and three pedal phalanges from three late Miocene localities in or near the Ukraine, and from two distal ends of tibiotarsi from the northern Caucasus near Armavir that were previously reported by Bendukidze (1972) as *Urmiornis maraghanus*. *Amphipelargus orientalis* (Kurochkin, 1981) was based on several tarsometatarsi, tibiotarsi, phalanges, and a fragment of cervical vertebra from lower Medial Pliocene deposits at Kalmakpai, eastern Kazakhstan, with a pedal phalanx from the middle Pliocene of Mongolia at Hirgiz-Nuur II being referred to the same species. *A. orientalis* was larger than *A. ukrainus* or *A. maraghanus*. Harrison and Walker (1982) proposed the new species *Urmiornis cracrafti* for the distal end of a tibiotarsus and portions of a femur from the late Miocene Siwalik series of Pakistan. This was distinguished from *Urmiornis* (= *Amphipelargus*) *maraghanus* mainly on the basis of smaller size, but, as Kurochkin (1981) notes, there is apparent sexual dimorphism in size in this group and it seems unlikely that *A. cracrafti* will ultimately prove distinct from all of the species of *Amphipelargus* proposed previously. In *Amphipelargus* the trochlea for digit II is entirely absent.

A problematical form is *Eleutherornis helveticus* Schaub, 1940, described from the anterior portion of a pelvis from the early middle Eocene of Switzerland. This was tentatively associated with *Struthio*, but Schaub also noted characters in which it agreed with carinates and differed from *Struthio* and all other ratites. *Eleutherornis* was eventually placed in its own family, Eleutherornithidae (Wetmore, 1951), in the Struthioniformes. Schaub himself stated that it would be unwise to base phylogenetic speculations on such fragmentary material. It is still not clear what the significance of *Eleutherornis* may be, if any, to the evolution of *Struthio*.

The Ostrich (*Struthio camelus*) is the largest living bird and is known in modern times only from Africa and Arabia, although there are historical records from the Middle East and Central Asia. Gaiduchenko and Tivanenko

(1978) have recorded eggs of *Struthio* from Holocene deposits in Transbaikalia and they raised the interesting possibility that ostriches were exterminated there by prehistoric man.

There is a relative abundance of Tertiary fossils of ostriches from Eurasia. The oldest remains yet ascribed to *Struthio* are a toe bone and egg shell fragments from the lower to middle part of the Upper Miocene of Turkey (Sauer, 1979). These were tentatively referred to the early Pliocene species *S. brachydactylus* Burchak-Abramovich. The next oldest specimens are the distal end of a tibiotarsus and a tarsal trochlea from the late Miocene (middle Sarmatian) of Moldavia, southwestern USSR, described as a new species, *Struthio orlovi*, by Kurochkin and Lungu (1970). This was smaller than the living species *S. camelus* or any of the fossil forms of *Struthio* yet discovered. An ostrich (*Struthio* sp.) the size of the living species, but differing in details of the tarsometatarsus, was reported from the late Miocene of Tunisia (Rich, 1972), and an ostrich is also known from the extensive fossil deposits at Langebaanweg, South Africa (Rich, 1980c), indicating that ostriches had dispersed to the southernmost parts of the continent by the early Pliocene.

Kurochkin and Lungu (1970) present a good review of the fossil record of *Struthio*, and I have tentatively followed their conclusions. They regard *Struthio brachydactylus*, known from much of a skeleton from the early Pliocene of Odessa Province, USSR, as a valid species that Sauer (1979, p. 496) has characterized as a "relatively small but heavily built ostrich with short and compact feet." They regard all other Pliocene and Pleistocene ostriches yet described as belonging to a single species, for which the name *Struthio asiaticus* Milne-Edwards has priority. This species had a very broad temporal and geographic range and is regarded by Kurochkin and Lungu as being the direct ancestor of the living species *Struthio camelus*. Remains of this species, to which innumerable names have been applied (see Brodkorb, 1963b; Kurochkin and Lungu, 1970), are known in deposits of early Pliocene to Pleistocene age from Greece and eastern Europe through the Ukraine and Kazakhstan to India and China. As Kurochkin and Lungu point out, this species appears to have changed in size through time and very likely may have exhibited clinal geographic differences in size over its broad range. Although their treatment may be somewhat of a nomenclatural oversimplification, it is probably a fairly accurate reflection of the evolutionary history of *Struthio* in the late Neogene and Quaternary.

There is considerable literature on the subject of fossil egg shells of ostriches or ostrichlike birds that is not without an element of interest, although the naming of new species on such material is not to be condoned. The most recent and extensive work on the subject is that of the late E. G. F. Sauer (this may be traced through the references cited in Sauer, 1979). Perhaps most significant in this line was the discovery of apparently "struthious" eggs in Miocene deposits on Lanzarote, in the Canary Islands (Rothe, 1964; Sauer and Rothe, 1972), although the identity of the birds that laid these eggs must be regarded as uncertain. A note of caution should be interjected concerning Sauer's unfortunate use of the term "aepyornith*oid*" (emphasis mine) to describe certain pore patterns found in egg shell fragments from Lanzarote, Africa, and Asia, and the intimation that the Aepyornithidae may have existed outside of Madagascar (Sauer, 1976). Such eggshell fragments were in one instance linked to a bone referred to *Struthio* (Sauer, 1979). Pore density, size, and shape have been shown to vary with egg weight (Tullett and Board, 1977) and it is unlikely that the configuration of pores has much taxonomic significance. There is no acceptable evidence of elephantbirds outside of Madagascar.

Apart from their paleognathous palate, the two primary attributes of ostriches are their flightlessness and the fact that they have but two toes, with distinctive, short, flattened phalanges. The geranoidid–eogruid–ergilornithid lineage also acquired these same attributes.

It is quite possible that most, if not all, of these fossil forms were flightless. Of great interest in this connection is the proximal end of a humerus from Lower Eocene (Wasatchian) deposits in Wyoming that, although unassociated, is of a size compatible with the hindlimb elements of geranoidids that were collected in the same vicinity (S. L. Olson and A. Feduccia, unpublished). This humerus is unquestionably from a flightless bird and in fact is remarkably similar to the proximal end of a humerus that Kurochkin (1976a, 1981) assigned to *Ergilornis* sp.

I believe that *Eogrus aeola* may have been flightless as well. The phalanx of the major digit that was referred to this species by Wetmore (1934, p. 9) was "suggestive of modern cranes but is somewhat smaller and appears slighter and weaker as though it came from a wing used only moderately." A coracoid from the type locality of *Eogrus aeola* was identified by Wetmore (1934) as that of an undetermined species of buteonine hawk (Accipitridae). This, however, is the only avian element of the pectoral girdle or wing found at Irdin Manha, other than the single finger bone. On examining the specimen, I find that it bears no similarity to the coracoid in the Accipitridae, but instead is much more like that in the Gruiformes. The sternal end is quite thin, however, and the procoracoid reduced, suggesting poor flight capability or even flightlessness.

The proximal end of a humerus from the early Oligocene at Khoer Dzan was demonstrated by Kurochkin (1976a, 1981) to have come from a flightless bird and he assigned it to *Ergilornis*. We now know, however, that at least one of the geranoidids had a very similar humerus and that *Eogrus*, too, may have been flightless, so this specimen could have come as easily from the eogruid *Sonogrus* as from *Ergilornis*, since both occur in the same deposits.

Two interesting undescribed specimens from Khoer Dzan shown to me by E. N. Kurochkin also possibly pertain to *Sonogrus* or *Ergilornis*, on the basis of size and the abundance of those forms in the deposits there. One is a peculiarly flattened distal end of an ulna having almost the appearance of that of a flightless alcid. The distal end of the ulna in *Struthio* is also very flattened. The other specimen is the dorsal portion of a cranium, which, although much smaller than that of *Struthio*, has a distinct impression for a salt gland running from inside the posterior margin of the orbit up onto the dorsal surface of the cranium, exactly as in *Struthio*. Furthermore, there appear to be articulating surfaces for the lachrymal and a posterior accessory bone that would have completed a ring around the aperture for the salt gland, just as in *Struthio*. On the other hand, the fossil cranium shows a distinct naso-frontal hinge, indicating that the skull was not rhynchokinetic and thus not paleognathous. Therefore, if this specimen pertains to *Sonogrus* or *Ergilornis*, and if the modern ostriches evolved from one of these Oligocene forms, then the paleognathous palate of *Struthio* would have to have evolved, presumably through neoteny, since the Oligocene.

In the morphological progression from the Geranoididae, to *Eogrus*, to *Sonogrus*, to *Ergilornis*, to *Amphipelargus*, there is increasing specialization in the distal end of the tarsometatarsus and in the toes. The inner trochlea becomes progressively reduced until it becomes vestigial in *Ergilornis rapidus* and is lost altogether in *E. minor* and in all of the species of *Amphipelargus*. Likewise, the phalanges of the toes become progressively shorter and flatter (Kurochkin, 1981). Thus, in both respects, we see this lineage becoming increasingly ostrichlike through time.

The fossils assigned to the Geranoididae, Eogruidae, and Ergilornithidae definitely suggest a derivation of ostriches from birds that have otherwise been associated with the Gruiformes. The evolutionary significance of these fossils has been curiously ignored over the years, as though the fact that these birds might be closely related to ostriches could not be accomodated. Let us now trace the history of the opinions concerning the relationships of these various fossils.

At the time Wetmore (1934) erected the new family Eogruidae for *Eogrus*, he mentioned its similarities not only to the Gruidae, but also to bustards, Otididae. I have emphasized where the geranoidid–eogruid lineage led rather than where it came from, and it remains to be determined whether these birds really belong in the Gruiformes and what their closest relatives are if they do. I would emphasize here that they do not possess the features that characterize the postcranial skeleton of the volant (Houde and Olson, 1981) or flightless paleognathous birds, however.

When Cracraft (1969) first studied the Geranoididae he tended, correctly, in my opinion, to emphasize their similarities to the Eogruidae. Later, however, although he still considered these two families to "share numerous features that suggest their derivation from a common ancestor," he placed them in separate superfamilies in the "infraorder Grui," with the Geranoididae being basal to the Bathornithidae and Idiornithidae (Cracraft, 1973a, p. 108). Except for advancing the poorly represented species *Eutreptornis uintae* as being "transitional" between the Geranoididae and Bathornithidae, Cracraft offered no evidence for a relationship between these two families, nor does he seem to mention any characters that would define the superfamily Geranoidea as a monophyletic group. As with the Bathornithidae (Mourer-Chauviré, 1981), Cracraft's earlier taxonomic insights appear more acceptable than those he propounded later (Cracraft, 1973a). I have examined new and better preserved specimens from the early Eocene of Wyoming that indicate the Geranoididae to be *very* close to, almost certainly confamilial with, the Eogruidae.

Both Cracraft (1973a) and Kurochkin (1976a, 1981) are in agreement that the Eogruidae and Ergilornithidae are closely related. Kurochkin (1976a) stressed the difficulties in distinguishing the elements of eogruids from those of ergilornithids and it might questioned whether it is really advisable to maintain them as separate families. Regardless, it is now evident that the Geranoididae, Eogruidae, and Ergilornithidae form a closely knit group; it remains for future studies to determine how many families should be recognized here. How, then, have the similarities of these birds to ostriches been treated?

When Mecquenem (1908) first reported *Urmiornis* (= *Amphipelargus*), he noted that the tarsometatarsus had only two trochleae and the bird therefore must have had only two toes, as in *Struthio*. On the other hand, he mentioned apparent similarities in the tibiotarsus to wading birds such as storks. In a later publication, Mecquenem (1925) stressed the similarities to wading birds, particularly cranes, and timorously omitted any specific mention of ostriches at all, stating only that the two-toed condition was presently limited to "running birds" (*oiseaux coureurs*). He considered that the specimens either represented a teratological example of a cranelike or storklike bird, or that the species may truly have lacked the inner trochlea, as in recent "running birds," of which two options he declared to prefer the former. Here we already see the unwillingness to accept as ostrichlike anything also showing traits of neognathous birds.

Lambrecht (1933) repeated part of Mecquenem's description of *Urmiornis* without comment, and placed the genus not just in the Gruiformes, but in the family Gruidae! Burchak-Abramovich (1951) described some of the specimens that were later named *Urmiornis ukrainus* by Kurochkin (1981). He compared *Urmiornis* in detail with *Struthio*, considered the possibility of convergence, and concluded that the similarities between the two genera must be due to relationship. His views have been largely overlooked or ignored since then, however.

In 1960, Kozlova described *Ergilornis* and *Proergilornis* from the early Oligocene of Mongolia, creating the family Ergilornithidae for them. This she placed in the order Gruiformes, but she made no mention of *Struthio* or *Urmiornis*, despite their being the only other genera in the class Aves that are known to have lost the inner toe.

Brodkorb (1967, p. 154) was the first to refer *Urmiornis* to the Ergilornithidae, which he placed in the Gruiformes. He was brave enough to suggest that the family was "possibly related to Struthionidae." Kurochkin (1976a, 1981) refers the Eogruidae and Ergilornithidae to the Gruiformes but does not discuss the possibility of relationships with *Struthio*. Cracraft (1973a) attributed the ostrichlike characters of the Ergilornithidae to convergence. Feduccia (1980b) was the only author since Burchak-Abramovich (1951) to stress the obvious connection between the smaller two-toed flightless running birds of the Tertiary of Asia and the ostriches, thereby provoking a caustic reply from Cracraft (1981a).

As I have indicated elsewhere (Olson, 1982c), Cracraft's reasons for denying an association between *Struthio* and the ergilornithids do not satisfy his own criteria for determining relationships. Cracraft (1973a, p. 118) lists 10 characters of the tarsometatarsus in which "ergilornithids differ from the struthionids and agree with the Gruoidea" as evidence of convergence. These are difficult to evaluate because it is not clear from his discussion on which genus each character is based. Characters 7 through 10, referring to the proximal end of the tarsometatarsus, must have been taken from *Urmiornis* (= *Amphipelargus*), because that part of the skeleton was not known in other ergilornithids at the time. But considering that *Urmiornis* was contemporaneous with fossil forms of *Struthio* and may have diverged from the line giving rise to *Struthio* as long ago as the Oligocene, one would expect to see some differences in more than 20 million years of evolution. After all, if there were no differences between *Urmiornis* and *Struthio* they would have been put in the same genus. If differences between taxa are not evidence of lack of relationship (Cracraft, 1981a), then no evidence in support of a hypothesis of convergence between the Ergilornithidae and Struthionidae has ever been advanced.

Why have not the ergilornithids and eogruids been widely acclaimed and publicized as the relatives of ostriches? The reason lies in the fact that the palate in the living ostrich is paleognathous. The reverence given to the possession of this character has outweighed all other considerations.

For perspective, let us summarize the possible sequence of events in the evolution of the ostrich from the standpoint of the paleontologist. The preliminary indications are that the Geranoididae, or at least some of them, were already flightless by the early Eocene. Birds of this group, which likely originated in North America, appear to have given rise to the subsequent radiation of eogruids and ergilornithids observed in Asia from the late Eocene onward. If so, they must have entered the Old World across the North Atlantic land connection during or before the early Eocene.

In the late Eocene of central Asia are running birds of the genus *Eogrus* that also may have been flightless and at the very least had reduced flying ability. The trochlea for the inner toe is reduced in *Eogrus* (Wetmore, 1934; Kurochkin, 1976a, 1981), more so than in the Geranoididae or in the Gruidae, for example. The Eogruidae persisted into the Oligocene in the genus *Sonogrus*, in which the tarsometatarsus and toes are somewhat more specialized than in *Eogrus*.

At some point prior to the early Oligocene the Eogruidae also gave rise to birds in which the inner toe was lacking or at best vestigial. In one of these, *Ergilornis minor*, the inner trochlea is present but greatly reduced, whereas in the other, *E. rapidus*, it is barely indicated. Both of these forms coexisted, along with *Sonogrus*, in the early Oligocene of central Asia. At least one, and perhaps all, of these birds were flightless.

Birds that may be derivatives of each of the early Oligocene lineages occur in Neogene deposits. The two-toed running bird *Amphipelargus*, known from the late Miocene and Pliocene of Eurasia, totally lacks the inner trochlea and thus may be descended from *Ergilornis rapidus*. A flightless two-toed running bird that retains a vestigial inner trochlea, and thus may have descended from *Ergilornis minor* or *Sonogrus*, still exists today—*Struthio*. Fossils of *Struthio* first appear in the late Miocene, so there is a gap in the record of roughly 20 million years, during which considerable evolution can be expected to have taken place. This gap is probably due mostly to the near absence of early and middle Miocene sediments in Asia.

The earliest ostrich based on diagnostic material, *Struthio orlovi*, from the late Miocene of eastern Europe, was smaller than any of the later forms, as were its Oligocene ancestors. Kurochkin and Lungu (1970) point out that the ancestors of *Struthio orlovi* would not have occurred in eastern Europe in the early Tertiary, as this area was then forested; an open steppe environment did not prevail here until the late Miocene. Such environments were present throughout most of the Tertiary in central Asia, however, where the eogruid and ergilornithid presumptive ancestors of ostriches are found. Ostriches were widespread in the Pliocene and are a typical component of *Hipparion* faunas (Kurochkin and Lungu, 1970). There appear to have been at least two lineages of *Struthio* in Europe and Asia at this time, *S. brachydactylus* and *S. asiaticus*, the latter being ancestral to the living *S. camelus*. Had *Struthio asiaticus* become extinct and left no living descendant, can there be any doubt that paleontologists would have reconstructed the history of *Struthio* from the palateless fossil record much as I have outlined above?

According to Cracraft (1974), ostriches were derived from a common ancestor with other ratites that inhabited Gondwanaland in the Mesozoic. If so, then how does one explain *Struthio* appearing in the Miocene of Europe and Asia with no known antecedents? The didactylous condition of the ostrich is unique among living birds. Is it parsimonious to postulate that flightless two-toed running birds in the Tertiary of Asia were derived once from a cranelike Paleogene ancestor and again from a hypothetical ratite that somehow got to Asia from Gondwanaland and has presumably been there since the Mesozoic without leaving any fossil record prior to the late Miocene? I think not. A better appreciation of the possible evolutionary significance of the Ergilornithidae and their relatives is long overdue.

3. *Remainder of Gruiformes*

Of the gruiform families that do not belong in the Cariamae or are not possibly involved in the evolution of the ostrich, the Psophiidae, Heliornithidae, Rhynochetidae, Eurypygidae, and Mesitornithidae have no published fossil record.

a. Rallidae. Elsewhere I have treated the fossil history of the Rallidae in some detail (Olson, 1977a). Apart from noting some middle Pliocene rails described by Kurochkin (1980) from western Mongolia, and a new genus and species (*Youngornis gracilis*) from the middle Miocene of China (Yeh, 1981), there is little new to be added to that account. *Youngornis* is based on a nearly complete skeletal impression in which, however, as illustrated, the humeri and ulnae appear much too robust, and the latter too curved, for any member of the Rallidae. The overall appearance of the specimen is more galliform in nature, and the relationships of this genus for the time being should be regarded as uncertain.

The Eocene tibiotarsi previously referred to the Rallidae cannot be assigned with certainty to that family (Olson, 1977a, p. 339). The earliest certain rails thus come from the late Oligocene to early Miocene of Europe. Fossil rails occur fairly regularly in various younger Tertiary deposits from Europe, Asia, and North America. The precise relationships of the earlier fossils to living genera of Rallidae still have not been determined and thus there is still little that the fossil record tells us about the early history of the family.

b. Apterornithidae. The strange birds from the Quaternary of New Zealand that are properly known as *Apterornis* Owen, which name has a week's priority over *Aptornis* Owen, have usually been thought of as rails but most definitely are not (Olson, 1977a). They were large, flightless birds with a unique jaw mechanism. Fully deserving of family status, *Apterornis* is not particularly closely related to any living family of Gruiformes but has a few suggestive resemblances to the Rhynochetidae of New Caledonia. *Apterornis* is nevertheless very different from *Rhynochetus.* Two forms of *Apterornis*, whether species or subspecies, may be separated on size—*otidiformis* (Owen) on the North Island and the larger *defossor* Owen on the South Island (S. L. Olson and R. L. Zusi, manuscript).

c. Gruidae (Including Aramidae). As used by Brodkorb (1967), the family Gruidae was much too inclusive. Cracraft (1973a) removed such taxa as *Eogrus, Geranoides,* and other early Paleogene taxa. Thus restricted, the Gruidae becomes a somewhat more manageable group. *Palaeogrus geiseltalensis* Lambrecht, from the middle Eocene of Germany, is synonymous with the palaeognathous ratite *Palaeotis weigelti* (P. Houde, personal communication, see also Section VIII,B). The species *Geranopsis elatus* Milne-Edwards was considered to be a nongruid by Cracraft (1973a), and it was assigned to the Idiornithidae by Mourer-Chauviré (1983b) as the type of a new genus, *Occitaniavis.* For the time being I would discount the Eocene species *Palaeogrus princeps* Portis, and *P. hordwelliensis* (Lydekker), as they are based only on distal ends of tibiotarsi. Cracraft (1973a, p. 84) noted that the holotypical tibiotarsus of *Eobalearica tugarinovi* Gureev is badly preserved, and he considered it unlikely to be a gruid; E. N. Kurochkin (personal communication) says that it is almost certainly referable to *Palaeogrus.* The identity of the holotypical rostrum of *Probalearica problematica* has already been questioned (Olson and Feduccia, 1980a).

