

THE GENERIC ALLOCATION OF *IBIS PAGANA* MILNE-EDWARDS, WITH A REVIEW OF FOSSIL IBISES (AVES: THRESKIORNITHIDAE)

STORRS L. OLSON

National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560

ABSTRACT—On the basis of characters of the tarsometatarsus, *Ibis pagana* Milne-Edwards from the early Miocene of France is assigned to the living genus *Plegadis*. *Plegadis gracilis* A. H. Miller and Bowman, 1956, from the late Pliocene of North America, is a junior homonym of *Milnea* (= *Plegadis*) *gracilis* Lydekker, 1891, and the new name *Plegadis pharangites* is proposed as a substitute. *Plegadis paganus* and *P. pharangites* constitute the only valid Tertiary paleospecies of Threskiornithidae. All other extinct taxa that have been referred to this family are here considered to be *Aves incertae sedis* except for *Theristicus wetmorei* Campbell and *Eudocimus peruvianus* Campbell, from the late Pleistocene of Peru, and the flightless Quaternary taxa *Apteribis glenos* Olson and Wetmore of Hawaii and *Xenicibis xympithecus* Olson and Steadman of Jamaica.

INTRODUCTION

The ibises and spoonbills form a distinctive group of waterbirds of nearly cosmopolitan distribution. Brodkorb (1963) has shown that the familial name Plataleidae Bonaparte, 1838, has priority over Threskiornithidae Richmond, 1917, for this group. In my first paper on fossil ibises (Olson and Wetmore, 1976), the decision to use Threskiornithidae was an editorial one, designed to conform with general usage. I have continued to apply this term for the same reason and for the sake of consistency. The Threskiornithidae is currently placed in the order Ciconiiformes, but this is partly an artificial assemblage of unrelated families (Olson, 1979; Olson and Feduccia, 1980). Although the affinities of ibises have not been precisely determined as yet, I believe them to be related to Gruiformes and Charadriiformes. The following is a critical revision of the fossil taxa that have been assigned to this family.

SYSTEMATIC PALEONTOLOGY

Order "CICONIIFORMES"
Family THRESKIORNITHIDAE
Genus *PLEGADIS* Kaup, 1829

PLEGADIS PAGANUS (Milne-Edwards), new combination
(Fig. 1B)

Ibis pagana Milne-Edwards, 1868, is a rather small species of ibis that was founded upon abundant remains from early Miocene (Aquitanian) deposits at Langy and Saint-Gerand-le-Puy, Dept. Allier, France. Lambrecht (1933) retained the species as *Ibis pagana*, but noted that Sharpe (1899) had previously listed it as *Eudocimus paganus*

(Lambrecht consistently misspelled the genus as "Eudocymus"). Because the generic name *Ibis* Lacépède, 1799, was ultimately applied to certain storks (Ciconiidae), Brodkorb (1963) listed this species as *Eudocimus paganus*, presumably because Milne-Edwards had made his comparisons chiefly with the living species *Eudocimus ruber*, to which he found *E. paganus* to be generally similar.

After examining specimens of *E. paganus* in the Smithsonian collections, I believe that the species should be referred to the genus *Plegadis*. Osteologically, the species of *Eudocimus* and *Plegadis* are rather similar, and these two living genera are probably closely related. *Plegadis*, however, has a peculiar conformation of the distal end of the tarsometatarsus not found in other ibises. In *Eudocimus* and most other genera of birds, there is a small intertrochlear foramen that begins within the distal vascular foramen and exits distally between the middle and outer trochleae. This intertrochlear foramen is inconspicuous when viewed from the anterior aspect (Fig. 1A). In *Plegadis*, the distal vascular foramen is situated much more proximally, and the proximal opening of the intertrochlear foramen is conspicuous, being located considerably farther distad, at the terminus of a deep groove, so the two foramina are clearly visible in anterior view (Fig. 1D). These foramina are closer together in the South American species *P. ridgwayi* (Fig. 1C) than in *P. falcinellus* (Fig. 1D) or *P. chihi*. In *Ibis pagana* (Fig. 1B) the condition of the foramina is clearly approaching that in living species of *Plegadis*, with the intertrochlear foramen situated at the distal end of a deep groove. Therefore, in this respect the species is more derived than *Eudocimus*, and for this reason I refer *Ibis pagana* to the genus *Plegadis*. If *Eudocimus* and *Plegadis* are each others' closest relatives (Mayr