Geranopsis hastingsiae Lydekker is known from a coracoid from the late Eocene Hordwell beds of England. This has the large pneumatic fossa in the sternal end of the dorsal surface that is characteristic of cranes. It is likely, therefore, that this species does in fact belong in the Gruidae. Cracraft (1973a) considered *Geranopsis* to be closest to *Balearica* among living cranes.

The species *Palaeogrus excelsus* (Milne-Edwards) is known from fairly abundant material from the early Miocene (Aquitanian) of France. Although clearly a crane, its inclusion in the Eocene genus *Palaeogrus,* the type of which is *P. princeps,* is suspect. Cracraft (1973a) did not present specific comparisons of *P. excelsus* with any modern members of the Gruidae.

The genus *Pliogrus* was created by Lambrecht (1933) for his species *P. germanicus,* known only from the distal end of a tibiotarsus and a fragment of scapula from the early Pliocene of Germany, and *Grus pentelici* (Gaudry) from the early Pliocene of Greece, to which specimens from France and Hungary were later assigned. Brodkorb (1952) designated *P. germanicus* as the type of *Pliogrus;* C. Mourer-Chauviré, J.-C. Balouet, Y. Jéhenne, and E. Heintz (manuscript) consider *Pliogrus* to be a valid genus but return the species *pentelici* to the genus *Grus.* They also describe a new species of *Grus* from the distal portion of a tarsometatarsus from the late Miocene (middle Turolian) of Afghanistan. This species is apparently different from *Grus miocenicus* Grigorescu and Kessler, 1977, also known from a tarsometatarsus from the Miocene (middle Sarmatian) of Romania (C. Mourer-Chauviré, personal communication).

I have examined the holotypical distal end of a tarsometatarsus of *Grus conferta* A. Miller and Sibley, from the early Pliocene of California, and found it to differ from modern species of *Grus* to the extent that its generic placement may be doubted. *Grus nannodes* Wetmore and Martin, from the Pliocene of Kansas, is known only from the distal end of a carpometacarpus, which is minimally diagnostic. Two species of *Grus,* one very large, are represented in the Lower Pliocene (Hemphillian) marine deposits at Lee Creek, North Carolina (S. L. Olson, unpublished).

From North America there is now a considerable representation of small to medium-sized cranes that are closely related to the modern African crowned cranes of the genus *Balearica.* I have examined specimens ranging in age from early Oligocene (Chadronian) to late Miocene (late Clarendonian or early Hemphillian). Some of these are known from complete or nearly complete skeletons. The putative limpkin *Aramornis longurio* Wetmore, from the early Miocene (late Hemingfordian) of Nebraska is in fact one of these *Balearica*-like cranes, as is *Probalearica crataegensis* Brodkorb from the early Miocene (Hemingfordian) of Florida. The more extensive new material shows that the latter is almost certainly referable to the genus *Aramornis,* which in turn may not be separable from *Balearica.* It is not certain whether any of the fossil gruids from the Old World belong with the *Balearica*-like cranes, although this is likely (see *Geranopsis,* above). Kurochkin and Ganya (1972) described *Probalearica moldavica* from the late Miocene (middle Sarmatian) of the Moldavian SSR, but it is known so far only from the distal end of a tibiotarsus.

My investigation into the morphology and literature of limpkins leads me to the conclusion that the Aramidae are no more than a subgroup of the Gruidae. It has long been recognized that the osteology of *Aramus* is purely cranelike, but it has been argued that limpkins are somehow intermediate between the Gruidae and the Rallidae because they supposedly have the internal anatomy of the latter. This fallacy, once having become established in the literature, was repeated until its origins were forgotten. I traced the idea that *Aramus* has rail-like internal organs back through the literature to its original source—Audubon's (1838) *Ornithological Biography.* Audubon had sent two specimens of *Aramus* in spirit for William MacGillivray to dissect in an attempt to resolve whether limpkins were more closely related to rails or to herons (Ardeidae), which was the debate in Audubon's time. MacGillivray's inspection of the viscera revealed, not surprisingly, that *Aramus* was more similar to the Rallidae than to herons. Thus, ever since Audubon it has been repeated that *Aramus* has the internal organs of a rail, whereas, in fact, no comparisons of it were ever made with the Gruidae. Not only is the osteology of *Aramus* very similar to that of the Gruidae (and distinct from the Rallidae), but an extensive comparison of the myology of *Aramus* (Allen, 1962) revealed that its musculature is also cranelike, being much more similar to that of *Balearica* than to either *Grus* or the Rallidae.

A variety of fossil taxa have been assigned to the Aramidae, most of them wrongly. Of those that Cracraft (1973a) recognized in this family, only *Badistornis aramus* Wetmore, known from a tarsometatarsus from the "middle" Oligocene (Orellan) of South Dakota, appears to be closer to *Aramus* than to some other genus of Gruidae. *Aramornis*, as I have already mentioned, is more closely related to *Balearica*. The distal end of a humerus from the late Oligocene (Whitneyan) of South Dakota that Wetmore (1942) described as *Gnotornis aramiellus* and placed in the Aramidae, is definitely not from any kind of limpkin and appears to be a heron (see Section X,B, Ardeidae). Cracraft (1973a) could find no evidence that the early Oligocene (Deseadan) South American species *Aminornis excavatus* Ameghino and *Loncornis erectus* Ameghino belonged in the Aramidae. The illustration (fig. 45 in Cracraft 1973a) of the holotype of *Anisolornis excavatus* Ameghino, from the early Miocene (Santacrucian) of Argentina, more closely resembles the tarsometatarsus in the Psophiidae than that of *Aramus*.

B. FAMILY INCERTAE SEDIS ARDEIDAE

The herons form a very distinctive family the precise relationships of which have never been determined. No acceptable evidence exists for associating them with the storks; Ligon (1967) placed these two groups in separate orders (Ardeiformes and Ciconiiformes) to emphasize their dissimilarity, and Rea (1983) likewise rejects a close relationship between herons and storks. There are, however, rather striking resemblances between the Ardeidae and the Mesitornithidae in pterylosis and the morphology of the tarsometatarsus (Olson, 1979).

The fossil record of herons is as good an example as exists of the perils one may encounter in uncritically following catalogs. Brodkorb (1963b) lists 17 paleospecies of Ardeidae going back as far as early Eocene. Yet virtually all of these either are not herons or are not distinguishable from living species.

Proherodias oweni Lydekker, based on a sternum from the early Eocene

(Ypresian) of England, was removed from the Ardeidae by Harrison and Walker (1978), although their reasons for placing it with the Presbyornithidae are not at all convincing. Shufeldt's supposed heron *Botauroides parvus*, of middle Eocene (Bridgerian) age in Wyoming, was later assigned to the "piciform" family Primobucconidae (Feduccia and Martin, 1976) and it is certainly not a heron (but see Section IX,B,1). The species Shufeldt named *Eoceornis ardetta*, also from the Bridgerian of Wyoming, and based on a fragmentary sternum, is likewise unlikely to be a heron, if it can be identified at all.

The holotypical ulna of *Goliathia andrewsi* Lambrecht, from the late Eocene or early Oligocene of Egypt, was considered to belong to the Pelecanidae by Harrison (1979c), whereas Brodkorb (1980) referred it to the Balaenicipitidae. The published illustrations of the specimen support Brodkorb's view, as does the fact that a more diagnostic element of a balaenicipitid is now known from the same area (T. Rasmussen, personal communication). *Ardea piveteaui* Brunet, 1970, was based only on the shaft of an ulna from the late Eocene (Ludian) of France that cannot possibly be identifiable to genus or species. Harrison (1979c) considered that it was not a heron in any case. *Ardea rupeliensis* Van Beneden, 1873, from the early Oligocene (Rupelian) of Belgium, is practically a *nomen nudum* and was regarded as Incertae Sedis by Brodkorb (1978). Brodkorb (1980) also placed *Ardeacites molassicus* Haushalter, from the Mio–Pliocene of Bavaria, in Incertae Sedis, as the illustration of the holotypical humerus, now lost, is not heronlike.

Ardea similis Fraas, later removed to *Botaurites* by Lambrecht (1933), is based on the distal end of a tibiotarsus from the middle Miocene Steinheim basin in southern Germany. The illustrations in Fraas (1870) show clearly that this specimen is from a large phasianid, possibly *Miophasianus altus*.

Among several species of birds named from the late Miocene of Germany by von Ammon (1918) were two supposed herons: *Ardea brunhuberi*, based on the proximal end of a carpometacarpus, and *Botaurites avitus*, based on a cervical vertebra. Brodkorb (1980) showed that the carpometacarpus was from a cormorant, and he used the new combination *Phalacrocorax brunhuberi* for this species in the erroneous belief that this was an earlier name for the species *Phalacrocorax praecarbo* von Ammon, from the same deposits. Although the carpometacarpus of what was to become "*Ardea*" *brunhuberi* was illustrated in an earlier publication by von Ammon (1911), it was neither named nor described therein. This name also dates from von Ammon's 1918 publication, although Brodkorb's action as first reviser nevertheless makes *P. praecarbo* a synonym of *P. brunhuberi*. In examining von Ammon's (1981) illustrations of the cervical vertebra of the supposed heron *Botaurites avitus*, from the same deposits, I have found that this species, too, is almost certainly from a cormorant of the same size, so that this name likewise is best synonymized with *Phalacrocorax brunhuberi*.

Brodkorb (1980) regarded the holotypical femur of *Ardea lignitum* Giebel, from the late Pliocene of Germany, to be from an owl of the genus *Bubo*. In a similar vein, my examination of Milne-Edwards' (1867–1871) illustration of the distal end of the holotypical humerus of *Ardea perplexa* from the middle Miocene at Sansan, France, revealed that this is also from a large owl. A late Miocene humerus that Milne-Edwards (1867–1871) named *Ardea aureliensis* has not been illustrated or restudied and its affinity with the Ardeidae thus remains to be confirmed.

The material of the extinct genus and species *Palaeophoyx columbiana* McCoy, from the Pleistocene of Florida, was shown to consist of the coracoids of the modern bittern *Botaurus lentiginosus*, and the ulna of the modern barn owl *Tyto alba* (Olson, 1974a). It is possible, but highly unlikely, that *Butorides mauritianus* Günther and E. Newton, from late Quaternary deposits on Mauritius, is specifically distinct from the wide-ranging modern species *B. striatus*. Thus, of the 17 paleospecies of herons in Brodkorb's (1963b) catalog, only *Proardea amissa*, from the Paleogene of France, *Ardea polkensis* and *Nycticorax fidens*, from the Pliocene of Florida, and *Nycticorax megacephala* Milne-Edwards, from the Quaternary of Rodriguez, are actually herons that are likely to be separable from modern species.

Although the holotypical tarsometatarsus of *Proardea amissa* (Milne-Edwards, 1892), from the Eo–Oligocene Phosphorites du Quercy, was never illustrated, C. Mourer-Chauviré (personal communication) assures me that it is from a heron, and it is thus the earliest known member of the family. From the Oligocene Fayum series in Egypt there are several true herons and a peculiar heronlike rostrum that differs greatly from all living members of the Ardeidae and will have to be assigned to a new family (T. Rasmussen, personal communication). The next oldest named form of ardeid would probably be *Gnotornis aramiellus* Wetmore, 1942, originally described as a limpkin (Aramidae: Gruiformes) from the distal end of a humerus from the late Oligocene (Whitneyan) of South Dakota. I have examined the holotype and found that it is definitely not from a limpkin, although it is very similar to the humerus in the Ardeidae. It does not appear to be referable to any modern genus. Slightly younger is *Proardeola walkeri* Harrison, 1979c, described from a complete tarsometatarsus from early Miocene (Aquitanian) deposits at Chavroche, Allier, France. *Proardeola* is possibly synonymous with *Proardea* (C. Mourer-Chauviré, personal communication).

Other species described since Brodkorb (1963b) that have been assigned to the Ardeidae are all Neogene or Pleistocene in age and were described from single bones: *Zeltornis ginsburgi* Balouet, 1981, from the early

Miocene (probably late Burdigalian) of Libya; *Ardeagrandis arborea* Kurochkin and Ganya, 1972, from the late Miocene (Sarmatian) of Moldavia, USSR; *Nyctanassa kobdoena* Kurochkin, 1976b, from the middle Pliocene of western Mongolia (generic allocation doubtful); *Ardea howardae* Brodkorb, 1980, from the late Pliocene of Ethiopia; *Botaurus hibbardi* Moseley and Feduccia, 1975, from the late Pliocene of Kansas, and *Butorides validipes* K. E. Campbell, 1976a, from the Pleistocene of Florida.

Because the Paleogene taxa of herons have not been adequately compared with living genera in order to determine their affinities within the Ardeidae, there is little that is informative about the sketchy fossil history of the Ardeidae, a family that superficially once appeared to have a rather good fossil record.

C. Family Incertae Sedis Podicipedidae

In looking beyond their obvious specializations for diving, I cannot see that the grebes (Podicipedidae) would be out of place in the Gruiformes. This is not a new idea, but it has received some more recent support from studies of the musculature of the neck (Zusi and Storer, 1969, p. 48). The similarities in the skull of the grebe *Podilymbus*, for example, and that of subgrebes (Heliornithidae), or even rails (Rallidae), are sufficient to suggest that a gruiform relationship for grebes should be thoroughly explored.

Unfortunately, despite their aquatic habits and dense bones, grebes have a relatively poor fossil record. Until 1982, the earliest known grebe was *Podiceps oligocaenus*, based only on the distal end of a femur. This came from the John Day beds in northern Oregon, which were originally attributed to the Oligocene, but later to the early Miocene (Brodkorb, 1963b). Svec (1982) described a new genus and species, *Miobaptus walteri*, apparently most similar to *Tachybaptus*, from the proximal end of a humerus, a coracoid, and several pieces of tarsometatarsi from Lower Miocene (Aquitanian) deposits at Dolnice, Cheb Basin, Czechoslovakia.

M. A. Bell has forwarded for my examination some associated wing bones of a medium-sized grebe from diatomites of the Truckee Formation in Nevada, which are early Pliocene or at most late Miocene in age (Bell, 1974). There is a species of *Podiceps* from the early Pliocene (Hemphillian) at Lee Creek, North Carolina, that is possibly the same as *Podiceps pisanus* (Portis) from the Pliocene of Italy. Reference to other Pliocene grebes from California, Arizona, Kansas, and Idaho may be found in Brodkorb (1963b) and Murray (1967). These are all very similar to extant grebes. With further study, I am confident that the fossil genera *Pliodytes* Brodkorb and *Pliolymbus* Murray will prove to be inseparable from living genera.

D. CHARADRIIFORMES

This order has a long fossil history, with its earliest known members appearing in the late Cretaceous (see Graculavidae). Only recently has it been recognized just how diverse the Charadriiformes really are, as at least two families traditionally placed elsewhere are now known to belong here. These are the Phoenicopteridae, formerly of the Ciconiiformes (see Olson and Feduccia, 1980a) and the Pedionomidae, formerly of the Gruiformes (see Olson and Steadman, 1981). Even with this, the order still does not have its full complement of living members, as the bustards (Otididae) are likewise charadriiform.

For the present I have divided the order into two informal categories—the ancient "transitional" Charadriiformes, and the "higher" Charadriiformes. The first group consists mainly of late Cretaceous and early Cenozoic fossil genera, along with the Burhinidae and Plataleidae (Threskiornithidae *auct.*). In some respects these birds bridge the differences between the Gruiformes and the Charadriiformes, although their apparently derived features are those of the latter order. From this group, which includes *Presbyornis*, the Anseriformes arose.

1. *The "Transitional" Charadriiformes*

This is a disparate amalgam of archaic birds that lack certain typical charadriiform features such as the expanded ectepicondylar spur of the humerus found in most of the "higher" families (except Jacanidae), yet possess other characters (e.g., occipital fontanelles, four-notched sternum) that are seldom or never met with in the Gruiformes. These were the predominant birds in the late Cretaceous avifaunas of New Jersey and Wyoming. How diverse they were in their feeding adaptations at that time is unknown. The early Paleogene bird *Presbyornis*, which had the head of a duck on the body of a shorebird, belongs in this group and indicates that the entire order Anseriformes had its origins here.

I have already called attention to the mosaic nature of the ibises (Plataleidae), which combine gruiform and charadriiform characters (Olson, 1979). The desmognathous palate and the increased pneumaticity of the skeleton, particularly the humerus, have contributed to mask the affinities of the family. It is interesting that fossils belonging to the Graculavidae, as well as those of *Presbyornis*, are frequently identified as being ibislike.

a. Burhinidae. The Burhinidae are anamalous in several respects. I have included them here because they do not clearly belong with the "higher" Charadriiformes and because their postcranial skeleton has many similarities to that in the Cretaceous Graculavidae.

The fossil history of the thick-knees has been reviewed by Bickart (1982), who described the only known Tertiary species, *Burhinus lucorum*, on a humerus from the early Miocene (Hemingfordian) of Nebraska. Extinct Pleistocene taxa have been described from Kansas (*Burhinus aquilonaris* Feduccia, 1980) and the Bahamas (*Burhinus bistriatus nanus* Brodkorb—see Olson and Hilgartner, 1982). The supposed burhinid *Milnea gracilis* from the Miocene of France was shown to be an ibis (Cracraft, 1972a), providing another instance of the confusion that the similarities between various of the "transitional" Charadriiformes have caused. Bickart (1982) suggested that the habitat requirements of modern species of burhinids are sufficiently varied as to compromise their use as paleoecological indicators, at least in the Tertiary, although the assumption that taxa in the Pleistocene of the New World were inhabitants of open plains and prairies is probably not invalidated.

b. Plataleidae. Numerous fossil birds representing a fair diversity of species have been recovered from the middle Eocene (Lutetian) Messel oil shales in Germany, although as yet only two names have been proposed for any of them. Hoch (1980) presents a useful review of the history of this important locality. Specimens from the Messel pit are usually preserved as crushed complete or partial articulated skeletons. The first species of bird named from Messel was *Rhynchaeites messelensis* Wittich, 1898, originally described in the charadriiform family Rostratulidae. The other taxon named from this site, *Plumumida lutetialis* Hoch (1980), was placed in the Charadriiformes, family Incertae Sedis. With several better preserved new specimens, Peters (1983) was able to show that *Rhynchaeites messelensis* is actually a small, rather primitive ibis, and that *Plumumida lutetialis* is a junior synonym of the same species. *Rhynchaeites* is the earliest certain ibis and had a distinctly ibislike skull, a fused notarium, and pneumatic humerus as in the modern members of the family. Other elements, however, such as the coracoid, are decidedly like those in the Charadriiformes, which contributed to *Rhynchaeites* being twice independently assigned to that order. Peters (1983, p. 26) considers that *Rhynchaeites* strongly corroborates the hypothesis that ibises "are close to the group from which Gruiformes and Charadriiformes arose," as had been proposed previously (Olson, 1979).

A review of the remaining fossil record of ibises (Olson, 1982a) showed that the earliest certain ibis, apart from *Rhynchaeites*, is *Plegadis paganus* (Milne-Edwards), known from abundant material from the early Miocene (Aquitanian) of France. This species was smaller and slightly less specialized in tarsal morphology than modern species of *Plegadis*. The only other certain species of Tertiary ibis is *Plegadis pharangites* Olson, from the late Pliocene of Texas and Kansas. Fossils of *Eudocimus* spp. have also been reported from the Pliocene of North Carolina and Florida. Other Tertiary ibises appear to range of the family into the Neogene. He referred *Paracrax antiqua* (Marsh) from the Oligocene of Colorado (formerly thought to be a galliform) to the Bathornithidae and named two new species, *Paracrax wetmorei* and *P. gigantea*, from the late Oligocene of South Dakota. The holotype of *Paracrax wetmorei* consists of a partial, associated skeleton with a bizarre sternum vaguely reminiscent of that of the Hoatzin (*Opisthocomus*).

In 1968, Cracraft considered the Bathornithidae to be related to the Cariamidae and to belong in the the suborder Cariamae. The illustrations of the bones of *Paracrax wetmorei*, particularly the coracoid, along with Cracraft's (1968) comparisons and discussion, indicate that this was an entirely reasonable and correct conclusion. Then, however, Cracraft began studying an accumulation of crushed and fragmentary Eocene specimens in several different genera that ultimately came to rest in Wetmore's (1933a) gruiform family Geranoididae. Through some intricate convolutions, Cracraft (1969, 1971a, 1973a) managed to disassociate the Bathornithidae from the Cariamae completely, and the family wound up with the Geranoididae in the suborder Grues. He made little or no attempt to explain away the characters that first led him to assign the Bathornithidae to the Cariamae. Mourer-Chauviré (1981) has noted this inconsistency and has reconfirmed the cariamid affinities of the Bathornithidae, which she considers to be only a subfamily of the Cariamidae. For the present, I would maintain the Bathornithidae as a separate family, consisting of the two genera *Bathornis* and *Paracrax*. *Eutreptornis uintae* Cracraft, 1971a, from the late Eocene (Uintan) of Utah, was described in the Bathornithidae but differs considerably from *Bathornis* or *Paracrax* and should be considered of doubtful affinity.

To begin untangling more of the *Bathornis* enigma, let us now return to the *Trigonias* quarry in Colorado from which the first species of *Bathornis* was described. The type species of the genus, *Bathornis veredus*, was based on the distal end of a tarsometatarsus. The putative vulture *Palaeogyps prodromus*, from the same site, was based on the distal end of a tibiotarsus and a referred proximal end of a tarsometatarsus with a square, blocklike hypotarsus. A specimen in the Carnegie Museum of Natural History (CM 20365), consisting of an associated tarsometatarsus and toes, also from the Oligocene of Colorado, shows, however, that these two taxa are based on bones of one and the same species of bird (Fig. 6). The distal end of the Carnegie tarsometatarsus is identical to the holotype of *Bathornis veredus* and the proximal end is identical to the like portion associated with the holotypical tibiotarsus of *Palaeogyps prodromus*.

When I first examined the holotypical distal portion of tarsometatarsus of the putative rail *Palaeocrex fax*, I found that it had been very poorly preserved and prepared. The trochleae had not been aligned properly when repaired, and one segment of the shaft had even been glued in backwards.

be based on misidentified or undiagnostic specimens. *Minggangia changgouensis,* a supposed ibis from the late Eocene of China (Hou, 1982), is known only from the distal end of a tibiotarsus and the distal end of an ulna, neither of which is sufficient to diagnose new taxa of Eocene birds.

Two Quaternary genera, *Apteribis* Olson and Wetmore, 1976, of Molokai and Maui in the Hawaiian Islands, and *Xenicibis* Olson and Steadman, 1977, of Jamaica, are significant in showing great departure from the typical morphology of ibises. Both of these insular genera were flightless and had reduced wings and pectoral girdle combined with short, robust hindlimb elements.

c. Graculavidae and Presbyornithidae. I have treated these two families together, as their postcranial morphology is quite similar. The Presbyornithidae includes the very instructive early Tertiary charadriiform–anseriform mosaics of the genus *Presbyornis* and the Graculavidae tentatively comprises the majority of presumably neognathous Cretaceous birds hitherto described. The following summary is taken largely from Olson and Parris' (manuscript) study of the Cretaceous birds of New Jersey and Olson and Feduccia's (1980b) discussion of *Presbyornis.*

With these birds it is best to work backwards through time, as it would have proven almost impossible to interpret the Cretaceous fossils without an understanding of the early Paleogene genus *Presbyornis,* which has provided one of the best clues ever found to the origin of a major group of birds.

Fossils of *Presbyornis* have been reported from the early Eocene of the western United States and Argentina, and additional fossils are now known from the Paleocene of Utah (S. L. Olson, unpublished) and the Paleocene of Mongolia (E. N. Kurochkin, personal communication). Several species, differing at least in size, are known, but considerable revisionary work is still needed to determine just how many can be recognized, and under what means. *Nautilornis* Wetmore and *Telmabates* Howard, both of which are types of family-group names, are synonyms of *Presbyornis.*

Presbyornis was a highly gregarious charadriiform bird whose bones are often found in incredibly dense concentrations. Virtually all significant elements of the skeleton have been recovered. The skull and hyoid apparatus are unmistakably ducklike, showing that *Presbyornis* had the uniquely derived double-piston filter-feeding apparatus that characterizes the Anseriformes (Olson and Feduccia, 1980a). Despite these specializations, other aspects of the skull morphology (e.g., pterygoid, quadrate, and palatines) are primitive compared to living Anseriformes. In its postcranial skeleton, *Presbyornis* shows little similarity to Anseriformes, being a slender, long-legged wading bird (Fig. 8). On this basis, it would have to be placed with the "transitional" Charadriiformes.

Presbyornis shows that the Anseriformes evolved from a primitive cha-

FIG. 8. Reconstructed skeleton of the early Eocene *Presbyornis*, a bird that provides positive evidence linking the Anseriformes and the "transitional" Charadriiformes. This fossil runs so contrary to long established dogma that many ornithologists either have refused to believe in its existence or will not accept its significance. The fossils, however, do not lie. (Illustration by Jaquin B. Schulz, from Olson and Feduccia, 1980b.)

radriiform ancestor and cannot have been derived from the Galliformes (Olson and Feduccia, 1980a). It should be noted here that biochemical comparisons between the Anseriformes and the "higher" Charadriiformes, which latter may have branched off after the Anseriformes originated, are not likely to provide useful data bearing on the relationships of ducks and geese. Such comparisons should be between the Anseriformes, ibises, and the Burhinidae, in order to provide a meaningful test of the relationships of the Anseriformes. There is no evolutionary possibility of the Anseriformes having arisen from the Galliformes (or vice versa). Consequently, should biochemical tests indicate otherwise, the problem then becomes one of determining why the biochemical data in question do not provide reliable phylogenetic information.

With knowledge of the osteology of *Presbyornis* it has proven possible to make some sense of the various taxa of birds that had been described from the late Cretaceous (Maastrichtian) of New Jersey (Olson and Parris, manuscript). These were originally proposed as cormorants, shorebirds, and rails, but all are now seen to be charadriiforms. *Graculavus velox* Marsh is known from the proximal end of a humerus that is very similar to the humerus in

Presbyornis. *Telmatornis priscus* Marsh (including *T. affinis* Marsh and *Graculavus pumilis* Marsh) is known from proximal and distal ends of humeri and a referred tibiotarsus, tarsometatarsus, carpometacarpus, and pedal phalanx. It is a smaller species than *Graculavus velox* and seems to be somewhat burhinidlike but is nevertheless still more similar to *Presbyornis*. The humeri of "*Telmatornis*" *rex* Shufeldt are very stout and curved, being more ducklike in proportions than the humeri of *Telmatornis* or *Presbyornis* and a new generic name is required for this species. *Laornis edvardsianus* is known only from the distal end of a tibiotarsus that is quite similar to that of *Presbyornis* but that came from a very large bird, the size of a crane.

All of these birds from the Cretaceous of New Jersey appear to be more similar to each other and to *Presbyornis* than to any modern family of birds. The oldest available name for them is Graculavidae, with which, for the time being, the Telmatornithidae, Laornithidae, and Palaeotringinae may be synonymized. This may be something of an oversimplification; if more of the skeleton were known for these Cretaceous birds it might be possible to recognize more than one family. There is no guarantee that all, or any, of these birds had the ducklike feeding adaptations of *Presbyornis*, for which reason the family Presbyornithidae may tentatively be retained. Some may have been more like typical shorebirds than *Presbyornis*, whereas others, such as "*T*." *rex*, appear to have been more ducklike in their postcranial skeleton than *Presbyornis*.

The only other late Cretaceous fauna with a number of birds of more or less modern appearance is that from the Lance Formation (Maastrichtian) of Wyoming. Brodkorb (1963c) recognized eight species of birds in these deposits that he described as loons, flamingos, shorebirds, and ichthyornithiforms. Olson and Feduccia (1980a) have already suggested that the supposed loons and flamingos belong with the Charadriiformes. The supposed ichthyornithiform was referred to the genus *Apatornis* by Brodkorb (1963c), but he later transferred it to the charadriiform family Cimolopterygidae in a new genus *Palintropus* Brodkorb (1970a). *Apatornis celer* Marsh, from the late Cretaceous (Coniacian) of Kansas, has been referred to its own family, Apatornithidae, and has been placed with the Ichthyornithidae in the Ichthyornithiformes. Howard (1955), however, considered that *Apatornis* was very similar to *Telmabates*, which we now know to be a synonym of *Presbyornis*. It is quite likely that the entire known avifauna of the Lance Formation, as well as *Apatornis*, may consist of "transitional" charadriiforms and that the families Cimolopterygidae, Torotigidae, Lonchodytidae, and Apatornithidae may be subject to synonymization. Another apparently related taxon is the Dakotornithidae, based on *Dakotornis cooperi* Erickson, 1975, a supposedly ibislike bird from the Paleocene of North Dakota (Olson, 1982a).

Except for two bones from New Jersey that may belong to primitive procellariiforms (Olson and Parris, manuscript), all other late Cretaceous birds that are clearly related to modern neognaths appear to be part of a great radiation of "transitional" Charadriiformes that had at least some similarity to *Presbyornis*. They ranged in size from that of a small species of *Burhinus* to that of a large crane. If "*Telmatornis*" *rex* was really ducklike, it may indicate that the Anseriformes branched off from the Charadriiformes before or during the late Cretaceous, although no true anseriforms have yet been found in deposits older than early Oligocene.

2. *The "Higher" Charadriiformes*

In this category, the following families either have not been identified in Tertiary deposits or have no fossil record: Rostratulidae (see Section X,D,1,b, Plataleidae), "Phalaropodidae," Dromadidae, Thinocoridae, Pedionomidae, and Chionididae. Bessonnat and Michaut (1973) have briefly noticed and illustrated a complete skeleton, including even the tracheal rings, of a limicoline charadriiform from the early Oligocene (Lower Stampian) of France. It has a rather short bill, long legs, and lacks the hallux. This specimen would certainly repay more detailed study.

a. Jacanidae. The only supposed jacana listed by Brodkorb (1967) was *Rhegminornis calobates* Wetmore, from the Miocene of Florida. This, however, was later shown to be a galliform having probable affinities with turkeys (Olson and Farrand, 1974; Steadman, 1980). Subsequently, a real jacana, *Jacana farrandi*, was described from the middle Pliocene (Hemphillian) of central Florida (Olson, 1976c), thus establishing that the family was indeed present in the Tertiary of North America. *J. farrandi* was slightly larger than the modern forms of *Jacana*. Three species of Jacanidae, including one much larger than any existing form, have been found in the Oligocene Jebel Qatrani Formation in the Fayum region of Egypt (T. Rasmussen, personal communication).

b. Scolopacidae. In the absence of any modern discussion of the fossil members of the Scolopacidae, or even a portion of them, it is difficult to say much specific about the paleontological history of the family. Brodkorb (1967) lists 20 Tertiary paleospecies ranging in age from late Eocene to late Pliocene. All are from either Europe or North America. Many of these are undoubtedly correctly assigned to family, but the generic placement of most, particularly the taxa from older deposits, may be doubted.

The earliest taxon listed by Brodkorb (1967) is *Limosa gypsorum* (Gervais) from the late Eocene of France. This seems not to have been illustrated and Milne-Edwards (1867–1871) makes it clear that the material was poorly preserved and difficult to interpret. Milne-Edwards queried its placement in

Numenius, in which genus it had been described by Gervais. Brodkorb (1967, p. 187) put it in *Limosa*, although he noted that its generic position was "very doubtful." On the basis of brain casts, Mlikovsky (1981) removed the species to the Rallidae, creating the new genus *Montirallus* for it. There is still ample room to doubt that this species has found its proper place in the taxonomic scheme.

The next oldest species referred to the Scolopacidae is *Totanus edwardsi* Gaillard from the Eo–Oligocene Phosphorites du Quercy; this is unquestionably a limicoline charadriiform and C. Mourer-Chauviré (personal communication) would create a new genus for it in the Scolopacidae. *Paractitis bardi* Weigel from the early Oligocene (Chadronian) of Saskatchewan is known only from the scapular end of a coracoid and so tells us little of scolopacid evolution. The remaining fossil scolopacids listed by Brodkorb (1967) are all Neogene or younger and there is scarcely one of them that I would be prepared to accept at face value, at least at the generic level. The species *Totanus tereuelensis* Villalta, 1963, based on the distal end of a humerus from the late Miocene (Pontian) of Spain, is not included in Brodkorb (1967). The illustration of the holotype shows a specimen with a much deeper brachial depression than found in *Totanus* (= *Tringa*) and that appears almost gull-like. A revision of the fossil forms of this family is obviously needed.

c. Charadriidae. The Tertiary record of the Charadriidae as reflected in Brodkorb (1967) proves to be entirely illusory. *Dolichopterus viator* Milne-Edwards (not Aymard), from the early Oligocene (Sannoisian) of France, has already been relegated to Incertae Sedis (Olson, 1978a). At the American Museum of Natural History I have examined the holotype of *Charadrius sheppardianus* Cope from the "middle" Oligocene (Orellan) of Colorado. This consists of the hindlimbs and pelvis of a bird in a slab, but the preservation is such that it is impossible even to assign the specimen to order, much less to genus. It, too, should be relegated to Aves Incertae Sedis. I have also examined the holotypical tibiotarsus of *Limicolavis pluvianellus* Shufeldt from the early Miocene of Oregon, and I was not particularly surprised to find that it is not from a shorebird at all, but is instead from a duck. The illustration of the humerus of *Vanellus selysii* Van Beneden, from the early Oligocene (Rupelian) of Belgium, is insufficient to be certain even of the ordinal affinities of the specimen. Although it does appear that it may have had an expanded ectepicondylar process, as in most Charadriiformes, Van Beneden's judgment of its being a lapwing cannot be relied upon without examining the actual specimen.

d. Haematopodidae. With the removal of *Paractiornis* to the Glareolidae, the entire Tertiary history of the oystercatchers is contained in two bones (Olson and Steadman, 1979). One of these is a tibiotarsus from the middle Pliocene of Florida that was originally described as a new genus and species, *Palostralegus sulcatus* Brodkorb, but Olson and Steadman (1979) synonymized *Palostralegus* with *Haematopus*. The other specimen is a humerus referred to *Haematopus* from the early Pliocene (Hemphillian) at Lee Creek, North Carolina. Each of these fossils is from an oystercatcher slightly larger than modern *H. palliatus* but otherwise not much different.

e. Recurvirostridae. Despite the fact that the Recurvirostridae must have been in existence for a long time, having given rise to flamingos, which are known at least as far back as the middle Eocene (Olson and Feduccia, 1980a), the fossil record for the family is almost nonexistent. Of those taxa listed under the Recurvirostridae by Brodkorb (1967), *Presbyornis* has been shown to be a charadriiform ancestor of ducks that belongs in its own family. *Coltonia recurvirostra* Hardy, while possibly referable to *Presbyornis*, is based upon a specimen so fragmentary that no positive determination can be made of it (Feduccia and McGrew, 1974; personal observation). The only named fossil species in the family is now *Recurvirostra sanctaeneboulae* Mourer-Chauviré (1978b) from the late Eocene–early Oligocene (Ludien) of France. This, however, is known only from the proximal end of an ulna, which is not particularly informative. Even less so is the distal end of an ulna from the middle Miocene of California that L. H. Miller (1961) assigned to *Recurvirostra* sp.

f. Phoenicopteridae. It has been demonstrated that flamingos are in no way closely related to storks, as once thought, but are instead derived from the Recurvirostridae and belong in the order Charadriiformes (Olson and Feduccia, 1980a). The fossil history of the Phoenicopteridae was reviewed by Olson and Feduccia (1980a), from which much of the following summary is taken.

The earliest certain flamingo is *Juncitarsus gracillimus* Olson and Feduccia, from the middle Eocene (Bridgerian) of Wyoming. This species was intermediate in size between the largest modern Charadrii and the smallest modern flamingos. As should be expected of a primitive flamingo, *Juncitarsus* shares even more characters with the Recurvirostridae than do its modern relatives. The tarsometatarsus is extremely long and slender and is essentially like that of a stilt (*Himantopus*), except for the broad, flamingolike intercotylar knob. The thoracic vertebrae are not fused into a notarium as in modern flamingos, and they resemble those in the Recurvirostridae, as do the pedal phalanges. The humerus is flamingolike, however, in being pneumatic and lacking an ectepicondylar spur. The anterior cervical vertebrae were evidently highly specialized and elongated as in modern flamingos.

A representative of the modern genus *Phoenicopterus*, *P. croizeti* Gervais, occurs in the late Oligocene to early Miocene (Aquitanian) deposits of France and has also been reported from contemporaneous deposits in Germany (Martini, 1974) and Czechoslovakia (Svec, 1981). It differs from living species in having had a straighter bill.

As noted by Olson and Feduccia (1980a), the postcranial osteology of modern species of flamingos is quite uniform and several authors have recognized only one genus rather than three. The differences between the genera consist almost entirely of specializations of the bill. The discovery in the early Miocene of Kenya of a flamingo (*Phoenicopterus aethiopicus* Harrison and Walker, 1976d) with a bill morphology intermediate between that of *Phoenicopterus* and *Phoenicoparrus* (including *Phoeniconaias*) is of considerable interest, but there seems to be little point in erecting yet another genus (*Leakeyornis*) for this species on account of its intermediate nature, as was done by Rich and Walker (1983). Because the bill morphology of *Phoenicoparrus* is more specialized than that of *Phoenicopterus* (Olson and Feduccia, 1980a), the characters that *P. aethiopicus* shares with the former could be viewed as derived characters that would ally the species with *Phoenicoparrus*, although I would prefer to place all these forms in a single genus *Phoenicopterus*. *P. aethiopicus* evidently shows that the divergence in bill morphology seen in the living birds had already started to take place by the early Miocene.

Extinct species of modern-type flamingos are known from the Pliocene and Pleistocene of North America and Mexico (Brodkorb, 1963b) and from the Miocene to Pleistocene of Australia, where flamingos no longer exist, despite having been rather diverse in the past (Rich and Van Tets, 1982). A. H. Miller (1963a) named a new genus and species of flamingo, *Phoeniconotius eyrensis*, from the Miocene of Australia, but so far it is known only from the distal end of a tarsometatarsus and a few phalanges, so it is not very informative.

In the same deposits with *Phoenicopterus croizeti* (including those in Germany and Czechoslovakia) were several species of flamingos belonging to the genus *Palaelodus* Milne-Edwards. These have shorter tibiotarsi and shorter, more laterally compressed tarsometatarsi than *Phoenicopterus* and are thought to have been more specialized for swimming. The morphology of their bill is not certainly known (Olson and Feduccia, 1980a; Cheneval, 1983). Several large species of a very similar genus, *Megapaloelodus*, are known from early Miocene to early Pliocene deposits in North America, with one or two other species occurring in the Aquitanian of France. Palaelodidlike flamingos are known also from the Miocene of Australia (Rich and Van Tets, 1982). *Palaelodus* and *Megapaloelodus* have often been separated in their own family but are best included in the Phoenicopteridae (Olson and Feduccia, 1980a). Because both *Palaelodus* and modern flamingos have a notarium, Storer (1982, p. 94) points out "that either *Palaelodus* diverged from the line of the Recent flamingos subsequent to the time of *Juncitarsus* or that the notarium evolved independently in both the *Palaelodus* and the modern flamingo line."