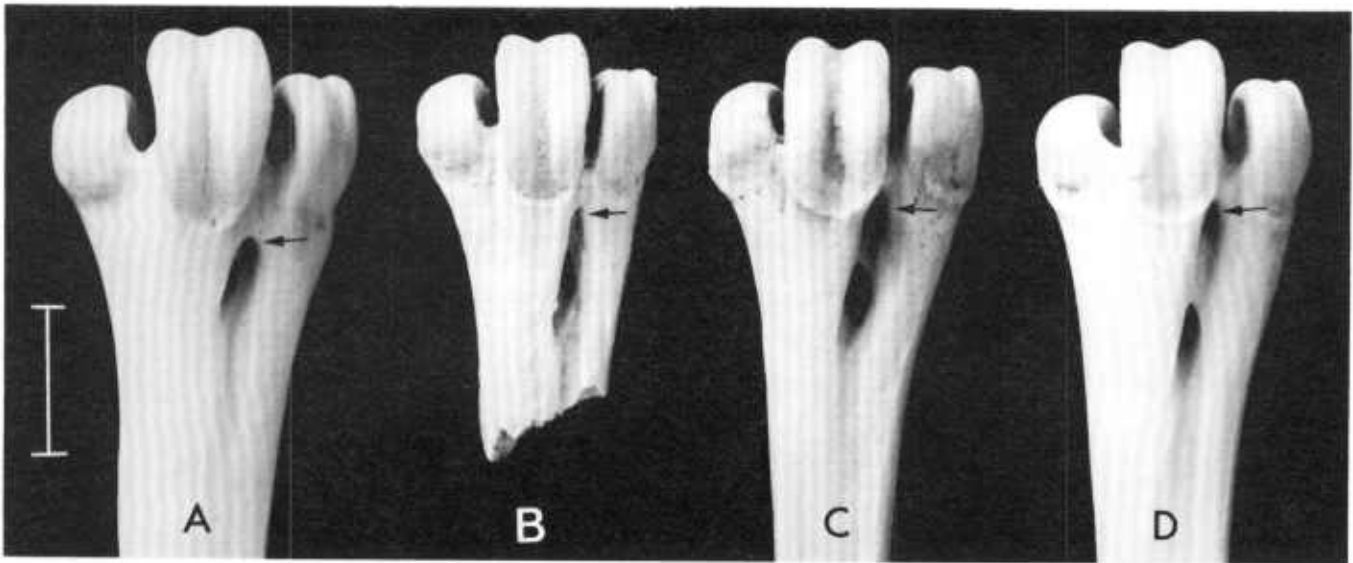


FIGURE 1. Distal ends of right tarsometatarsi of the fossil species *Plegadis paganus* (B) compared with the Recent species *Eudocimus albus* (A), *Plegadis ridgwayi* (C), and *P. falcinellus* (D). Arrows indicate location of proximal opening of intertrochlear foramen. Scale equals 5 mm for all specimens.

and Short, 1970, have suggested synonymizing these genera), then the occurrence of a species of *Plegadis* in the early Miocene implies that species similar to the more primitive genus *Eudocimus* must have been in existence before that time.

Lydekker (1891) founded *Milnea gracilis*, which he thought to be a new genus and species of Burhinidae (Charadriiformes), upon a complete humerus from the same deposits as *Plegadis paganus*. Cracraft (1972:43) determined that this humerus belonged to an ibis "con-specific with *Eudocimus paganus* or at least very closely related to it." Whether this taxon can be recognized as specifically distinct depends upon how much size variation one admits within *Plegadis paganus*, but a proper analysis of the abundant material of this species in European museums remains to be conducted. Regardless, *Milnea gracilis* Lydekker would either become *Plegadis gracilis* or a synonym of *Plegadis paganus*.

PLEGADIS PHARANGITES, new name

Within the genus *Plegadis*, Lydekker's name *gracilis* antedates *Plegadis gracilis* A. H. Miller and Bowman (1956) from the late Pliocene (Blancan) of Cita Canyon, Randall County, Texas, and the new name proposed above is required as a replacement. It is derived from Greek *pharax*, a chasm or ravine, in reference to the type locality.