It was previously noted that *Palaelodus steinheimensis* Fraas, from the late Miocene of Germany, belongs in the Anatidae (Olson and Feduccia, 1980a). Cheneval (1983) has reviewed the remaining species of *Palaelodus*, concluding that there are three species in the Aquitanian of France, with *P. minutus* becoming a synonym of *P. gracilipes*, and *P. goliath* being removed to the genus *Megapaloelodus*. In the Smithsonian collections is a cast of a tarsometatarsus from the museum in Basel indicating a species of *Megapaloelodus* in the Aquitanian of France much larger than *M. goliath*. In the American Museum of Natural History is a tarsometatarsus of yet another species of *Megapaloelodus* of similar size from the middle Miocene (Clarendonian) of Texas (see Olson and Feduccia, 1980a, p. 45).

g. *Glareolidae.* As of the appearance of Part 3 of Brodkorb's "Catalogue" (1967), there was no fossil record for the family Glareolidae. This changed dramatically with the nearly simultaneous appearance of studies by Ballmann (1979) and Olson and Steadman (1979). Modern glareolids are strictly Old World in distribution, and some doubt exists that the family constitutes a natural group. As yet there is still no fossil record for any of the coursers (Cursoriinae), but the pratincoles (Glareolinae) now have a most interesting history.

Olson and Steadman (1979) showed that *Paractiornis perpusillus* Wetmore, from the early Miocene (Arikareean) of Nebraska, was not a diminutive oystercatcher, as originally described, but a pratincole very similar to the modern genus *Glareola*. It is as yet known only from a single tarsometatarsus, and Olson and Steadman hesitated to synonymize the genus *Paractiornis* without being able to determine how different the remainder of the skeleton might be, although it is possible that *Paractiornis* is inseparable from *Glareola*. In any case, the specimen provides proof of the existence of pratincoles in the New World, and it will be of interest to know how prevalent these birds may have been there and when they died out.

Ballmann (1979) has documented an extraordinary collection of 137 bones of glareolids from the middle Miocene Nördlinger Ries in southern Germany. Most elements of the skeleton are represented, and these come from at least two, and perhaps as many as four species. One of these was referred to the modern genus *Glareola* as *G. neogena*. This was a rather small species, the size of Recent *G. nuchalis* or *G. lactea* and closely related to the former. A second fossil species differed from modern pratincoles sufficiently to merit its own genus and was named *Mioglareola gregaria*. Most of the skeleton was recovered, including the skull and mandible. The genus is characterized partly by its short, wide bill. This species, although the size of modern *G. pratincola*, is nevertheless more similar to the smaller species *G. nuchalis*. A few other specimens from the same locality appeared to come from a second unnamed species of *Mioglareola*, and a few others came from a glareolid of uncertain generic affinities. Ballmann used the internal structure of the humerus to show that these pratincoles were breeding when their bones were deposited and from this he was able to make inferences about probable climatic conditions in southern Germany in the middle Miocene.

h. Otididae. That the bustards are usually placed in the Gruiformes can be credited to the weight accorded the opinion of Hans Gadow. Gadow (1893) was confident that the Otididae belonged either in the Gruiformes or the Charadriiformes and proceeded to list a number of their similarities to the Limicolae. He then mentioned a few weak characters (e.g., "double-flecked eggs") supposedly supporting a gruiform relationship. Controverting the bulk of his own evidence and the conclusions of Fürbringer (1888), who placed the Otididae in the Charadriiformes, Gadow (1893, p. 188) considered that bustards could be regarded as some sort of "steppe rails." Steppe rails they have been ever since.

Nevertheless, the gruiform affinities of the Otididae have been seriously questioned by some modern authors (e.g., Hendrickson, 1969) and I have found the osteology of the Otididae to be very divergent from that of any gruiform family but very similar to that of the coursers (Cursoriinae, Glareolidae). Within the Cursoriinae, the Egyptian Plover, *Pluvianus aegyptius*, is very distinct and has the most similarities to the bustards, the holorhinal skull, for example, being very like that in the Otididae. Accordingly, I have placed the Otididae in the Charadriiformes, pending further investigation into their anatomy.

The bustards have a poor fossil record that tells us almost nothing about their evolutionary history. The earliest supposed bustard is *Palaeotis weigelti* Lambrecht, 1928, from the middle Eocene (Lutetian) Geiseltal brown coal in Germany, but this is now known to have been a flightless, paleognathous bird (Section VII,B) possibly related to one of the living groups of ratites (P. Houde, personal communication).

There appears to be some doubt as to the exact provenance of the type specimen of *Otis affinis* Lydekker (see Brodkorb, 1967), but it came from Bavaria and is either middle or late Miocene in age. Lambrecht (1933) shows the holotype to be most of a very crushed skeleton on a slab. Lydekker (1891) characterized it as having the exact proportions of *Otis* (= *Chlamydotis*) *undulata*, which is apparently why Brodkorb (1967) placed it in *Chlamydotis*, although such a refinement of its generic affinities is probably not warranted due to the nature of the specimen. Lambrecht's illustration is not clear enough to make out details of the pedal phalanges, but if Lydekker's

(1891) statement that these elements in the fossil are indistinguishable from those in a modern bustard is correct, then *Otis affinis* may well be a bustard, as the pedal phalanges in the Otididae are diagnostic by their extreme shortness. There are also undescribed remains of bustards in the old collections from the Phosphorites du Quercy, France, that are either late Eocene or Oligocene in age (Mourer-Chauviré, 1982, personal communication).

Gryzaja odessana Zubareva is an enigmatic fossil from the early Pliocene of the Ukraine. Brodkorb (1967) cites the pertinent literature on the subject, nearly all of which is in Russian or Ukrainian. The species was originally described from two distal ends of tibiotarsi from different individuals, both of which exhibited a very peculiar laterally compressed and expanded shaft. So strange were these that they were thought at first to come from some sort of swimming bird. Later, more specimens of tibiotarsi and tarsometatarsi were found, also with the shafts flattened laterally and swollen anteroposteriorly. It was then determined that the coracoids from the same deposits that had been described as a bustard, *Chlamydotis pliodeserti* Serebrovsky, belonged to *Gryzaja*, which was then interpreted as a peculiarly specialized bustard (Voinstvensky, 1959). Remains of several different individuals were recovered, so the configuration of the bones of *Gryzaja* is not a result of some pathological aberration. I can think of no functional explanation for the expanded shaft of the tibiotarsus. Brodkorb (1967) made a new family, Gryzajidae, for the genus, but E. N. Kurochkin (personal communication) assures me that *Gryzaja* is a bustard that is best retained in the Otididae.

i. Stercorariidae. The only fossil species hitherto recognized in the Stercorariidae is *Stercorarius shufeldti* Howard from Fossil Lake in the Pleistocene of Oregon. There is, however, a Tertiary species that is probably a jaeger but that has not been recognized as such. The illustration of the humerus that Milne-Edwards (1867–1871) referred to his species *Larus desnoyersii*, from the early Miocene (Aquitanian) of France, shows a single, large pneumatic fossa, as also noted by A. H. Miller and Sibley (1941). If this humerus is correctly referred, then the species cannot belong to the genus *Larus*, in which the humerus is not pneumatic and has two deep tricipital fossae. Such a humerus is characteristic of the Stercorariidae, however, and the possibility that *L. desnoyersii* should be referred to this family should be confirmed by examination of specimens.

Among the fossils in my care are specimens of several additional species of Stercorariidae. One of these is a partial associated skeleton from the middle Miocene (Barstovian) Calvert Formation of Maryland that belongs to a species of *Stercorarius* that is considerably smaller than any living member of the family. From the same formation are bones of a larger species as well. At least two species of Stercorariidae have been found at the Lee Creek mine in North Carolina. One of these is known from the distal end of a humerus about the size of that of *S. parasiticus* but that shows diagnostic differences. The other is a tarsometatarsus from a species the size of the modern birds that are usually placed in the genus *Catharacta*, although I can find no osteological basis for continuing to recognize the genus *Catharacta*. Stercorariids are so rare in the Lee Creek deposits that it has not been possible to determine whether the few specimens came from the Lower Pliocene (Hemphillian) Yorktown Formation or the underlying Medial Miocene (Barstovian) Pungo River Formation. In any case, it is evident that a variety of jaegers and skuas have been present in the North Atlantic from the early Miocene onward.

j. Laridae. Among the fossils listed under the Laridae by Brodkorb (1967), the early Eocene genus *Halcyornis* Owen has subsequently been referred to the Coraciiformes (Harrison and Walker, 1972); regardless of its affinities, it does not appear to be a gull. The affinities of *Rupelornis definitus* Van Beneden from the early Oligocene (Rupelian) of Belgium have not been confirmed and Van Beneden is known to have misidentified several fossil birds. *Ocyplanus proeses* De Vis, from the late Pleistocene of Australia, has been reidentified as a flamingo (Rich and Van Tets, 1982).

All of the taxa that appear under the Sterninae in Brodkorb's catalogue are suspect. *Sterna milne-edwardsii* Riabinin, from the Miocene of the Georgian SSR, is based on a very poorly preserved and fragmentary skeletal impression in a slab, the whereabouts of which is now unknown (E. N. Kurochkin, personal communication). The illustration cannot be identified except to say that the tarsometatarsus is much too long for a tern. The two species from the late Pleistocene (Lujanian) of Argentina named in the fossil genus *Pseudosterna* Mercerat were never illustrated, have never been reexamined, and are unlikely to represent extinct taxa.

I have examined the holotype of *Larus pristinus* Shufeldt from the early Miocene of Oregon and consider it to be of indeterminate affinities. The specimen is the proximal end of a tibiotarsus that is not only worn but appears to be from a juvenile individual, despite Shufeldt's (1915) claim to the contrary. A. H. Miller and Sibley (1941, p. 566) likewise regarded it as "of doubtful allocation." *Larus desnoyersii* is probably a jaeger of some sort (see Section X,D,2,i, Stercorariidae).

Mourer-Chauviré (1982) lists the Laridae among the birds found in the Eo–Oligocene Phosphorites du Quercy, France, which would be the earliest record of the family. Among named forms, the earliest gulls are *Larus elegans* and *L. totanoides* from the early Miocene (Aquitanian) deposits of France. *Larus elegans* is apparently abundant in these deposits, with *L. totanoides* being a rarer, slightly larger and more robust form (Milne-Edwards, 1867–1871). Ballmann (1976b) considers these species to be closely related to each other but too primitive for inclusion in the modern genus

Larus. Although Brodkorb (1967, p. 206) intimated that *Larus elegans* might be a tern, a referred skull that I examined in the Smithsonian collections is clearly that of a gull and is much closer to *Larus* (*sensu lato*) than to any other modern genus of Lari. Compared to modern forms, the Aquitanian gulls are diminutive and had a more primitive humerus and a rather long, slender tarsometatarsus.

Svec (1980) has described *Larus dolnicensis* on the distal end of a humerus from the early Miocene of Bohemia, but from the illustration of the specimen it appears quite worn and seems to lack the deep brachial depression characteristic of *Larus*. *Larus elmorei* Brodkorb, from the Pliocene Bone Valley Formation in Florida is the only other species of *Larus* yet named from the Tertiary. Grigorescu and Kessler (1977) identified the proximal end of an ulna from the late Miocene (Sarmatian) of Romania as *Larus* sp., and several unnamed species of *Larus* are represented among the extensive early Pliocene (Hemphillian) material from Lee Creek, North Carolina, all being uncommon.

The only other Tertiary species described in the Laridae is *Gaviota niobrara*, named from a distinctive distal end of a humerus from the late Miocene of Nebraska (A. H. Miller and Sibley, 1941). I have examined the holotype and concur with Miller and Sibley that *Gaviota* is a larid (not a stercorariid) that is generically distinct from all living members of the family.

k. Alcidae. Modern alcids are pelagic, wing-propelled diving birds that are confined to the Northern Hemisphere. Much of the more interesting aspects of their fossil history resides in thousands of fossils that have been recovered from the Miocene beds of Chesapeake Bay in Maryland and Virginia and from Lower Pliocene marine deposits exposed in a phosphate mine at Lee Creek, North Carolina. With the exception of a few specimens, however (Olson, 1977d, 1984a), most of the newer material has not been mentioned in print. Consequently, much of what follows is original information.

The earliest supposed alcids, *Nautilornis avus* and *N. proavitus*, were described from crushed and fragmentary bones from the early Eocene (Wasatchian) Green River Formation of Utah, for which Wetmore (1926b) made a distinct subfamily, the Nautilornithinae. Feduccia and McGrew (1974) showed that these were not alcids but are instead referable to the genus *Presbyornis*, now known to be a charadriiform near the ancestry of Anseriformes (Olson and Feduccia, 1980b).

The earliest alcid therefore becomes *Hydrotherikornis oregonus* A. H. Miller (1931), from the late Eocene of Oregon. This is known from a single tibiotarsus that Miller considered to be sufficiently distinct from the Alcinae as to suggest its placement with the Nautilornithinae. Because, as we have seen, *Nautilornis* does not belong in the Alcidae, the affinities of *Hydro-*

therikornis within the Alcidae must now be considered uncertain. D. W. Steadman (personal communication) has reexamined the holotype of *Hydrotherikornis* and concludes that it is indeed correctly assigned to the Alcidae. At this point, *Hydrotherikornis* tells us little other than that an alcid was present in the eastern Pacific in the late Eocene.

The next alcids from the Pacific are of late Miocene age. Representatives of the Fraterculini have been recorded from late Miocene to late Pliocene deposits in California and Baja California (*Cerorhinca dubia* L. H. Miller, 1925; *Cerorhinca minor* Howard, 1971; *Cerorhinca* sp. Howard, 1968; Fraterculini gen. and sp. indet. Howard, 1978), as have various small auklets (*Aethia rossmoori* Howard, 1968; *Aethia* sp. Howard, 1978; ?*Endomychura* sp. Howard, 1971; *Brachyramphus pliocenum* Howard, 1949; *Ptychoramphus tenuis* L. H. Miller and Bowman, 1958). Howard (1982) has reported additional fossils of small alcids and suggested the possibility that the species *Aethia rossmoori* may belong to some other genus.

Murres and guillemots of the genera *Uria* and *Cepphus* have lately been documented in the late Miocene (Clarendonian, Hemphillian) of California (Howard, 1978, 1981, 1982; Barnes *et al.*, 1981). Three of these have been named—*Uria brodkorbi* Howard, 1981, based on an impression preserving much of the skeleton, including the skull; *U. paleohesperis* Howard, 1982; and *Cepphus olsoni* Howard, 1982.

The most abundant and best known of the Tertiary seabirds of the eastern Pacific are the mancalline alcids. These were flightless and paralleled the great auks (*Pinguinus*) in their adaptations for wing-propelled diving, except that they were even more specialized. Howard (1966a, 1976, 1982) has described two species in the presumptive ancestral genus *Praemancalla* from the late Miocene (Clarendonian) of California. This genus is superseded in Pliocene (Hemphillian, Blancan) deposits of California and Baja California by the genus *Mancalla,* of which five species have been recognized (Howard, 1970, 1971; Olson, 1981b). Three of these species occur in the San Diego Formation (Olson, 1981b) and a different combination of three species has been found in the Lawrence Canyon Local Fauna (Howard, 1982), which raises the possibility that four species of *Mancalla* may have coexisted in the Pliocene. A third problematical genus and species, *Alcodes ulnulus,* known from a single distinctive ulna from the late Miocene (Clarendonian) of California, has tentatively been associated with the mancallines (Howard, 1968).

Although the mancalline alcids are usually speurated as a subfamily, Mancallinae, it is my opinion that this treatment overemphasizes their diving adaptations. It is highly likely that the mancallines are more closely related to a particular genus or group of genera now included in the Alcinae, rather than being the "sister group" of all other alcids. The discovery of a complete skull and mandible of *Mancalla* by R. M. Chandler (in preparation) should greatly aid to clarify the relationships of the genus.

In the Atlantic, the fossil record of the Alcidae is even more extensive than in the Pacific, but, as mentioned, little has been published on it as yet. Fossil alcids have come mainly from middle to late Miocene deposits of the Chesapeake Bay region of Maryland and Virginia (Calvert Formation *et seq.*), early Pliocene deposits in North Carolina (Yorktown Formation), and middle Pliocene deposits in central Florida (Bone Valley Formation).

The earliest Atlantic alcid is *Miocepphus mcclungi* Wetmore from the middle Miocene (Barstovian) Calvert Formation of Maryland and strata of equivalent age in North Carolina. There is a second, slightly larger undescribed species, probably of *Miocepphus*, also in the Calvert beds (Olson, 1984a). Wetmore (1940) considered *Miocepphus* to share similarities with *Cepphus*, but Howard (1978, p. 21) and I agree in disassociating *Miocepphus* from *Cepphus*, with the former being part of the Atlantic radiation of *Alca*-like auks.

An associated skull, mandible, and wing of an alcid from later in the Miocene of Virginia (Olson, 1984a) indicates a bird with a fairly slender bill with the tip swollen but not laterally compressed as in *Alca*. It seems to parallel *Uria* in some respects but the humerus shows that it is not closely related to that genus.

One of the more important alcid genera in the Tertiary of the Atlantic is *Australca*, originally described from the Bone Valley Formation of Florida by Brodkorb (1955). Brodkorb's assessment of *Australca grandis* as being on the road to flightlessness is erroneous, however, as he had mistakenly associated wing elements from a much smaller species with the holotypical coracoid of *A. grandis*. The fossil species *Uria antiqua*, from North Carolina, was once thought to be from the Miocene but is actually early Pliocene in age and is referable to the genus *Australca* rather than *Uria* (Olson and Gillette, 1978). Thousands of bones of *Australca* have been recovered from lower Pliocene (Hemphillian) deposits at the Lee Creek phosphate mine in North Carolina. It is not at all certain at this point just how many species of *Australca* are represented here, although there appears to have been a considerable radiation in this group. The more abundant larger forms are intermediate in size between *Alca torda* and *Pinguinus impennis*. The morphology of the skull and mandible is likewise intermediate between these two modern species, although somewhat more like *Pinguinus*, whereas the wings show no approach towards flightlessness. Several premaxillae from Lee Creek show that there are two sibling species included among the abundant large *Australca* remains, and it may prove impossible to determine to which of these species the names *A. grandis* and *A. antiqua* apply.

Also from Lee Creek are smaller species of the Atlantic alcid radiation, some of which must certainly be referable to the genus *Alca*. I have received a cast of the type of *Uria ausonia* Portis from the Pliocene of Italy and would assign it either to *Alca* or *Australca*. It is considerably smaller than *A. grandis* and is definitely not referable to *Uria*. Specimens identical to the type of *A. ausonia* occur in the Lee Creek deposits in North Carolina.

Among the Atlantic fossil alcids is a partial associated skeleton from the late Miocene of Virginia (Olson, 1984a) that I would tentatively refer to *Australca*. It is, however, from a species much larger than *A. grandis*, being about the size of *Pinguinus impennis* (the humerus is longer, the coracoid slightly smaller) yet that shows no modifications towards flightlessness and was clearly volant. This controverts Storer's (1960, p. 697) speculation that: "the maximum size obtainable by flying alcids appears to be near that of the murres (*Uria*) or the Razor-bill (*Alca*)."

In the early Pliocene deposits at Lee Creek there are two additional large alcids. One of these, *Pinguinus alfrednewtoni*, Olson, 1977d, is an ancestral form of the Greak Auk and differs only in minor details from *P. impennis*. The other, of which there is scant material, was even larger than *Pinguinus* and was apparently also flightless; its relationships are as yet unclear.

Among the early Pliocene remains from Lee Creek I have identified a few very small alcid fossils as probably belonging to the genus *Alle*. There are also a fair number of specimens from two species of puffins (*Fratercula*). One of these species is about the size of *Lunda cirrhata* and could well be related to it. I cannot, however, distinguish *Lunda* from *Fratercula* osteologically and do not consider it to be a valid genus. The other species is somewhat smaller than the modern Atlantic Puffin (*F. arctica*). These specimens are the only indication so far of puffins in the Tertiary of the Atlantic.

The only fossil from the Atlantic that has correctly been referred to *Uria* is *U. affinis* Marsh, based on a humerus from Pleistocene marine sediments in Maine that were deposited along the edge of the melting Wisconsinan glacier about 12,000 years ago (see Ray and Spiess, 1981). Although likely to be referable to one or the other of the two modern species of *Uria*, this specimen is larger than any of the living subspecies of *Uria* now found in the Atlantic and instead is nearest in size to the Pacific form *U. lomvia arra*. The important point to be made here is that among the thousands of fossil alcid bones recovered from the Miocene and Pliocene of the western Atlantic, there is not a single specimen belonging to the genus *Uria*. The same holds true for *Cepphus*.

As now understood, the fossil record of the Alcidae requires that we modify certain ideas that have been advanced concerning zoogeography and relationships within the family (Storer, 1945, 1952; Udvardy, 1963). There is still no reason to doubt a Pacific origin for the Alcidae, but the logic for this rests as much with the diversity observed there as with fossil evidence.

In previous discussions of zoogeography of the Alcidae, it has been considered probable that dispersal between the two oceans was through northern seaways and I accept this probability. The most difficult part of reconstructing the history of the Alcidae is in explaining how the first alcids arrived in the Atlantic. This would most likely have been after the early Eocene, as until then there was a continuous land connection between North America and Europe across the North Atlantic. According to the fossil record available at present, there were only a few species of rather small alcids (*Miocepphus*) in the middle Miocene of the western mid-Atlantic. By the early Pliocene, however, there was a diverse radiation of the family there that included *Alca, Australca,* and *Pinguinus,* as well as certain undescribed genera. *Alle,* too, may be part of this radiation.

An unexpected discovery is that *Uria* apparently is not part of this Atlantic radiation, despite the fact that many workers have considered *Uria* to be closely related to *Alca* and to have originated in the Atlantic (e.g., Storer 1945, 1952; Udvardy, 1963). We have seen, however, that whereas *Uria* occurs in the Pacific in the late Miocene, it is utterly unknown in the Atlantic until the Pleistocene. The same is true for *Cepphus.* This suggests that a reevaluation of the relationships of *Uria* is needed. Perhaps the genus is more closely related to some of the much smaller Pacific murrelets such as *Endomychura.* It might also share a close common ancestor with the mancallines.

Another interesting phenomenon is the occurrence of two species of *Fratercula* in the early Pliocene of the Atlantic. As these are representatives of what has probably rightly been considered to be a Pacific group of alcids, and as no specimens of *Fratercula* have as yet been found in the Miocene of the Atlantic, this occurrence indicates dispersal from the Pacific to the Atlantic in the late Miocene. This interpretation is in accord with other evidence indicating a very brief inundation of the Bering land bridge in the late Miocene (Hopkins, 1967). At this time there was an interchange between the marine organisms of the two oceans, and the preponderance of these went from the Pacific to the Atlantic rather than vice versa. The only possible indication that alcids may have dispersed from the Atlantic to the Pacific at this time are two fragmentary late Miocene fossils from California that Howard (1968, p. 15) referred to as "*Alca* sp.". Better material is needed before we can feel confident that *Alca* entered the Pacific in the late Miocene and subsequently perished.

E. ANSERIFORMES

The Anhimidae have no fossil record. The more important aspects of the fossil history of the Anatidae are summarized in Olson and Feduccia (1980b). As we have seen, the Anseriformes evolved from a primitive charadriiform ancestor through birds similar to *Presbyornis*. One species, "*Telmatornis*" *rex* Shufeldt, from the late Cretaceous of New Jersey, had more ducklike humeri than its relatives but is not certainly an anseriform and has been retained in the order Charadriiformes.

With the removal of the late Eocene (Uintan) species *Eonessa anaticula* Wetmore from the Anatidae (Olson and Feduccia, 1980b), the oldest certain anatids are the genera *Romainvillia* Lebedinsky and *Cygnopterus* Lambrecht, from the early Oligocene of France and Belgium, respectively. These were rather large forms, the size of geese, but of uncertain affinity. Another enigmatic form, *Paranyroca magna* A. H. Miller and Compton, 1939, known only from tarsometatarsi from the early Miocene (Arikareean) of South Dakota, was considered so unusual in possessing only two calcaneal ridges on the hypotarsus, among other characters, that it was made the type of a new family, Paranyrocidae. Brodkorb (1964) demoted it to a subfamily of Anatidae, which seems more in keeping with its overall morphology.

Anatids are not common as fossils until the Neogene. In many Pliocene and Pleistocene freshwater deposits, ducks and geese are the dominant group of birds. Thus, if the Anatidae arose as early as the Cretaceous, the absence or rarity of their fossils in the Paleogene is difficult to understand. The various fossil species of Anseriformes are carefully and conservatively treated by Howard (1964, 1973), who correctly notes that the generic determinations of many of these species, particularly those described by earlier workers, should not be accepted at face value. Likewise, species-level determinations, particularly of Pleistocene fossils, are subject to inaccuracies. For example, all of the supposedly extinct species of ducks named by C. W. De Vis from the Pleistocene of Australia were synonymized with living species (Olson, 1977b).

It appears that the principal radiation of modern tribes and genera of Anatidae took place by the Miocene, regardless of how long the family may have been around previous to that. The ducks from the early Miocene (Aquitanian) of France have been regarded as difficult to place even in a modern tribe (Howard, 1964; Olson and Feduccia, 1980b; P. Ballmann, personal communication), but J. Cheneval now considers that they can be placed in the fossil genus *Dendrochen* A. Miller and referred to the Dendrocygninae (C. Mourer-Chauviré, personal communication). By the middle Miocene, highly derived mergansers of the modern genus *Mergus* were already in existence, as shown by a pelvis associated with both tibiotarsi and tarsometatarsi from the Calvert Formation (Barstovian) of Virginia that was described as a new species, *Mergus miscellus* Alvarez and Olson, 1978. A middle Miocene anatid (*Sinanas diatomas*) has been described from diatomites in Shandong Province, China (Yeh, 1980), but is of uncertain affinities.

The modern shelducks of the tribe Tadornini are practically worldwide in distribution except for their absence in North America. This does not reflect their past history, as several species of tadornines have been described from Pleistocene deposits in North America (Howard, 1964, 1973; Short, 1970). A fragmentary ulna, referred only to tribe, from the middle Miocene Calvert Formation in Maryland, shows that the Tadornini had been in North America at least since the middle Miocene (Alvarez and Olson, 1978). Well preserved fossils very similar to the modern genus *Tadorna* have also been obtained from the middle Miocene Nördlinger Ries in Germany (P. Ballmann, personal communication).

F. CICONIIFORMES

As used here, the Ciconiiformes has a radically different composition from that traditionally accorded it. The flamingos have been removed to the "higher" Charadriiformes, the ibises to the "transitional" Charadriiformes, and the herons are considered Incertae Sedis but probably related to the Gruiformes (Olson, 1979; Olson and Feduccia, 1980a). On the other hand, the three remaining families (Scopidae, Ciconiidae, and Balaenicipitidae) have been augmented by the Teratornithidae and Vulturidae, which can no longer be considered as part of the Falconiformes (Ligon, 1967; Jollie, 1976–1977; König, 1982; Rea, 1983).

1. *Ciconiidae*

Storks have a reasonably good fossil record, though as yet it is not readily comprehended. Of the Tertiary taxa listed by Brodkorb (1963b), *Tantalus* (= *Ibis* = *Mycteria*) *milneedwardsii* Shufeldt has been shown to be synonymous with the galliform *Miophasianus altus* (Milne-Edwards) (Olson, 1974b), *Amphipelargus majori Lydekker* has been referred to the gruiform family Ergilornithidae (Harrison, 1981), and *Propelargus cayluxensis* Lydekker has been transferred to the Idiornithidae (Mourer-Chauviré, 1983b). *Ciconiopsis antarctica* Ameghino, from the early Oligocene of Argentina, cannot be accepted as a stork without restudy. Two of the paleospecies of storks named from the Quaternary or latest Tertiary of Australia by De Vis are instead flamingos (Rich, 1976), and one of the three others is a megapode (Van Tets, 1974).

Other supposed early storks are the three species named from distal ends of tarsometatarsi from the late Eocene to Oligocene Phosphorites du Quercy in France (Gaillard, 1908; Lydekker, 1891). Two of these, however, *Pelargopappus stehlini* Gaillard and *P. trouessarti* Gaillard, have now been shown to be the same as the secretarybird *Amphiserpentarius schlosseri* Gaillard, from the same deposits, which must now be known as *Pelargopappus schlosseri* (Mourer-Chauviré and Cheneval, 1983). Likewise, these same authors have shown that the supposed stork *Pelargopappus magnus* (Milne-Edwards) is the early Miocene (Aquitanian) representative of this same genus of secretarybird.

The earliest certain stork is *Palaeoephippiorhynchus dietrichi* Lambrecht, 1930, known from a skull and mandible from the early Oligocene of the Fayum series in Egypt. *Palaeoephippiorhynchus*, incidentally, is the longest generic name in the class Aves (M. D. Bruce, personal communication). Two early Miocene species that are also storks, *edwardsi* Lydekker from France, and *olseni* Brodkorb from Florida, were described in the genus *Propelargus*, the type species of which, as mentioned, has been transferred to the Idiornithidae. Cheneval (1984) has redescribed the former in a new genus as *Grallavis edwardsi*. This species is now known from most of the skeleton and is most similar to species in the living genus *Ephippiorhynchus*, but also shares characters with *Leptotilos*. The generic position of "*Propelargus*" *olseni* is now very uncertain.

Additional Tertiary storks have been reported from France, Florida, Nebraska, Ukraine, Tunisia, Kenya, India, Pakistan, Mongolia, and Romania (Brodkorb, 1963b; Short, 1966; Zubareva, 1948; Hill and Walker, 1979; Harrison, 1974, 1980a; Harrison and Walker, 1982; Kurochkin 1982b; Grigorescu and Kessler, 1977). These are for the most part based on isolated fragments.

2. *Scopidae*

The only fossil record of this family is the distal end of a tarsometatarsus and a partial coracoid from the early Pliocene of South Africa that have been described as a new species, *Scopus xenopus* (Olson, 1984b). This was slightly larger than the living species *S. umbretta* and had a foot structure reminiscent of that in the Pelecaniformes, possibly indicating that the fossil species swam more than the living form.

3. *Balaenicipitidae*

The Shoebill (*Balaeniceps rex*) is the only living member of this peculiar family, and combines characters of storks and pelecaniforms (Cottam, 1957; Feduccia, 1977b; Olson, 1979). The species is now confined to marshes in east-central Africa. The distal end of a tarsometatarsus from the late Miocene of Tunisia was conditionally listed as "cf. Balaenicipitidae" by Rich (1972, p. 50). Harrison and Walker (1982) referred this specimen to their new genus and species of balaenicipitid, *Paludavis richae,* based on two tarsal trochleae from the late Miocene Siwalik series in northern Pakistan. Better material would be desirable before one could feel confident about extending the range of this family to Asia, although such a distribution is not unlikely. The other fossil referred to this family is the holotype of the putative heron *Goliathia andrewsi* from the Eo–Oligocene Fayum series in Egypt, which Brodkorb (1980) transferred to the Balaenicipitidae (see Section X,B, Ardeidae). This assignment seems all the more likely given the discovery of additional material of Balaenicipitidae in the same beds (T. Rasmussen, personal communication).

4. *Teratornithidae*

The literature and present knowledge of the teratorns has been conveniently summarized by K. E. Campbell and Tonni (1980, 1982, 1983). These gigantic soaring birds were long known only from the late Pleistocene of North America. They have usually been placed near the Vulturidae and have even been included in that family by some authors. The Teratornithidae nevertheless constitute a perfectly distinct group that shares important similarities with such nonraptorial birds as the storks and Pelecaniformes, as well as with the Vulturidae. Their exact phylogenetic position is under investigation by Campbell and Tonni and for the present it is sufficient to say that the teratorns will probably add evidence to that already available for a derivation of the Vulturidae from a nonfalconiform ancestral stock.

Teratornis merriami L. Miller is the best known teratorn, having been described from the late Pleistocene of Rancho La Brea, California, where most of its skeletal elements have been recovered. Fossils of this species have been collected also in Florida, Arizona, Nevada, and Mexico (Brodkorb, 1964; Lundelius *et al.*, 1983). *T. merriami* is estimated to have had a wing span of 3.5 to 3.8 m and a weight of ~15 kg (K. E. Campbell and Tonni, 1980). A second species, *T. incredibilis* Howard, is known from three rather undiagnostic specimens from California and Nevada that range in age from early to late Pleistocene. These fossils indicate a tremendous bird, with an estimated wing span of 5.2 to 5.9 m. A third teratorn, *Cathartornis gracilis* L. Miller, is rather enigmatic, as it is known only from two tarsometatarsi from Rancho La Brea that are somewhat longer and more slender than those of *T. merriami.*

More astonishing even than *Teratornis incredibilis* was the discovery of a fourth species of teratorn, *Argentavis magnificens* K. E. Campbell and Tonni, 1980, in the late Miocene (Huayquerian) of Argentina, that surpassed in size anything thought possible for a volant bird. This is known from a partial associated skeleton including portions of the skull, wing, and leg bones. The wing span of this bird was estimated at 7 to 7.6 m and its weight was calculated at 120 kg.

The discovery of *Argentavis* now suggests that the teratorns arose in South America and spread to the North American continent only after the late Pliocene closure of the Panamanian seaway. Because of their large size and soaring habits, they must have been restricted to open prairie and savanna-like habitats. K. E. Campbell and Tonni (1982, 1983) have estimated the weights and wing dimensions of the various teratorns and hypothesized that they were predatory rather than scavenging birds, with vulturelike flight but better adapted for terrestrial locomotion than the members of the Vulturidae.

5. *Vulturidae (Cathartidae* auct.)

If the available fossil record is any guide, the so-called New World vultures are definitely misnamed, as their early history is almost completely confined to the Old World. Let us first dispose of the taxa that probably do not belong in this family. *Lithornis vulturinus* Owen, from the early Eocene of England, belongs with the volant paleognathous birds (Houde and Olson, 1981) that are so prevalent in the same deposits from which the holotype (later destroyed) of *L. vulturinus* came (P. Houde, personal communication). *Eocathartes robustus* Lambrecht, from the middle Eocene (Lutetian) brown coals of Geiselthal, Germany, is known from a partial crushed skeleton that is almost certainly not a vulturid (P. Houde, personal communication). The putative hornbill *Geiseloceros robustus* Lambrecht may belong to the same species (see Section IX,G,1). *Teracus littoralis* Milne-Edwards, from the early Oligocene of France, has been placed in Incertae Sedis (Olson, 1978a). *Palaeogyps prodromus* Wetmore, from the early Oligocene of Colorado, and *Neocathartes grallator* Wetmore, from the late Eocene of Wyoming, are both referable to the family Bathornithidae in the gruiform suborder Cariamae (see Section X,A,1,b, Bathornithidae). *Phasmagyps patritus* Wetmore, from the early Oligocene (Chadronian) of Colorado, is known from the distal end of a tibiotarsus that has some superficial resemblances to the Vulturidae. My examination of the holotype reveals several striking departures from that family such that the relationships of this fragment must be considered problematical.

The fossil species *Vultur patruus* (Lönnberg) was supposed to be from Pliocene deposits in Bolivia, but these were later shown to be Pleistocene, and *V. patruus* was synonymized with the living species *V. gryphus* (K. E. Campbell, 1979). Thus, the species *Sarcoramphus kernense* (L. Miller) and *Pliogyps fisheri* Tordoff from the Pliocene of California and Kansas, respectively, provide the only pre-Pleistocene evidence of the Vulturidae in the New World. Important among newer references to Pleistocene taxa are Howard's (1974) description of the postcranial skeleton of the extinct vulture *Breagyps clarki* (L. Miller) from the tar pits at Rancho La Brea, California, Arredondo's (1976) recognition of a condor in the Quaternary of Cuba, and K. E. Campbell's (1979) descriptions of one new genus and three new species of Vulturidae from tar seeps in northwestern Peru.

Most Old World fossils of the Vulturidae were reviewed by Cracraft and Rich (1972). The species *Diatropornis ellioti* (Milne-Edwards) and *Plesiocathartes europaeus* Gaillard, both from the late Eocene to Oligocene Phosphorites du Quercy, France, are considerably smaller than any modern members of the family. Cracraft and Rich (1972) considered them to be definitely referable to the Vulturidae, as does Mourer-Chauviré (1982). Cracraft and Rich (1972) removed *Amphiserpentarius schlosseri*, also from the Phosphorites du Quercy, from the Sagittariidae to the Vulturidae, but this was in error as the species actually is a secretarybird (Mourer-Chauviré and Cheneval, 1983).

A vulturid larger than *Diatropornis* or *Plesiocathartes* has been found in the early Oligocene of Mongolia (E. N. Kurochkin, personal communication), which establishes that the family was present in Asia at about the same time as in Europe. Crusafont and Villalta (1955) described *Plesiocathartes* (?) *gaillardi* on the distal end of a tarsometatarsus from the early Miocene (Burdigalian) of Spain, but their publication appears to have been entirely overlooked and the species has not been critically evaluated.

Thus, we see that the Vulturidae have been in the Old World at least since the middle Paleogene, whereas their presence in the New World cannot be confirmed until late in the Neogene.

G. PELECANIFORMES

The Pelecaniformes have an extensive and most interesting fossil record. Before elucidating this, it is first necessary to dispense with two families that were included in this order by Brodkorb (1963b), but that are not pelecaniform.

The Elopterygidae was created by Lambrecht (1933) for three disparate taxa: *Elopteryx nopcsai* Andrews (1913), based on the proximal end of a femur and two distal ends of tibiotarsi from the late Cretaceous of Romania; *Eostega lebedinskyi* Lambrecht, 1929, based on a mandible from the middle Eocene of Romania; and *Actiornis anglicus* Lydekker, 1891, based on the proximal end of an ulna from the late Eocene of England. What the fancied connection may have been between these three taxa is impossible to perceive. Brodkorb (1963b) modified the composition of the family by removing *Actiornis* to the Phalacrocoracidae (where it does not belong, see Section X,G,5,d), while including the species *Argillornis emuinus* (Bowerbank). The various specimens included under *Argillornis emuinus* appear to be referable to the Pelagornithidae. Lambrecht (1929) regarded the mandible of *Eostega* as being intermediate between *Sula* and *Phalacrocorax*. It is quite possibly pelecaniform, but needs comparison with other Eocene Pelecaniformes such as *Prophaethon*, *Limnofregata*, and *Protoplotus*, before its familial allocation can be determined. It is probable that the lectotypical femur of *Elopteryx nopcsai* is nonavian (see Section VI) and thus this species, which carries with it the family name Elopterygidae, should be regarded only as Vertebrata Incertae Sedis.

Cladornis pachypus Ameghino, known from the distal end of a tarsometatarsus from the early Oligocene (Deseadan) of Argentina, was originally considered to be some sort of a terrestrial penguin. Simpson (1946) would not have it as such, but had no suggestion as to its real affinities. In attempting to do something with the Cladornithidae, Wetmore (1951, pp. 2–3) stated that "the only suggestion that has come to me is that possibly [it] may belong in the order Pelecaniformes, in which I have placed the family tentatively in the suborder Odontopteryges." He later created a separate suborder, Cladornithes, for the family (Wetmore, 1960). Examination of the illustration of the holotype in Ameghino (1895, fig. 35) supports Simpson's (1946, p. 25) categorization of this as an "extraordinary bone." To me it appears to be from some sort of very large and extremely weird land bird, possibly even tending towards being zygodactyl. It is probably as far from the mainstream of avian evolution, and as far removed from the Pelecaniformes, as, for example, the hornbill genus *Bucorvus*.

1. *Suborder Phaethontes*

a. Prophaethontidae. This family was erected by Harrison and Walker (1976a) for *Prophaethon shrubsolei* Andrews, 1899a, known from an associated skull, mandible, sternum, pelvis, coracoid, and partial femur and tibiotarsus from the early Eocene (Ypresian) of England. The obvious similarity of the skull to that of *Phaethon* led Andrews (1899a) to place *Prophaethon* in the Phaethontidae, in which he was followed by subsequent authors (e.g., Lambrecht, 1933; Brodkorb, 1963b). In *Prophaethon*, however, the pelvis is narrow and elongate, somewhat as in diving birds, and the tibiotarsus is large and bears well developed cnemial crests. This is quite in contrast with *Phaethon*, in which the pelvis is short and wide, and the hindlimb is greatly reduced and nearly functionless. Harrison and Walker (1976a) interpreted *Prophaethon* as having similarities not only with *Phae-*

thon but also with the Procellariiformes and particularly the Charadriiformes. Because of its supposedly "intermediate" nature, they not only proposed that *Prophaethon* be given separate familial status, but also elevated it to the rank of a monotypic order, Prophaethontiformes. This is unjustified and does nothing to clarify relationships.

Whereas its considerable differences from *Phaethon* justify the retention of a family Prophaethontidae, similarities in the skull to *Phaethon*, and the clearly pelecaniform features of the sternum, indicate that *Prophaethon* should be placed in the Pelecaniformes in the suborder Phaethontes. The characters of "intermediacy," particularly those that are supposedly like the Charadriiformes, all appear to be primitive. A reanalysis of *Prophaethon* would likely provide some valuable information concerning the possible close relationship between the Pelecaniformes and Procellariiformes (see also Section X,G,2, Pelagornithidae).