Plegadis pharangites was based on the proximal portion of a tarsometatarsus (the holotype), the distal portion of an ulna, and a carpometacarpus. The species was diagnosed as being similar to living species of *Eudocimus* and *Plegadis*, but smaller. The only reason given for its generic placement was that "it appears to be more closely related to *Plegadis* in size" (Miller and Bowman, 1965:40). The

temporal significance of the Cita Canyon locality is treated in Steadman's (1980) discussion of fossil turkeys.

Collins (1964) referred certain specimens from the slightly older Rexroad fauna (Blancan) of Kansas to living South American species of ibises, but Mosely and Feduccia (1975) questioned whether this material could even be correctly assigned to genus. Collins assigned two distal ends of tibiotarsi to *Plegadis gracilis* (= *P. pharangites*), and Mosely and Feduccia tentatively referred the proximal end of a tarsometatarsus from the Saw Rock Canyon locality of the Rexroad Formation to this species.

EUDOCIMUS Wagler, 1839

EUDOCIMUS spp. (Fig. 2)

With the removal of *Ibis pagana* from *Eudocimus* to *Plegadis*, the only published fossil record for *Eudocimus* is an indeterminate species in the middle Pliocene deposits of the Bone Valley Formation in central Florida (Brod-korb, 1972). This record was based on the distal end of a tarsometatarsus that I examined, but did not compare, at the University of Florida. Another occurrence is provided by the distal end of a right tibiotarsus from the lower Pliocene Yorktown Formation at Lee Creek, North Carolina (see Olson 1977d, and Olson and Steadman 1979a, for information on other fossil birds from this locality). This specimen (USNM 181027; Fig. 2) differs from *Plegadis* in the better developed tubercle on the supratendinal bridge, the relatively narrower and deeper posterior intercondylar sulcus, and the heavier shaft. It is identical to Recent *Eudocimus albus* in size and all other details, except that the proximal border of the posterior face of the articular surface extends farther proximally on the external side in the fossil, whereas this border is straight in *E. albus*. Other

fossils referable to *Eudocimus* are Quaternary in age (see below).

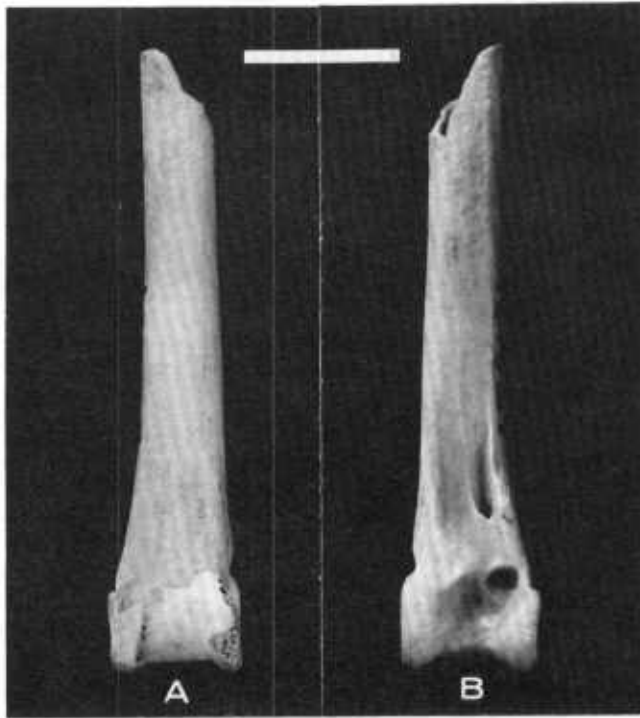


FIGURE 2. Anterior (A) and posterior (B) views of the distal end of a right tibiotarsus of *Eudocimus* sp. (USNM 181027) from the lower Pliocene Yorktown Formation of North Carolina. Arrow indicates the only point of difference between this specimen and the comparable element in the living species *E. albus* (see text). Scale equals 1 cm.