Prophaethon is of further interest in having a very long, open nostril, similar to that seen in embryos and juveniles of modern Pelecaniformes (Olson, 1977c), but unlike most adult members of the order, in which the nostrils are nearly or entirely ossified. The primitive, open condition of the nostrils is also found in the early Eocene frigatebird *Limnofregata* (see Section X,G,3, Fregatidae).

b. Phaethontidae. The three modern species of tropicbirds (*Phaethon*) are the only recognized representatives of this peculiar family. Their relationships have been questioned in the past, but their totipalmate foot, positioning of the salt glands within the orbit, and lack of an incubation patch are apparently derived characters shared with the remainder of the Pelecaniformes.

No fossils have as yet been described that can be referred to the Phaethontidae. In the Smithsonian collections, however, there are an associated humerus, coracoid, and scapula from the middle Miocene (Barstovian) Calvert Formation of Maryland that appear to belong to a highly distinctive new genus of Phaethontidae that in some respects is more specialized than *Phaethon*. This genus cannot have been ancestral to the modern tropicbirds, and it thus indicates more diversity within the family than was hitherto known.

2. *Suborder Odontopterygia*

Pelagornithidae. The pseudodontorns, as I shall call them, were an extraordinary group of gigantic marine gliding birds with very large bills bearing numerous pointed toothlike projections (Fig. 9) that in reality are only bony extensions of the rostrum and mandible. Their bones were excessively thin, and as a consequence these birds are known mainly from disassociated

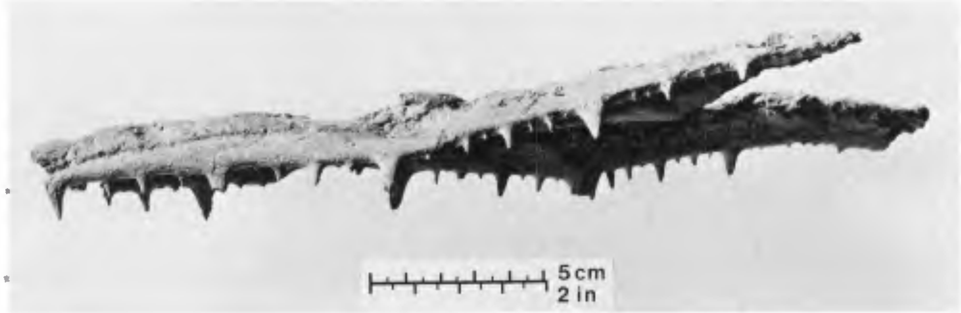

FIG. 9. Partial rostrum of a large pseudodontorn (probably *Osteodontornis orri:* Pelagornithidae) from the middle Miocene (Barstovian) Round Mountain silt in California, showing the bony toothlike projections that characterize this family. (Photograph by Victor E. Krantz.)

fragments that are very imperfectly preserved. The only exception to this is the holotype of *Osteodontornis orri*, from the late Miocene of California, which includes the skull and associated limb elements represented by essentially two-dimensional mineralized bone or impressions, plus scattered feather impressions (Howard, 1957a). The many fragments of pseudodontorns that have been discovered and described have been placed in a number of different living and extinct families, not all of which have been associated with the Pelecaniformes. The group is in dire need of a comprehensive and sensible revision, and as this would be incomplete without some of the material currently in my charge, the blame for the lack of such a revision must rest with me. Much of the following appraisal is the result of my preliminary investigations.

Harrison and Walker (1976b) reviewed the pseudodontorns, but their results are completely unrealistic. For example, they recognize six species, in five genera, in three families in the Lower Eocene deposits of the Isle of Sheppey alone. They present no evidence, however, that the rostrum they assign to the Pseudodontornithidae, and humeri they assign to the Dasornithidae, are not referable to one or the other of the two species of Odontopterygidae that they recognize on the basis of skulls.

From my examination of specimens and the literature, I believe that all the various pseudodontorns clearly belong to a single family. The oldest available name for this group is Pelagornithidae Fürbringer, 1888. Synonyms of this name are Odontopterygidae Lydekker, 1891, Cyphornithidae Wetmore, 1928, Pseudodontornithidae Lambrecht, 1933, and perhaps Dasornithidae Harrison and Walker, 1976b, provided that Harrison and Walker have correctly assigned the very imperfect cranium of *Dasornis londinensis* Owen to the pseudodontorns.

The first appearance of the family is in the early Eocene (Ypresian) of the

Isle of Sheppey, England. Of the plenitude of taxa of pseudodontorns recognized by Harrison and Walker (1976b) in these deposits, the best known is *Odontopteryx toliapica* Owen, 1873, based on a partial skull and mandible, although this may not be the oldest name available for the species. Without reference to the specimens it is impossible to assess the status of the various nominal taxa from Sheppey, but from perusing the text and illustrations in Harrison and Walker (1976b) I cannot find evidence that there are more than two species of pseudodontorns represented, a large one and a somewhat smaller one. These may perhaps be referable to two distinct genera. The names that would be assigned to these taxa cannot be determined without a revision that takes into account the fact that bird skeletons consist of more than one bone.

The next occurrence of the family is an incomplete sternum from the middle Eocene of Nigeria that Andrews (1916) named *Gigantornis eaglesomei* and considered to belong to a gigantic bird somewhat like the Procellariiformes and Pelecaniformes but perhaps more similar to the latter. Brodkorb (1963b) placed *Gigantornis* with the albatrosses (Diomedeidae) but Rich (1974, p. 169) has correctly pointed out the many pelecaniform characteristics of the specimen and removed *Gigantornis* to the Pelecaniformes, where it "most probably represents a family separate from any of the living families of that order." The similarity of the sternum of *Gigantornis* to that of a pseudodontorn in the Smithsonian collections from the Miocene of Oregon, convinces me that *Gigantornis* is referable to the Pelagornithidae. The reconstruction of the sternum of *Gigantornis* in Halstead and Middleton (1976) is evidently based on the sternum of *Diomedea* and is inaccurate, as the fossil is actually more nearly complete than they indicate.

Tonni and Cione (1978) and Tonni (1980) have documented a fragment of rostrum, unquestionably from a pseudodontorn, from the Tertiary deposits of Seymour Island, Antarctica, that have yielded so many fossil penguins. These deposits are now believed to be late Eocene in age. The Antarctic specimen came from a bird of particularly immense size. This occurrence indicates that pseudodontorns were probably worldwide in distribution by the Eocene.

Several specimens of very large marine birds that are almost certainly pseudodontorns have been recognized from the Charleston region of South Carolina. The first of these to be described was the distal end of a femur that Shufeldt (1916) named as a gigantic gooselike bird, *Palaeochenoides mioceanus*. Wetmore (1917) recognized this as a pelecaniform and later (Wetmore, 1928) referred the species to a new family, Cyphornithidae, based on *Cyphornis* Cope, 1894, from the Miocene of British Columbia (see below). Hopson (1964) discusses three additional specimens from South Carolina: a fragment of a mandible that he referred to *Pseudodontornis*, the distal end of a tarsometatarsus that he tentatively referred to *Paleochenoides*, and a very fragmentary piece of tarsometatarsus that he named *Tympanoneisiotes wetmorei* and referred to the Cyphornithidae.

All of the above specimens were attributed to the Lower Miocene Hawthorne Formation, the type section of which is in north-central Florida, but none of them was found in place. Robert Weems of the U. S. Geological Survey (personal communication) informs me that, although the stratigraphy of the marine deposits in the Charleston area is complex, the Hawthorne Formation does not appear anywhere near there. These fossils are probably either from the Cooper or Chandler Bridge Formations, which are late Oligocene (Chattian–see Sanders, *et al.*, 1982) in age. I have also examined a distal portion of a rostrum of a pseudodontorn from the Ashley Formation, taken from the Cooper River in South Carolina. The age of the holotype of *Tympanonesiotes* may be a bit more doubtful, as there is a "phantom" unit in the vicinity of the type locality that has yielded reworked fossils of late Miocene age but for which no lithological evidence has yet been found. The specimen is indeed reworked—to the extent that about all that can be said about *Tympanonesiotes* is that it was a large bird.

The only other Oligocene pseudodontorn of which I am aware is *Caspiodontornis kobystanicus* (Aslanova and Burchak-Abramovich, 1982) represented by a skull and mandible from middle Oligocene deposits of the Apsheronian Peninsula, Caucasus. This is the only example of the family known from Asia. The validity of the genus can be determined only by a revision of the entire family, however.

There are fairly numerous examples of pseudodontorns from Miocene deposits. The first of these to be described was based on a huge humerus from the middle Miocene of France that Lartet (1857) named *Pelagornis miocaenus*. If anyone were to offer a prize for the most unimaginative name ever applied to a fossil, this would be my nomination. To be confronted with an avian humerus nearly two feet long and distinguish it by a name that means simply "Miocene seabird," requires an unenviable dullness of spirit. Anyhow, Lartet considered *Pelagornis* to be related to albatrosses, whereas Milne-Edwards (1867–1871) regarded its similarities as being with the Pelecaniformes, particularly the Sulidae.

The deposits in which *Pelagornis* was obtained appear to me to have had a seabird fauna nearly identical with that in the middle Miocene (Barstovian) Calvert Formation of Maryland and Virginia. Over the years, about a dozen fragmentary specimens of pseudodontorns have come to the Smithsonian collections from these deposits, a few of which have been briefly noticed (Olson, 1984). It is not certain how many taxa are represented here, but it is quite likely that *Pelagornis*, perhaps even the species *P. miocaenus*, is present.

There are also a few pseudodontorn remains, mostly distal ends of femora, collected from the spoil piles at the Lee Creek phosphate mine in North Carolina. Most avian specimens here come from the Lower Pliocene (Hemphillian) Yorktown Formation (Olson 1977d; Olson and Steadman, 1979), but some come from the underlying Pungo River Formation, which is in part equivalent in age to the Calvert. I suspect that the few pseudodontorns recovered here were derived from the older beds. From the femora, I would guess that there may be three species of pseudodontorns represented in combined material from the Calvert and Pungo River Formations.

A vexatious enigma is the species that was originally described by Spulski (1910) as *Odontopteryx longirostris,* for which Lambrecht (1930) later created the genus *Pseudodontornis.* This was based on a reasonably well preserved skull and mandible that was obtained from a dealer who in turn had purchased it from a Brazilian sailor. The age and provenance of the fossil are unknown and in the meanwhile the specimen appears to have been lost. It is not impossible that *Pseudodontornis* is a synonym of *Pelagornis.* However, as this is one of the more widely recognized of the various generic names that have been used for species in this group, and is also among the more descriptive, I have continued to use "pseudodontorn" as a convenient term for all the pelagornithids.

A number of specimens of pseudodontorns have been recovered from the Pacific coast of North America, the first of which was a much abraded proximal end of a huge tarsometatarsus that Cope (1894) named *Cyphornis magnus.* Wetmore (1928) studied this in as much detail as the specimen allowed and concluded that it was a pelecaniform bird for which he created the family Cyphornithidae. The deposits in British Columbia from which this specimen was probably derived have been thought to be early Miocene in age (Wetmore, 1928; Brodkorb, 1963b).

Howard (1957a) described a new genus and species, *Osteodontornis orri,* from a nearly complete skeletal impression with bone fragments from Upper Miocene (Clarendonian) shales in California. She recognized a separate order, Odontopterygiformes, consisting of the families Odontopterygidae and Pseudodontornithidae, to which latter she assigned *Osteodontornis.* Other fragmentary remains from late Miocene deposits in California have also been assigned to *O. orri* (Howard and White, 1962; Howard, 1978). In addition, I have examined two fragmentary wing bones of pseudodontorns from the middle Miocene (Barstovian) Round Moutain Silt in the Los Angeles County Museum collections, and much of a rather well-preserved rostrum in the Smithsonian collections from the same deposits (Fig. 9).

Five additional specimens of pseudodontorns in the Smithsonian collections were obtained by the late Douglas Emlong in the early and middle Miocene Nye and Astoria Formations in Oregon. These are almost certainly referable to the same genus as the California birds. There is a great likelihood, however, that *Osteodontornis* is a synonym of the earlier name *Cyphornis*. The Pacific coast pseudodontorns nevertheless do appear to be generically distinct from those known from the Miocene of the Atlantic.

Apart from the Eocene rostral fragment reported from Seymour Island by Tonni and Cione (1978) and Tonni (1980b), the only occurrences of pseudodontorns in the Southern Hemisphere have been in New Zealand. Howard and Warter (1969) described a partial skull and mandible with an associated femur from the South Island as *Pseudodontornis stirtoni*. The age of this specimen is uncertain but was determined to be no younger than late Pliocene and no older than early Miocene. Brodkorb (1971b, p. 174) listed this as "Upper Pliocene," but Fordyce (1982) has reviewed stratigraphic complexities at the type locality and cautions against citing a definite age for the specimen. If it actually were Pliocene or younger, it would be the only pseudodontorn yet found in rocks younger than Miocene. Scarlett (1972) reported the proximal end of a humerus of a pseudodontorn (incorrectly identified as the distal end), also from the Canterbury district of the South Island, that came from rocks of middle to late Miocene age.

Thus we see that the pseudodontorns were widespread through most of the Tertiary, being known from the Eocene of England, Nigeria, and Antarctica, the Oligocene of South Carolina and the Caucasus, and the Miocene of France, Maryland, Virginia, North Carolina, California, Oregon, British Columbia, and New Zealand.

Opinion has vacillated concerning the relationships of the pseudodontorns. They are generally recognized as having affinities both with the Procellariiformes and the Pelecaniformes, although it is usually accepted that they share more characters with the latter. Howard (1957a) recognized a separate order, Odontopterygiformes, for the group, but later (e.g., Howard, 1978) included them in the Pelecaniformes. Harrison and Walker (1976b) continued to recognize the pseudodontorns as a separate order because of their "intermediate" nature.

The apparently derived characters of the pseudodontorns argue for their placement in the Pelecaniformes. For example, the salt glands are completely within the orbit (Fig. 10), as in Pelecaniformes, in marked contrast to Procellariiformes and most other marine birds, in which the salt glands are in furrows on top of the skull. On the other hand, the distal end of the tarsometatarsus that Hopson (1964) assigned to *Palaeochenoides*, and which must surely have come from a pseudodontorn, has almost no pelecaniform characters and closely resembles the same element in albatrosses. As is already apparent, the entire group should be subject to a critical reevaluation at all levels. One of the goals of such a treatment should be to assess the bearing that the pseudodontorns have on a hypothesis deriving the Pelecaniformes and Procellariiformes from a close common ancestor.

Most of the pseudodontorns were truly gigantic. Howard (1957a) esti-

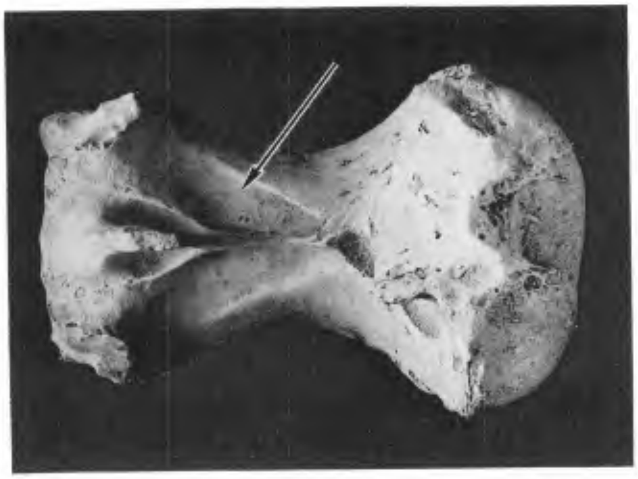

FIG. 10. Ventral view of the cranium of a large pseudodontorn (Pelagornithidae) from the middle Miocene (Barstovian) Astoria Formation in Oregon (the posterior portion, at the right, has been worn away, leaving an endocast of the brain). The large depressions for the salt glands (arrow) in the roof of the orbit provide evidence for placing the Pelagornithidae in the Pelecaniformes. (Photograph by Victor E. Krantz.)

mated a wingspan of 14 to 16 feet for *Osteodontornis orri,* and if anything I would gauge this as an underestimate, with 18 to 20 feet (5.5 to 6 m) being quite likely for the material I have examined from the Miocene of Oregon. The bones of these birds are extremely light and thin, more so even than those of frigatebirds. The pseudodontorns were unquestionably marine gliding birds that must have filled a niche somewhat like that of albatrosses. The structure of the proximal end of the humerus is unique among birds. The pectoral crest is squared in outline and situated far distally from the head. There is a unique large protuberance on the shaft at the level of the proximal end of the pectoral crest that may have functioned either as a point of insertion for M. coracobrachialis cranialis, or as point of origin of the distal head of M. biceps brachii, inasmuch as the bicipital crest is all but absent, as in most Pelecaniformes. In addition, the head of the humerus and the dorsal and ventral tubercles are all in virtually the same proximodistal plane, and the head in proximal view is an oblong diagonal. It thus appears that the nature of the humeral articulation was such as to have restricted the normal rotary movement of the head in the glenoid facet. At the same time, the muscles that counter the forces that raise the wing above the horizontal were greatly strengthened. Possibly pseudodontorns were incapable of sustained flapping flight and if so would have had to rely almost entirely on winds to provide lift.

The bony pseudoteeth in the pseudodontorns are not particularly well reinforced. Furthermore, they are of irregular lengths, with longer teeth being interspersed with several shorter ones. Prey items would therefore have to have been soft-bodied for the smaller teeth to have had any holding function at all. This suggests that the principal food of pseudodontorns may have been squid and other unshelled cephalopod mollusks.

4. *Suborder Fregatae*

Fregatidae. Modern frigatebirds comprise a single genus (*Fregata*) of marine birds that are specialized aerialists that feed from the surface of the water. Their skeleton is very highly pneumatic; they have very long wings, short legs and feet, and a strongly fused pectoral girdle. The only fossil frigatebird, apart from Quaternary remains of recent species, is *Limnofregata azygosternon* Olson, 1977c, known from a complete skeleton and additional referred specimens from the Lower Eocene (Wasatchian) Green River Formation of Wyoming. This interesting species is considerably more primitive than *Fregata.* The skeleton, with the possible exception of the humeri and femora, appears not to have been pneumatic. There is no fusion of the coracoids to the furcula and sternum as in *Fregata;* the wing is shorter and the legs somewhat longer; the nostril is open and unossified. These and other differences necessitate *Limnofregata* being placed in its own subfamily, Limnofregatinae. Nevertheless, the reduced hindlimb, the short, wide sternum and pelvis, and the well developed pectoral crest of the humerus indicate its affinities with the Fregatidae (Olson, 1977c).

Limnofregata may have occupied a somewhat gull-like niche on the large inland lakes that were characteristic of the early Eocene landscape of Wyoming, Colorado, and Utah. This suggests that the strictly oceanic modern frigatebirds are relicts of a group once more widespread and ecologically more diverse.

4. *Suborder Pelecani.*

Pelecanidae. The Tertiary record of pelicans is not particularly enlightening, with most of the literature on the subject having been published in the nineteenth century. *Liptornis hesternus* Ameghino, from the middle Miocene (Santacrucian) of Argentina, is known only from a large cervical vertebra that was not illustrated and that was only questionably referred to the Pelecanidae in the first place. Lambrecht (1933) referred it to the superfamily "Sulides" without putting it in a family. As with so many of Ameghino's taxa, *Liptornis* should be placed in Aves Incertae Sedis until restudied.

Considerable confusion surrounds the name *Protopelicanus cuvierii*

Reichenbach, 1853, based on a femur from the late Eocene (Ludian) Paris Basin. It was proposed by Reichenbach (1853—date of publication *fide* Richmond 1917, p. 615, footnote) for a scapula and a femur that were illustrated and briefly mentioned by Cuvier (1825). Lambrecht (1933) inexplicably carried this as "*Protopelecanus* [*sic*] sp. Reichenbach 1851." Brunet (1970) gives a good synonymy and correctly recognizes Reichenbach as the author of *Protopelicanus cuvierii*, whereas Harrison (1979b) errs in regarding Reichenbach's name as a *nomen nudum.* Brunet listed the femur as the holotype and did not discuss the scapula originally mentioned by Cuvier and by Reichenbach, so the femur may now be regarded as the lectotype. Brunet (1970, p. 16) considered *Protopelicanus* to be a typical pelican, somewhat more specialized than living species of *Pelecanus.* Harrison (1979b) considered that the femur of *Protopelicanus* was most similar to that of the Sulidae, although lacking the pneumatic foramen, and he removed the genus to that family. Brunet's illustrations indicate to me that *Protopelicanus* is indeed a pelecaniform, but probably not a pelican. As the femur in the Pelagornithidae is also sulidlike and nonpneumatic, I do not feel that *Protopelicanus cuvierii* can be confidently referred to the Sulidae, however, and the species requires additional study and comparison.

The oldest certain pelican is *Pelecanus gracilis* Milne-Edwards, which is rather rare in the Lower Miocene (Aquitanian) fossiliferous deposits of France. *Pelecanus intermedius* Fraas, from the middle Miocene Nördlinger Ries and Steinheim Basin of Germany, is represented by fairly abundant material including the skull and mandible (Fraas, 1870; Lydekker, 1891). A cranium of the same age from the Nördlinger Ries was differentiated as *P. fraasi* by Lydekker (1891).

Pelecanus tirarensis A. H. Miller, 1966a, is a small species known from several fragmentary tarsometatarsi from deposits in South Australia that are now considered to be Miocene in age (Rich and Van Tets, 1981). Two early Pliocene species, *P. cautleyi* and *P. sivalensis*, were described by Davies (1880) solely from the distal ends of ulnae from the Siwalik Hills in India. *P. sivalensis* was only tentatively assigned to *Pelecanus*, however. Lydekker (1891) referred portions of femora and radii to *P. cautleyi*, from which it appears likely that at least one species of pelican actually does occur in the Siwalik fauna. More recently, Harrison and Walker (1982) have referred a few poorly preserved fragments from the Siwaliks to *P.* cf. *sivalensis.*

Additional species of *Pelecanus* have been named from the early Pliocene of the Ukraine (*P. odessanus* Lambrecht) and the late Pliocene of Idaho (*P. halieus* Wetmore), the latter being known only from the proximal end of a radius. In the Smithsonian collections are two distal ends of femora of *Pelecanus* from the lower Pliocene (Hemphillian) deposits at Lee Creek, North Carolina, that are from a species considerably larger than either of the two extant species of pelicans in the New World.

Rich and Van Tets (1981) reviewed the Quaternary pelicans of Australia and New Zealand, named a new small species, *Pelecanus cadimurka*, from Australia, and elevated *P. conspicillatus novaezealandiae* Scarlett of New Zealand to full specific rank as *Pelecanus novaezealandiae*.

5. *Suborder Sulae*

a. Sulidae. Sulids have an extensive fossil record, with well over 20 paleospecies having been named. These are in great need of revision, but it is beyond the scope of this chapter to treat all of the various taxa. Rather, I shall confine myself to calling attention to some of the more recent literature on the subject and making a few general observations.

I know of no good evidence that any of the species listed in Brodkorb (1963b) are incorrectly referred to the Sulidae. Species described subsequently are *Morus magnus* Howard, 1978, a very large gannet from the late Miocene of California, and *Sarmatosula dobrogensis* Grigorescu and Kessler, 1977, from the late Miocene (Sarmatian) of Romania.

Harrison (1975b,c) erected three new genera and a new family for three species of sulids named by Milne-Edwards, one of which he removed to the Phalacrocoracidae. This was evidently done without reference to any of the actual specimens and I find myself in almost perfect disagreement with all of Harrison's conclusions.

The oldest fossil referred to the Sulidae is *Sula ronzoni* Milne-Edwards from the early Oligocene of France. The type is a partial pelvis still in matrix. As illustrated by Milne-Edwards (1867–1871) it is badly broken and difficult to interpret. Harrison's (1975b) reasons for placing it in the Phalacrocoracidae are not at all convincing and the status of the genus *Prophalacrocorax* that he proposed for it can only be determined upon examination of the holotype, if then.

The next earliest sulid is *Sula arvernensis* Milne-Edwards from the late Oligocene of France, which is based on a pelvis and sternum, also in a block of matrix. As illustrated by Milne-Edwards, the posterior border of the sternum differs from that of modern sulids in being four-notched, a primitive condition that is seen also in *Limnofregata* (Olson, 1977c) but not in modern frigatebirds. Harrison (1975b) proposed the preoccupied name *Parasula* for this species (later replaced by *Empheresula* Harrison, 1975c), but whether such a distinction is justified remains to be determined. *S. arvernensis* could be merely a somewhat more primitive species of a modern genus. I have examined roughly contemporaneous fossils of sulids from the late Oligocene of South Carolina in the Charleston Museum that do not differ substantially from modern genera.

Additional fossil species that have been assigned to the modern genus *Sula* have been described from the Miocene and Pliocene of California and Florida (Brodkorb, 1963b). Paleospecies of *Morus* occur in the Miocene of California, the Pliocene of Florida, and the mid-Atlantic coast of the United States (Brodkorb, 1963b). The presence of *Morus reyanus* Howard, 1936, in the late Pleistocene (Rancholabrean) of California shows that gannets persisted into the Quaternary in the North Pacific, where they no longer occur.

Sulids are abundant in the Medial Miocene and Lower Pliocene deposits of Maryland, Virginia, and North Carolina, and most of those that I have examined appear to be referable to *Morus* rather than *Sula*. These two genera are very distinct osteologically and their differences can be discerned at least as far back as the middle Miocene. There is no justification, therefore, for combining *Morus* with *Sula*.

The genus *Microsula* comprises two quite small sulids from the middle Miocene of France [*M. pygmaea* (Milne-Edwards)] and Maryland (*M. avita* Wetmore, the type of the genus). *Microsula* has been regarded either as a subgenus of *Sula* (Wetmore, 1938) or as a distinct genus (Brodkorb, 1963b). One of the main characters used by Wetmore (1938) to distinguish *Microsula* was the lack of pneumaticity in a carpometacarpus that he referred to *M. avita*. I have found, however, that this specimen is from a larger species of sulid that is fairly common in the same formation. Certain of the middle Miocene sulids from the western Atlantic have bones that are decidedly less pneumatic than in modern members of the family, but it is doubtful that this is of generic consequence. Harrison (1975b), who, it must be remembered, evidently based his conclusions on Milne-Edwards' illustrations, placed *M. pygmaea* in its own genus, *Pseudosula*, and made this the type of a new family, Pseudosulidae. This is absurd. Milne-Edwards' (1874) illustrations clearly show that *M. pygmaea* is a sulid; furthermore this species could well prove to be conspecific with *M. avita*. The considerable material of the latter that I have examined suggests that *Microsula* may be a small form of *Morus*. A species similar to *M. avita* but distinct from it occurs in Upper Oligocene deposits of South Carolina (S. L. Olson, unpublished).

Three additional genera have been recognized in the Sulidae: *Miosula* and *Palaeosula* from the Miocene and Pliocene of California (Brodkorb, 1963b), and *Sarmatosula* from the late Miocene of Romania (Grigorescu and Kessler, 1977). These were distinguished from other sulids by differences in the proportions of the elements of the wing, particularly by the shorter length of the ulna in comparison with that of the humerus. These taxa need further study, both to determine their relationships to each other and to ascertain their precise relationships to more typical sulids. They might possibly represent an adaptive mode similar to that through which the ancestors of the Plotopteridae may have passed.

b. Plotopteridae. The recognition of the Plotopteridae was one of the more exciting recent advances in avian paleontology. These flightless, wing-propelled diving birds were remarkably convergent towards penguins and alcids in their pectoral apparatus, but clearly were derived from the suborder Sulae of the Pelecaniformes (Olson and Hasegawa, 1979; Olson, 1980b). The family was originally and correctly diagnosed on a single fragment of coracoid from the early Miocene (Arikareean) of California that was described as *Plotopterum joaquinensis* (Howard, 1969). *Plotopterum* was rather small compared to other members of the family, being only as large as a medium-sized cormorant.

The only other form as yet named in the family is *Tonsala hildegardae* Olson, 1980b, from the late Oligocene of Washington State. This is known from a partial associated skeleton and was larger than all but the largest two species of living penguins. Remains of several different species of Plotopteridae have been recovered from various late Oligocene to early Miocene sites in Japan (Hasegawa *et al.*, 1979). Most of these were large to very large birds, with the largest previously known having been estimated at 2 m or more in length (Olson and Hasegawa, 1979). Since then, Y. Hasegawa has sent me a cast of a stupendous femur from Japan belonging to an even larger species. This bone has a total length of almost 225 mm, and came from the largest diving bird yet known.

Several partial associated skeletons have been found, and almost all skeletal elements are known from one or another species in the family. Hasegawa *et al.* (1977) described and illustrated a femur from the early middle Miocene of central Japan that they identified as "Phalacrocoracidae ? gen. et sp. indet." I have examined and compared a cast of this specimen and found it to be much more similar to the femur of *Anhinga* than that of *Phalacrocorax*, for which reason this specimen is likely to be from a plotopterid (see below). Its size would be compatible with that of *Plotopterum* itself.

Thus the Plotopteridae are known to range in age from late Oligocene to middle Miocene, after which they disappear. A relation between the extinction of giant penguins and the giant plotopterids and the evolutionary ascendancy of seals and porpoises has been suggested (Olson and Hasegawa, 1979; Olson, 1980b), although the mechanism of extinction lies entirely in the realm of speculation.

The most striking feature of the Plotopteridae is their modification of the wing into a paddle-like flipper similar to that of penguins and flightless alcids. The proximal end of the humerus is remarkably penguinlike, whereas the distal end is more alcidlike. The radius, ulna, and carpometacarpus are foreshortened, the last having a long, low first metacarpal as in flightless alcids. The blade of the scapula is very wide and thin, as in penguins. The plotopterids have a typically pelecaniform sternum, however, with the furcula articulating strongly with the apex of the carina. The elements of the hindlimb show their greatest similarity to the Anhingidae among the Pelecaniformes. The Plotopteridae provide a spectacular example of convergent evolution while at the same time contributing to make the Pelecaniformes one of the most morphologically diverse orders in the class Aves.

c. Anhingidae. The earliest fossil referred to the Anhingidae is *Protoplotus beauforti* Lambrecht, 1931a, described from a nearly complete skeleton from Sumatra originally thought to be late Eocene in age but possibly younger. This very interesting specimen is now being restudied and is considered as probably being referable to a new family (P. V. Rich, personal communication). Although the modern anhingas (*Anhinga*) have a highly specialized skull and cervical vertebrae, their postcranial osteology I find to be more primitive than that of cormorants (Phalacrocoracidae). The hindlimb in the flightless penguinlike Plotopteridae is more similar to that in *Anhinga* than that of any other pelecaniform (Olson, 1980b). Almost certainly the Anhingidae, Plotopteridae, and Phalacrocoracidae have a close common ancestry. It will be of interest to determine how similar *Protoplotus* may be to such an ancestor.

Anhinga pannonica Lambrecht, 1916, was described from a cervical vertebra and a referred carpometacarpus from Hungary from deposits originally regarded as early Pliocene but now placed in the late Miocene. Rich (1972) assigned a cervical vertebra and a portion of a humerus from the late Miocene of Tunisia to the same species, which she characterized as being slightly larger than modern *Anhinga anhinga,* with the more elongate and slender cervical vertebrae that distinguish the living species *A. rufa* from *A. anhinga.* Harrison and Walker (1982) assigned two fragmentary fossils from the late Miocene Siwalik series in Pakistan to *A.* cf. *pannonica.* Additional diversity of the Anhingidae in the Tertiary is indicated by *Anhinga grandis* Martin and Mengel, 1975, based on the distal end of a humerus from the Kimball Formation of Nebraska. This was regarded by Martin and Mengel to be late Pliocene but has subsequently been determined as being of Hemphillian age (Breyer, 1981) and is latest Miocene. This species was approximately 25% larger than modern *Anhinga anhinga.* Brodkorb and Mourer-Chauviré (1982) described a third paleospecies, *Anhinga hadarensis,* from late Pliocene to early Pleistocene (3.5 to 1.5 million years ago) deposits in Ethiopia and Tanzania. This they assumed to be ancestral to the living species *A. rufa.*

There is less diversity in anhingas in the Quaternary than was apparent previously, however, as both *Anhinga parva* of Australia and *Anhinga nana* of Mauritius and Madagascar were shown to be synonyms of small living species of *Phalacrocorax* (A. H. Miller, 1966b; Olson, 1975b). Although A. H. Miller (1966b) considered that *Anhinga laticeps* De Vis, based on a cranium from the late Pleistocene of Australia, was probably a valid species, Brodkorb and Mourer-Chauviré (1982) considered this debatable in the absence of additional fossil material.

I fully concur with Brodkorb and Mourer-Chauviré (1982) that it is inappropriate to regard the Anhingidae as forming a subfamily of the Phalacrocoracidae. Furthermore, it should be noted that despite the modern tendency to regard all the living species of *Anhinga* as constituting a superspecies (e.g., Bock and Farrand, 1980), this is not the case. Beddard (1982) discussed cranial differences and Harrison (1978) called attention to the differences in structure of the hypotarsus between *Anhinga anhinga* and the Old World members of the genus. There are many other osteological distinctions as well, such as the principal opening in the anterior wall of the braincase, which is large in *Anhinga anhinga* and much smaller in the Old World forms. It is possible that the Old World anhingas constitute a superspecies, but the New World anhinga is definitely not part of it.

d. Phalacrocoracidae. The noncormorants listed in this family by Brodkorb (1963b) include *Graculavus, Actiornis*, and *Phalacrocorax mediterraneus*. The two species of *Graculavus* from the late Cretaceous of New Jersey are charadriiform, as first noted by Shufeldt (1915). These are "transitional" charadriiforms with similarities to the Burhinidae and Presbyornithidae (Section X,D,1,c). *Actiornis anglicus*, from the late Eocene of England, is not a cormorant (Harrison and Walker, 1976c), but its true affinities are uncertain (Olson, 1982a). Cracraft (1971a) has shown that *Phalacrocorax mediterraneus* Shufeldt, from the early or middle Oligocene of Colorado, belongs in the gruiform family Bathornithidae and he synonymized the species with *Paracrax antiqua* (Marsh).

The earliest cormorant is an undescribed genus, near *Phalacrocorax*, from the Eo–Oligocene Phosphorites du Quercy, France (Mourer-Chauviré, 1982; personal communication). Following this are the four species that Brodkorb (1963b) lists from lower Miocene deposits in France, Florida, and Oregon. Additional Tertiary species are known from the late Miocene of France, Germany, and California, and the Pliocene of Italy, Florida, Idaho, California, and Oregon (Brodkorb, 1963b; Martini, 1974). Two of the Pliocene species were revised by Murray (1970). There is little doubt that these various forms are indeed cormorants, and all have been referred to the living genus *Phalacrocorax*. It should be noted that two supposed species of herons have been shown to be the same species as *Phalacrocorax praecarbo* von Ammon, which now becomes *P. brunhuberi* (see Section X,B, Ardeidae). Additional Tertiary species described subsequent to Brodkorb (1963b) are *Phalacrocorax anatolicus* Mourer-Chauviré, 1978a, from the early Miocene of Turkey, *P. ibericum* Villalta, 1963, from the late Miocene (Pontian) of Spain, *P. lautus* Kurochkin and Ganya, 1972, from the late Miocene (Sarmatian) of Moldavia, *P. mongoliensis* Kurochkin, 1971, and *P. reliquus* Kurochkin, 1976b, both from the middle Pliocene of Mongolia, and *P. goletensis* Howard, 1965, and *P. chapalensis* Alvarez, 1977, from the Plio–

Pleistocene of Mexico. Abundant cormorant remains from the early Pliocene of South Africa are mostly from a form ancestral to the living species *Phalacrocorax capensis;* a very few are referable to a smaller cormorant of the "*Microcarbo*" group (Olson, 1983b, 1985d; H. F. James, manuscript). Intraspecific variation in *Phalacrocorax capensis* and its Pliocene antecedent is so great (H. F. James, manuscript) as to call into question the validity of most of the species of fossil cormorants based on isolated fragments.

It is difficult to know what to make of *Pliocarbo longipes* Tugarinov, 1940, from the early Pliocene of the Ukraine. This was described from a worn tarsometatarsus and a referred femur. The size and proportions of the tarsometatarsus do seem different from typical cormorants, but the illustrations of it are too poor even for certain familial verification.

Harrison (1979a) made a new genus and species, *Valenticarbo praetermissus,* for a supposed cormorant from the late Pliocene to early Pleistocene portion of the Siwalik series in India. The "holotype" is a century-old plaster cast of the proximal end of a tarsometatarsus lacking part of the hypotarsus—the whereabouts of the original being unknown. This must be very near the acme of zealotry for naming new species of fossil birds. It is highly doubtful that the genus *Valenticarbo* could be shown to be valid, even if a specimen of it did exist.

As with so many families of birds, there is little to be said about the evolutionary history of the Phalacrocoracidae in the absence of a comprehensive modern revision. The family first appears in the late Eocene or early Oligocene of Europe and the living genus *Phalacrocorax* appears in the early Neogene and radiated widely subsequently.

H. PROCELLARIIFORMES

1. Diomedeidae

First, to eliminate the nonalbatrosses from further discussion, it should be noted that *Gigantornis* has been removed to the pseudotoothed birds (see Pelagornithidae). *Manu antiquus* Marples, from the early Oligocene of New Zealand, is based solely on a fragmentary furcula that differs considerably from that of living albatrosses; its affinities are indeterminable without additional specimens.

Of greater interest is *Plotornis delfortrii* Milne-Edwards, 1874, described from a tarsometatarsus and humerus from the middle Miocene of France. Despite the fact that Milne-Edwards clearly believed this species to be closest to albatrosses, both Lambrecht (1933) and Brodkorb (1963b) placed *Plotornis* in the Procellariidae. The illustrations with the original description show beyond doubt that *Plotornis delfortrii* is an albatross, and only when it can be compared with the full range of variation in *Diomedea* will we be able to determine if it really deserves a separate genus, although the species is smaller than any extant member of the family. The distal end of a humerus from the middle Miocene (Barstovian) Calvert Formation of Maryland in the Smithsonian collections is very similar to the humerus illustrated for *P. delfortrii* and is perhaps from the same species (S. L. Olson, unpublished). A similar humeral fragment from the Upper Oligocene (Chattian) Chandler Bridge Formation (Sanders *et al.*, 1982) of South Carolina appears to be from a slightly different species, but is clearly closely related to *P. delfortii* and provides the earliest record for the family Diomedeidae (S. L. Olson, unpublished).

Although only these smallest of albatrosses are known from the middle Miocene of the Atlantic, two species of *Diomedea* have been described from the middle Miocene (Barstovian) of California. One of these, *D. milleri* Howard, 1966c, is smaller than extant albatrosses but nevertheless was larger than *Plotornis*. The other, *Diomedea californica* L. Miller, is a large species, about the size of recent *D. albatrus* or larger, known from distal portions of a tarsometatarsus, humerus, and tibiotarsus (L. H. Miller, 1962; Howard, 1966c, 1978). The same, or a closely related species, seems to have been relatively common in the middle Miocene of Oregon, where seven specimens, including three skulls, have been obtained from the Astoria Formation (S. L. Olson, unpublished). These skulls are of interest in that they show considerably less ossification, as for example around the nostril, than do modern albatrosses. Until feather hunters nearly exterminated the species, *Diomedea albatrus* was the common inshore albatross along the coast of the eastern Pacific. Evidently there has been an albatross of similar size in this niche at least since the middle Miocene. Howard (1982) discusses the occurrence of bones of smaller, unnamed albatrosses from several late Miocene sites in California.

The only published Tertiary records of the family from the Southern Hemisphere are *Diomedea thyridata* Wilkinson, 1969, known from an incomplete rostrum from the late Miocene of Victoria, Australia, a single toe bone of an albatross somewhat larger than *D. albatrus* from the early late Miocene of the Valdez Peninsula in Argentina (Olson, 1984c), and the proximal end of a tarsometatarsus of a smaller species from the early Pliocene of South Africa (Olson, 1983b, 1985a).

Albatrosses are common in the Lower Pliocene (Hemphillian) marine deposits at Lee Creek, North Carolina, where at least four species may be represented, including one the size of *D. californica* (S. L. Olson, unpublished). A tibiotarsus from the Pliocene Bone Valley Formation of Florida was referred by Wetmore (1943) to the Pleistocene species *Diomedea anglica*, but this assignment is doubtful. The Bone Valley specimen also differs from the tibiotarsus in any of the species from Lee Creek. The proximal end of a carpometacarpus in the Smithsonian collections provides another specimen of *Diomedea* from Bone Valley.