OTHER PUTATIVE TERTIARY IBISES

Tertiary and older records of ibises other than *Plegadis paganus* and *P. pharangites* all prove unsatisfactory. *Plegadornis antecessor* Wetmore, 1962, which was described as forming a new family of ibis-like birds from the Cretaceous of Alabama, was shown to belong with the toothed birds of the genus *Ichthyornis* (Olson, 1975a). *Ibidopsis hordwelliensis* Lydekker, 1891, based on the distal end of a tibiotarsus from the upper Eocene of England, was removed to the Rallidae by Cracraft (1973), although it is doubtful that the specimen can be confidently identified (Olson, 1977a:339, 343).

A humerus from the Paleocene of North Dakota was described as a new genus and species, *Dakotornis cooperi*, in a new family, the Dakotornithidae, supposedly similar to ibises (Erickson, 1975). The one-sentence diagnosis of the family is insufficient for the purpose, and the humerus of *Dakotornis* is of a type similar to that found in several different families of possibly primitive birds. It differs from all known ibises in not being pneumatic. The identity of early Tertiary birds usually cannot be determined from single elements, and without additional material there is no way to ascertain whether *Dakotornis* had any relationship with ibises.

Five nominal species from the Eocene of England have either been proposed in, or referred to, the Threskiornithidae by Harrison and Walker (1971, 1976, 1977). The reader is referred to Steadman's (1981) evaluation of the paleontological methods and results of these authors.

Harrison and Walker (1971) named a new genus and species of supposed ibis, *Proplegadis fisheri*, on the basis of an incomplete distal end of a humerus from the early Eocene London Clay at Sheppey, Kent, England. The specimen appears to be considerably water-worn, so that it is very doubtful that it was found in place. Such fragments, even in unworn condition, simply cannot be used to determine the nature and affinities of early Tertiary birds (Olson, 1977c:31). Harrison and Walker's illustrations of the type of *Proplegadis fisheri* show the bone to bear a closer resemblance to the humerus in tropicbirds (Phaethontidae: Pelecaniformes) than to that in ibises. This is particularly apparent in the straighter shaft in internal view, and the relatively narrower shaft and less expanded distal end in palmar view. *Proplegadis* may possibly be referable to the fossil genus *Prophaethon* Andrews, 1899, of the same deposits, which is known from a significant portion of the skeleton that unfortunately does not include the humerus. Regardless, the assignment of *Proplegadis* to the Threskiornithidae is dubious and the genus should be regarded as *incertae sedis*.

The species *Lithornis vulturinus* Owen, 1841, was originally described as a vulture from a sternum and a few associated bones embedded in a nodule from the early Eocene London Clay. The holotype was destroyed in the Second World War and only Owen's (1841, 1846) two indifferent line drawings of it remain. For this reason, Cracraft and Rich (1972) rightly considered that the affinities of *Lithornis* could no longer be determined. Nevertheless, Harrison and Walker (1977) attempted to transfer the species to the Threskiornithidae, based only on Owen's equivocal illustrations, which they had redrawn. In the absence of a specimen, I follow Cracraft and Rich in regarding the relationships of *Lithornis* as indeterminate.

Harrison and Walker (1976) described a new genus and species, *Gigantibis incognita*, as a supposed giant ibis based on a damaged proximal end of a femur from the upper Eocene of Hordle, Hampshire, England. Neither the diagnosis nor the description mention how this taxon resembles or differs from other taxa in the family, and Harrison and Walker do not provide a single reason for assigning the specimen to the Threskiornithidae. Their illustrations show the neck of the femur to be quite elongated, with the head markedly set off from the neck. Thus the specimen bears not the slightest resemblance to the femur in the Threskiornithidae and to me appears more similar to that of Galliformes. *Gigantibis incognita* is not an ibis and should be relegated to *Aves incertae sedis* until its true affinities can be determined.

Actiornis anglicus Lydekker, 1891, was based on the proximal end of an ulna, also from the upper Eocene of Hordle, that Lydekker assigned to the Phalacrocoracidae. Harrison and Walker (1976) transferred this taxon to the Threskiornithidae and referred two humeri and a portion of the shaft of a tarsometatarsus to the same species. One

of these humeri is the type of *Elomis(?) anglicus* Lydekker, 1891, which had previously resided in the Phoenicopteridae. Harrison and Walker's illustrations show the holotypical ulna of *Actiomis anglicus* to have the olecranon much less pronounced than in ibises. I would agree that this specimen is not from a cormorant, but neither is it clearly from an ibis.

The humerus of *Elomis(?) anglicus* Lydekker rather resembles that of an ibis, but Harrison and Walker's illustration shows the attachment of the anterior articular ligament to be much more extensive and the brachial depression more restricted than in the Threskiornithidae, in which respects the specimen more nearly resembles *Palaelodus* (Phoenicopteridae). The genus *Elomis* Milne-Edwards is based on specimens now lost and its affinities are not certain, although they may possibly lie with the Phoenicopteridae (Olson, 1978). I do not regard any of the specimens referred to *Actiomis anglicus* or *Elomis anglicus* as having been convincingly shown to belong in the Threskiornithidae.

Ibidopodia palustris Milne-Edwards, 1868, was founded on a tarsometatarsus and incomplete skull from the Aquitanian of France. Brodkorb (1963) erroneously cites Lydekker (1891) as designating the skull as the lectotype, whereas Lydekker clearly regarded the tarsometatarsus as the type. Milne-Edwards' diagnosis of the genus and the generic name itself were based on characters of the tarsometatarsus. The identity of the skull of *Ibidopodia*, as well as that of other cranial elements from the Aquitanian of France referred to cranes (*Probalearica*, Gruidae) and flamingos (*Palaelodus*, Phoenicopteridae), has been questioned (Olson and Feduccia, 1980). The tarsometatarsus of *Ibidopodia palustris*, as noted by Milne-Edwards, differs from all known ibises in having a simple, block-like hypotarsus without distinct deep tendinal grooves. Milne-Edwards considered the distal end of the bone to show similarities to ibises, although his illustrations show the inner and outer trochleae to be more elevated relative to the middle trochlea than in living ibises. In view of these dissimilarities from all known members of the Threskiornithidae, it must be doubted that *Ibidopodia* is an ibis; it should be relegated to incertae sedis.

The supposed ibis *Protibis cnemialis* Ameghino, 1891, was based on the distal end of a tibiotarsus from the middle Miocene (Santa Cruz Formation) of Argentina. The poorly executed drawing of this specimen (Ameghino, 1895, fig. 42) shows a tibiotarsus that more closely resembles that of flamingos (Phoenicopteridae) than ibises. The familial allocation of most of Ameghino's taxa of fossil birds cannot be accepted without critical modern revisions (Tonni, 1980), and I place *Protibis* in incertae sedis pending its re-examination.

QUATERNARY IBISES

With four exceptions, all continental fossils of Threskiornithidae younger than the Pliocene have been referred to extant taxa. *Ibis condita* [sic; = *condita*] De Vis, 1906 (placed in *Carphibis* by Brodkorb, 1963) was described on the proximal end of a femur from the late Pleistocene

Kaitipiri sands at Wurdulumankula, near Lake Eyre, South Australia. *Platalea subtenuis* De Vis, 1892, was based on the proximal end of a femur and the distal end of a tibiotarsus from Plio-Pleistocene deposits in Queensland. The tibiotarsus proved to be referable to *Gallinula mortierii* (Rallidae), for which reason I designated the femur as the lectotype (Olson, 1975b). The majority of the fossil taxa named by De Vis that have been re-examined have proven invalid (e.g. Olson, 1975b, 1977b), and there is no reason to accept the above taxa as representing extinct ibises. I briefly examined the holotypical femora of *Ibis condita* and *Platalea subtenuis* at the Queensland Museum in 1974 and concluded that they came from birds of different families. My notes and sketches suggest that *Ibis condita* may be a flamingo (Phoenicopteridae). Both of these taxa should be treated as *Aves incertae sedis* until proper comparisons of the types can be made.

Campbell (1979) described two new species of ibises, *Theristicus wetmorei* and *Eudocimus peruvianus*, from late Pleistocene tarpit deposits in northern coastal Peru. These are well illustrated and described and are clearly ibises. Campbell provided evidence for late Pleistocene climatic changes on the coast of Peru that caused many extinctions in this area of relatively high endemism, so it is not unreasonable to expect extinct species of ibises here. I do entertain some reservations about *Eudocimus peruvianus*, however, as this was said to differ less from *E. alba* (found in the same deposits) than either differs from *E. ruber*. The living species *E. alba* and *E. ruber* are extremely closely related and were found to hybridize readily when *E. ruber* was introduced into southern Florida, so I would not expect osteological differences between these species to be of great significance.