Diomedea anglica Lydekker was based on a tarsometatarsus from the Lower Pleistocene Red Crag of Suffolk, England, to which species an ulna from the underlying Upper Pliocene Coralline Crag was referred. *D. anglica* was smaller than living *D. exulans* but larger than most other living albatrosses, and thus was similar in size to *D. californica*, the largest species of *Diomedea* from Lee Creek, and the species represented at Bone Valley. Although many systematic details remain to be worked out, it is evident that albatrosses were common in the North Atlantic in the late Tertiary and that their subsequent disappearance from that ocean was a Quaternary event.

2. *Procellariidae*

Plotornis delfortrii, as we have seen, is an albatross. *Argyrodyptes microtarsus* Ameghino, known from portions of a tibiotarsus and femur from the early Miocene ("Patagoniano") of Argentina, was originally described as a penguin. Although Simpson (1946) suggested only that it was not a penguin, Brodkorb (1963b) assigned it to the Procellariidae with no explanation. Tonni (1980a, p. 108) queried the familial identification but then added that its "placement in the Procellariidae . . . is quite probable." Without critical study, this species cannot add to our knowledge of evolution in the Procellariidae, even if it were correctly assigned to that family.

Early Pliocene faunas from the southwestern coast of South Africa have yielded the first Tertiary remains of subantarctic Procellariidae, including three species of prions of the genus *Pachyptila*, one of which was much larger than any living species, as well as unnamed species of *Procellaria*, *Calonectris*, *Puffinus*, and an enigmatic fulmarine petrel (Olson, 1983b, 1985a,b).

Fulmarus miocaenus Howard, 1984, based on a complete humerus from the middle Miocene (Barstovian) of California, was considerably smaller than the living species of *Fulmarus*, whereas *Fulmarus hammeri* Howard, 1968, known so far only from the proximal end of a carpometacarpus from the late Miocene (Clarendonian) of California, was somewhat larger than extant forms.

With the exception of these two species of *Fulmarus*, all other Tertiary fossils of Procellariidae from the Northern Hemisphere have been referred to the modern genus *Puffinus*. The earliest of these is *Puffinus raemdonckii* Van Beneden, based on a humerus from the early Oligocene (Rupelian) of Belgium. It was originally described as a gull, but the illustrations clearly show that Brodkorb (1962) was correct in referring it to the Procellariidae.

The specimen needs to be reexamined before it can definitely be stated to belong in the genus *Puffinus*, however. In the collections at Harvard University, I have examined the distal end of a humerus from the Upper Oligocene Ashley member of the Cooper Formation in South Carolina that is from a procellariid that does not seem to fit conveniently in any modern genus. In the collections of the Charleston Museum is a humerus of a small procellariid, the size of the modern species *Bulweria bulwerii* and not too different in morphology, from the Upper Oligocene (Chattian) Chandler Bridge Formation (Sanders *et al.*, 1982) in South Carolina. The preceding three specimens show that some diversity of shearwater and petrel-like birds existed in the Atlantic as early as the Oligocene.

The illustration of the holotype of *Puffinus arvernensis* Milne-Edwards (in Shufeldt, 1897), a tarsometatarsus from the early Miocene of France, seems to indicate that this species is more like a *Pterodroma* than a *Puffinus*. Elsewhere from the early Miocene is *Puffinus micraulax* Brodkorb, a very small species scarcely the size of the living Audubon's Shearwater (*P. lherminieri*). This is known from the distal end of a humerus from central Florida.

From middle Miocene through Pliocene marine deposits are several named species of *Puffinus* from France, Maryland, and California. The literature on these has been compiled by Howard (1978). In addition, there are many undescribed specimens of *Puffinus* from Medial Miocene and Lower Pliocene deposits in South Africa, Maryland, Virginia, and North Carolina (Olson, 1983b, 1985a,b, unpublished). A worldwide revision of the fossils belonging to this genus will be needed before the significance of this extensive fossil record can be fully appreciated. From my preliminary studies, however, it appears that most of the modern species-groups, or subgenera, of *Puffinus* were in existence by the middle Miocene, and there has been very little morphological change within these lineages in 15 million years or so. As an example, *Puffinus conradi* Cope, of which fairly numerous specimens have been recovered from the middle Miocene of the Chesapeake Bay area, differs only in minor details from the living species *Puffinus gravis*, and is of the same size and proportions.

The fossil record clarifies certain zoogeographical patterns in shearwaters. For example, the *Puffinus pacificus* group (subgenus *Thyellodroma*) is curiously absent from the Atlantic at present, but fossils are known from the early Pliocene of North Carolina, and a species belonging to this group persisted into the Pleistocene at St. Helena, where it became extinct well before the arrival of man (Olson, 1975c). As with the albatrosses, it appears that the rigors of the Pleistocene may have been felt more severely in the Atlantic than in other oceans.

3. *Pelecanoididae*

The only Tertiary record for the diving petrels is a new species, very close to *Pelecanoides urinatrix,* described from three bones from the early Pliocene of South Africa (Olson, 1985a), which is of interest in that no species of Pelecanoididae occurs in South African waters today. A presumptive Miocene record of the family in New Zealand was subsequently determined to be late Quaternary in age (T. Rich *et al.*, 1979).

4. *Oceanitidae (Hydrobatidae* auct.)

Presumably because of their very small size and pelagic habits, storm-petrels are seldom recovered from Tertiary deposits. Two specimens from the late Miocene of California have been referred to the genus *Oceanodroma.* One of these is a partial skeleton in a slab, the type of *Oceanodroma hubbsi* L. H. Miller, 1951, of Hemphillian age, and the other is a tarsometatarsus of a larger, but unnamed species from the Clarendonian (Howard, 1978).

The only other Tertiary records of the family come from the early Pliocene of South Africa, where a species ancestral to *Oceanites* ("*Pelagodroma*") *marinus* bred abundantly on islands adjacent to the coast, and where a fragment of a smaller species of *Oceanites* was also deposited (Olson, 1985a,b).

I. GAVIIFORMES

I am in complete agreement with Storer (1960) that loons (Gaviidae), grebes, and Hesperornithiformes are purely convergent in their similarities and did not share a common diving ancestor. I am less confident of his suggestion of a charadriiform ancestry for loons (Storer, 1956), however, and consider it likely that the Gaviiformes are more closely related to the Procellariiformes and Sphenisciformes, although the evidence is as yet quite tentative. These three orders can be associated by the fact that the young have two true successive coats of down preceding the juvenal plumage, whereas in other birds with two coats of down the second coat is actually the plumulaceous tips of the juvenal feathers (see Olson and Feduccia, 1980a, p. 34). Chandler (1916) found the structure of the down in loons to be most similar to that of penguins and more similar to Procellariiformes than to grebes. The downy young in these three orders are usually gray and unpatterned, quite unlike the boldly patterned young of grebes or the variously patterned young of most Charadriiformes. The loonlike bill and vertebrae of some Eocene penguins may also be of significance (see Section X,J).

In contrast to Storer (1956), I find the coracoid in the fossil loon *Colymboides* to be much more similar to that in the Procellariiformes than the

Charadriiformes. Storer (1956) maintained that *Colymboides* differs from Procellariiformes and agrees with Charadriiformes in having two, rather than three, proximal foramina in the tarsometatarsus, and three, rather than two, tendinal canals in the anterior part of the hypotarsus. Taking *Diomedea* to represent the Procellariiformes, I find only two proximal foramina and three incipient canals in the hypotarsus, so these alleged differences between *Colymboides* and Procellariiformes do not seem to hold.

It has been established that the Mesozoic genera *Enaliornis* and *Lonchodytes* are not loons (Martin and Tate, 1976; Olson and Feduccia, 1980a). *Eupterornis remensis* Lemoine from the Paleocene of France was originally described as gull-like (Lemoine, 1878) but for no apparent reason Lambrecht (1933) placed it near the loons and grebes, after which it was put in the Gaviidae by Brodkorb (1963b). The illustrations of the holotype (the distal end of an ulna and a phalanx) show no resemblances to loons; thus, *Eupterornis* is best ignored until the specimens are restudied.

The putative loon *Gaviella pusilla* is based only on the proximal end of a carpometacarpus of unknown age, supposedly from the vicinity of Lusk, Wyoming. I have examined this specimen and although it is similar to loons, it is equally similar to the carpometacarpus in the wing-propelled diving Pelecaniformes of the extinct family Plotopteridae. Without more material, and in the absence of precise data on locality and age, there is little point in cudgeling our brains over the affinities of this fragment.

Therefore, the earliest loons that are demonstrably loons are referable to the extinct genus *Colymboides*, which contains two species—*C. anglicus* Lydekker, from the late Eocene of England, and *C. minutus* Milne-Edwards, described from the early Miocene of France and also reported from Czechoslovakia (Svec, 1980). *Colymboides minutus* was a very small loon and is known from abundant, well preserved material. *Colymboides anglicus* was originally known only from a coracoid, but a humerus, a portion of a skull, and an ulna have recently been referred to this species (Harrison, 1976; Harrison and Walker, 1976c). The ulna was not illustrated, but the humerus, at least, appears to be correctly assigned to family.

Storer's (1956) detailed study of *Colymboides* shows it to have many primitive features as compared with modern loons. Yet according to Harrison (1976), *C. anglicus* had a wing proportionately much shorter than that of *C. minutus* or other loons, and was therefore supposedly not on the main line of evolution of the Gaviidae.

The species *Gavia egeriana* Svec, 1982, based on two distal ends of humeri, was described from Lower Miocene deposits in Czechoslovakia that have also yielded the remains of *Colymboides minutus* (Svec, 1982), thus establishing the contemporaneity of these two genera. *Gavia egeriana* was evidently smaller than any previously known species of *Gavia*, as is an undescribed species of *Gavia* known from several specimens from middle Miocene marine deposits in Maryland, Virginia, and North Carolina (S. L. Olson, unpublished). None of these specimens are comparable with those of *G. egeriana*, however.

A worn and polished distal end of a tibiotarsus of a loon "slightly smaller than modern *Gavia immer*", found on the shore of Chesapeake Bay in Maryland, was considered by Wetmore (1941) to have come from the middle Miocene Calvert Formation, but I am convinced from its large size that it must have come from overlying Pleistocene deposits. Wetmore (1962) himself later figured a fossil cranium of a loon, found under similar circumstances at very nearly the same locality, that he referred to *Gavia immer* and attributed to the Pleistocene.

Gavia brodkorbi Howard, 1978, is known from a complete ulna from Upper Miocene (Clarendonian) deposits of Orange County, California. This is larger than the ulna of the middle Miocene species from the western Atlantic mentioned above, but smaller than in any Pliocene loons. Howard (1982) has also reported a tarsometatarsus of a larger species of *Gavia* from the late Miocene (Hemphillian) of San Diego County, California. There are three species of *Gavia* from the Lower Pliocene (Hemphillian) Yorktown Formation at Lee Creek, North Carolina; one is smaller than any other Pliocene or modern species, another is nearly as large as *Gavia immer*, and another is intermediate in size (S. L. Olson, unpublished). None of these appears to be the same as any of the species of Pliocene loons from Florida or California (see Brodkorb, 1953, and Howard, 1978, for more on these forms).

It is an unappreciated fact that loons, in addition to being highly modified for foot-propelled diving, are also specialized for using the wings in underwater locomotion. Modern loons are known to use their wings occasionally in diving, especially in "spurts or turns" (Palmer, 1962, p. 34), and if their morphology is any indication, they probably use their wings underwater on a regular basis. Evidence for this lies in the analogy of their very long, low first metacarpal and the flattened, distally expanded ulna, with similar conditions found in flightless wing-propelled alcids and plotopterids. Storer (1956) has noted that in these respects *Colymboides minutus* is much less specialized than extant loons, whereas loons from later in the Miocene are intermediate (S. L. Olson, unpublished). Thus, since the early Miocene, loons have become increasingly better adapted for wing-propelled diving at the same time that the specializations of the hindlimb were being refined. If Harrison (1976) is correct in his appraisal of the wing proportions in the late Eocene loon *Colymboides anglicus*, then it would seem that specialization for wing-propelled diving may have arisen more than once in the gaviid lineage. The same may have happened in some even earlier loonlike stock to give rise to penguins.

J. SPHENISCIFORMES

The literature on the fossil record of penguins is considerable and has been discussed extensively in technical, semipopular, and popular form by G. G. Simpson (see Simpson, 1975, 1976, 1979, and references cited therein). Other recent publications on fossil penguins include those of Jenkins (1974), Cione *et al.* (1977), and Cione and Tonni (1981).

The earliest known penguins are from Upper Eocene deposits on Seymour Island, Antarctica, and in New Zealand. The record continues through the Tertiary, with fossil penguins also having been found in Australia, Argentina, and South Africa. There are no fossils known from outside the range of modern penguins.

By the late Eocene, penguins were already quite specialized for wing-propelled diving and show most of the specializations of the limb bones found in living penguins. Hitherto, there have been few or no fossil specimens to show the nature of the bill in these early penguins. Fortunately, I was able to study portions of a rostrum and mandible of one of the giant late Eocene species from Seymour Island which show that the bill was long, pointed, and daggerlike (Fig. 11), unlike any of the modern forms. In details, as well as in overall morphology, these specimens are quite loonlike. Additional specimens are under study by P. R. Millener, who has found that a large mandibular articulation and several large cervical vertebrae from the

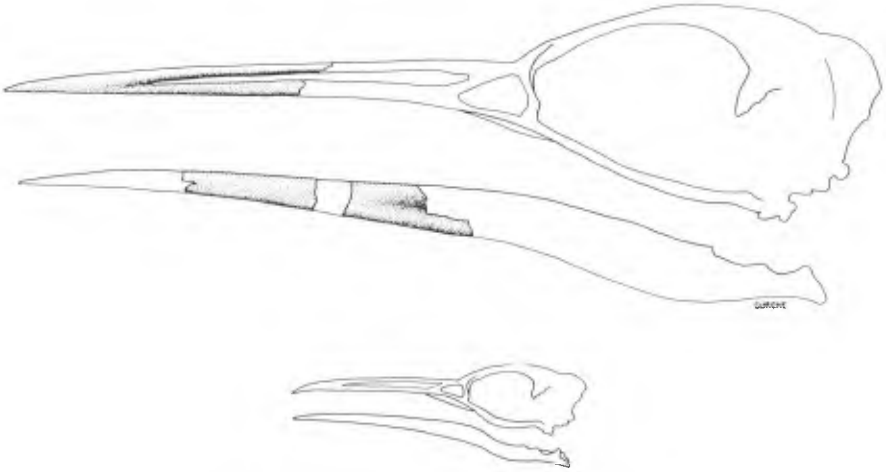

FIG. 11. Reconstructed skull of a giant late Eocene penguin (?*Palaeoeudyptes* sp.) from Seymour Island, Antarctica, based on specimens of rostrum and mandible (stippled) in the Smithsonian Institution collected by William Zinsmeister. This is contrasted with the skull of the King Penguin (*Aptenodytes patagonicus*, below), which has the longest skull of any living penguin. (Illustration by John Gurche.)

Seymour Island deposits are very different from modern penguins and are also extraordinarily loonlike. At this point it would appear that a close common ancestry between the Gaviiformes and Sphenisciformes is highly likely. The earlier penguins may have been adapted for spearing larger prey, whereas most of the modern forms are specialized for feeding partly or entirely on plankton (Zusi, 1974); those that take larger prey such as fish and squid, do not do so by spearing.

Simpson (1946) originally recognized five different subfamilies of penguins, four of which consisted exclusively of fossil taxa. He later "disowned" subfamilial designations but provided a summary of characters by which the genera of penguins could be placed in seven informal "groups" (Simpson, 1974). This is unsatisfactory in that it fails to provide a formal nomenclatural distinction for the group that includes the late Eocene penguins, at least some of which are now seen to be very distinct from living forms.

The living penguins constitute an extremely homogeneous group for which only feeding adaptations and head patterns provide consistent characters by which the species may be grouped into genera. There are no characteristics of the appendicular myology that are useful for defining genera (Schreiweis, 1982). I found that two of the postcranial characters by which Zusi (1974) was able to group species and genera result from differential ossification of ligaments that are present in all species; these characters do not appear to hold for certain Pliocene fossils (Olson, 1983b, 1985b, manuscript).

Many, if not most, of the Neogene genera of penguins that have been named were distinguished on the placement of the proximal vascular foramina of the tarsometatarsus. Given the variability inherent in the vascular system and the considerable intraspecific variability in the pattern of the foramina in the tarsometatarsus in living penguins, I suspect that few of the Neogene genera that have been proposed will bear up under close scrutiny. For the purposes of comparison with fossil postcranial elements, modern penguins may essentially be regarded as monogeneric because of their great homogeneity. Thus a fossil penguin for which the skull was unknown would have to differ significantly in postcranial osteology from *all* living penguins to have any claim to separate generic status. A revision of fossil penguins in which this principle was applied would doubtless give us a somewhat different picture of the former diversity of penguins, at least in the Neogene.

The much greater size of some of the fossil penguins, as well as of their contemporaneous ecological counterparts (Plotopteridae) in the North Pacific, has been the subject of speculation (Simpson, 1974, 1976; Olson and Hasegawa, 1979; Olson, 1980b). The disappearance of the larger members of both of these groups in the early Miocene coincides with the ascendancy of cetaceans and pinnipeds, but if these events are indeed related, an adequate mechanism for the extinction of the birds has yet to be advanced.

In contrast with the giant forms, Simpson (1981) has described a new genus and species, *Microdytes tonnii*, from presumptive late Oligocene deposits in Argentina, that was billed as "the smallest known penguin, living or fossil." The holotypical tarsometatarsus, however, is only 1.6 mm shorter than in the single specimen of the living species *Eudyptula minor* with which it was compared. This certainly cannot be representative of the size variation to be found in a species with six named geographic representatives ranging from Australia to New Zealand and the Chatham Islands. Whatever claim to fame the species *tonnii* may have on account of its small size, it will have to be known by another generic name because *Microdytes* is preoccupied by a genus of beetles (Olson, in press).

XI. Conclusion

If there is one overriding message to be conveyed by this chapter, it is that fossil birds are *not* rare. Furthermore, their significance to understanding evolution, systematics, biogeography, and the overall diversity of the class Aves can no longer be denied. Whereas E. Mayr (1983, p. 9) could claim that for twenty years no one attempted to refute his assertion that "not a single fossil bird has led to an improvement of the avian classification," such fossils as *Presbyornis*, *Juncitarsus*, and some of the Eocene penguins, for example, should now at least insure that a refutation will be attempted. Similarly, C. Patterson (1981) has contended that fossils seldom overturn theories of relationship. This may not always be the fault of the fossils, however, but of the scientists who will not accept the new insights provided by paleontology because of preconceptions based on incomplete or erroneous neontological studies. Whether fossils will actually result in an improvement in classification depends upon the degree to which the concrete evidence they provide is accepted.

The Eocene and Oligocene avifaunas of Quercy, France, which contain fossils of avian families that are now restricted to Australia, Africa, South America, and the Antilles (Mourer-Chauviré, 1982), are as good an example as exists of what the fossil record has to offer the biogeographer, who will now be compelled to consult the paleontological literature if his work is to have any cogency. And, as E. Mayr (1983, p. 10) has noted, fossils provide the *only* evidence from which we can learn about totally extinct lineages and the "adaptations and various radiations of birds in former geological periods." Although we can expect to keep hearing that fossils of birds are rare and that the avian fossil record is uninformative, henceforth it should be taken as a mark of ignorance in anyone who continues to parrot this canard.

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Note Added in Proof

A valuable paper by Cheneval (1984) concerning waterbirds from the early Miocene (Aquitanian) of France was received too late for inclusion in the text. It contains important new information regarding the Ardeidae (*Proardeola walkeri*), Plataleidae (*Plegadis paganus*), Phoenicopteridae (*Phoenicopterus croizeti*), Anatidae (*Dendrochen; Cygnopterus alphonsi* n. sp.), Ciconiidae (*Grallavis edwardsi*), Pelecanidae (*Miopelecanus* [n. gen.] *gracilis*), Sulidae (*Empheresula arvernensis*), Phalacrocoracidae (*Phalacrocorax littoralis* and *Nectornis* [n. gen.] *miocaenus*), Diomedeidae (*Plotornis arvernensis* n. comb.), and Gaviidae (*Colymboides minutus*).

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INDEX TO BIRD NAMES