Until recently, ibises had not been known to give rise to flightless forms on islands, as do rails (Rallidae) and other birds. The first such ibis described was *Apteribis gienos* Olson and Wetmore, 1976, bones of which were found in Pleistocene and possibly Holocene dune deposits on the island of Molokai, Hawaii. This species had reduced wings and a nearly keelless sternum. A partial skeleton from a lava tube on Maui was tentatively referred to *A. gienos*, but is now believed to represent a second species (Olson and James, ms). Subsequently, another flightless ibis, *Xenicibis xympithecus*, was described from cave deposits in Jamaica (Olson and Steadman, 1977, 1979b). *Apteribis* is now known from nearly the complete skeleton, and new material of *Xenicibis* includes the pelvis, ribs, radius, ulna, and an incredibly bizarre carpometacarpus, none of these elements having been known previously (Olson, in prep.).

CONCLUSIONS

Ignoring all misidentified, unsubstantiated, or inadequately documented taxa, the fossil record of the Threskiornithidae can be summarized as follows. The earliest and best represented Tertiary ibis is *Plegadis paganus* from the lower Miocene of France, which is smaller and slightly more primitive in its tarsal morphology than living species of *Plegadis*. The only other valid paleospecies of

Tertiary ibis is *Plegadis pharangites* from the late Pliocene of North America. Extinct Quaternary taxa include two species from late Pleistocene tarpit deposits in Peru (*Eudocimus peruvianus* and *Theristicus wetmorei*), and flightless species from Hawaii and Jamaica (*Apteribis gienos*, *Apteribis* sp., and *Xenicibis xympthecus*).

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REFERENCES

- Ameghino, F. 1891. Enumeración sistemática de las especies de las aves fósiles de la República Argentina. *Revista Argentina de Historia Natural* 1:441–453.
- 1895. Sur les oiseaux fossiles de Patagonie. *Boletín del Instituto Geográfico Argentino* [for 1894] 15(11–12):501–602.
- Andrews, C. W. 1899. On the remains of a new bird from the London Clay of Sheppey. *Proceedings of the Zoological Society of London* 1899:776–785.
- Brodkorb, P. 1963. Catalogue of fossil birds. Part 1 (Archaeopterygiformes through Ardeiformes). *Bulletin of the Florida State Museum, Biological Sciences* 7(4):179–293.
- 1972. New discoveries of Pliocene birds in Florida [abstract], p. 634 in *Proceedings of the XVth International Ornithological Congress*. E. J. Brill, Leiden, 745 p.
- Campbell, K. E., Jr. 1979. The non-passerine Pleistocene avifauna of the Talara Tar Seeps, northwestern Peru. *Royal Ontario Museum, Life Sciences Contribution* 118:1–203.
- Cracraft, J. 1972. A new Cretaceous charadriiform family. *Auk* 89(1):36–46.
- 1973. Systematics and evolution of the Gruiformes (class Aves). 3. Phylogeny of the suborder Grues. *Bulletin of the American Museum of Natural History* 151(1):1–127.
- and P. V. Rich 1972. The systematics and evolution of the Cathartidae in the Old World Tertiary. *Condor* 74(3):272–283.
- Collins, C. T. 1964. Fossil ibises from the Rexroad Fauna of the upper Pliocene of Kansas. *Wilson Bulletin* 76(1):43–49.
- De Vis, C. W. 1892. Residue of the extinct birds of Queensland as yet detected. *Proceedings of the Linnean Society of New South Wales* [for 1891] (2) 6:437–456.
- 1906. A contribution to the knowledge of the extinct avifauna of Australia. *Annals of the Queensland Museum* 6:1–25.
- Erickson, B. R. 1975. *Dakotornis cooperi*, a new Paleocene bird from North Dakota. *Scientific Publications of the Science Museum of Minnesota* (n.s.) 3(1):1–7.
- Harrison, C. J. O. and C. A. Walker 1971. A new ibis from the lower Eocene of Britain. *Ibis* 113:367–368.
- and ——— 1976. Birds of the British upper Eocene. *Zoological Journal of the Linnean Society of London* 59:323–351.
- and ——— 1977. Birds of the British lower Eocene. *Tertiary Research, Special Paper* 3:1–52.
- Lambrecht, K. 1933. *Handbuch der Palaeornithologie*. Gebrüder Borntraeger, Berlin, 1024 p.
- Lydekker, R. 1891. *Catalogue of the Fossil Birds in the British Museum (Natural History)*. British Museum (Natural History), London, 368 p.
- Mayr, E. and L. L. Short 1970. Species taxa of North American birds. *Publications of the Nuttall Ornithological Club* 9:1–127.
- Miller, A. H. and R. I. Bowman 1956. Fossil birds of the late Pliocene of Cita Canyon, Texas. *Wilson Bulletin* 68(1):33–46.
- Milne-Edwards, A. 1867–1871. *Recherches Anatomiques et Paléontologiques pour Servir à l'Histoire des Oiseaux Fossiles de la France*. 4 volumes. Victor Masson et Fils, Paris.
- Mosely, C. and A. Feduccia 1975. Upper Pliocene herons and ibises from North America. *University of Michigan Papers on Paleontology* 12:71–74.
- Olson, S. L. 1975a. *Ichthyornis* in the Cretaceous of Alabama. *Wilson Bulletin* 87:103–105.
- 1975b. The fossil rails of C. W. De Vis, being mainly an extinct form of *Tribonyx mortierii* from Queensland. *Emu* 75(2):49–54.
- 1977a. A synopsis of the fossil Rallidae, p. 339–373 in S. D. Ripley, *The Rails of the World*. David R. Godine, Boston 406 p.
- 1977b. The identity of the fossil ducks described from Australia by C. W. De Vis. *Emu* 77(3):127–131.
- 1977c. A lower Eocene frigatebird from the Green River Formation of Wyoming (Pelecaniformes: *Fregatidae*). *Smithsonian Contributions to Paleobiology* 35:1–33.
- 1977d. A great auk, *Pinguinis* [sic], from the Pliocene of North Carolina (Aves: *Alcidae*). *Proceedings of the Biological Society of Washington* 90(3):690–697.
- 1978. The nomenclatural status of the taxa of fossil birds attributed to Auguste Aymard. *Proceedings of the Biological Society of Washington* 91(2):444–449.
- 1979. Multiple origins of the Ciconiiformes. *Conference of the Colonial Waterbird Group (1978)*, *Proceedings* p. 165–170.
- and A. Feduccia 1980. Relationships and evolution of flamingos (Aves: *Phoenicopteridae*). *Smithsonian Contributions to Zoology* 316:1–73.
- and D. W. Steadman 1977. A new genus of flightless ibis (*Threskiornithidae*) and other fossil birds from cave deposits in Jamaica. *Proceedings of the Biological Society of Washington* 90(2):447–457.
- and ——— 1979a. The fossil record of the Glareolidae and Haematopodidae (Aves: *Charadriiformes*). *Proceedings of the Biological Society of Washington* 91(4):972–981.
- and ——— 1979b. The humerus of *Xenicibis*, the extinct flightless ibis of Jamaica. *Proceedings of the Biological Society of Washington* 92(1):23–27.
- and A. Wetmore 1976. Preliminary diagnoses of two extraordinary new genera of birds from Pleistocene deposits in the Hawaiian Islands. *Proceedings of the Biological Society of Washington* 89(18):247–258.
- Owen, R. 1841. Description of the fossil remains of a mammal (*Hyracotherium leporinum*) and of a bird (*Lithornis vulturinus*) from the London Clay. *Transactions of the Geological Society of London* 6:203–208.
- 1846. *A History of British Fossil Mammals and Birds*. John van Voorst, London, 560 p.
- Sharpe, R. B. 1899. *A Hand-List of the Genera and Species of Birds*. Volume 1. British Museum (Natural History), London, 303 p.
- Steadman, D. W. 1980. A review of the osteology and paleontol-

ogy of turkeys (Aves: Meleagridinae). Natural History Museum of Los Angeles County, Contributions in Science 330:131-207.

———. 1981. [Review of Harrison and Walker 1976, 1977—see above]. Auk 98(1):205-207.

Tonni, E. P. 1980. The present state of knowledge of the Cenozoic birds of Argentina. Natural History Museum of Los Angeles County, Contributions in Science 330:105-114.

Wetmore, A. 1962. Notes on fossil and subfossil birds. Smithsonian Miscellaneous Collections 145(2):1-17.