FOSSIL BIRDS AND EVOLUTION

By George Gaylord Simpson[1]

PALEORNITHOLOGY

One of the first textbooks of vertebrate paleontology, that published in 1898 by A. (later Sir Arthur) Smith Woodward devoted 14 pages, 3 percent of its text pages, to birds. It discussed particulars of only *Archaeopteryx, Hesperornis, Ichthyornis, Aepyornis* (not figured) and three moas. When I studied vertebrate paleontology at Yale in the mid-1920's the class received even shorter coverage of birds. As much time was devoted to "*Tetrapteryx,*" a "bird" that never existed, as to the two real fossil birds that were discussed. It was generally felt that fossil birds were too rare to have any great evolutionary interest beyond that engendered by *Archaeopteryx,* of which more later. That depreciative view is still sometimes encountered, but now rarely and without justification.

A decided change in this subject, and in attitudes toward it, began in the late 1920's and has been accelerating ever since. It is true that the late Alexander Wetmore published a short paper on a fossil bird as early as 1917 (Wetmore 1917) and long continued such studies, but he was primarily a neontologist and his career was centered on Recent birds. Hildegarde Howard published a long paper on a fossil bird in 1927, the start of a great career. She was certainly one of the first, perhaps the very first, to adopt paleornithology as a full-time specialty and to occupy a salaried position explicitly devoted to that speciality.

That many fossil birds were in fact known by 1930 is evident from Lambrecht's massive *Handbuch der Palaeornithologie* (1933). Even so, the first sentence of that work begins (in German), "As is known, the number of remains of fossil birds is comparatively very limited. . . ." The fossil record of birds is indeed still markedly incomplete, as is that of even such richly documented groups as, for instance, echinoderms or mammals. Nevertheless it is now far from negligible, as witness Brodkorb's *Catalogue of Fossil Birds* (1963, 1964, 1967, 1971a, 1978) and Fisher's chapter on Aves in the symposium volume on *The Fossil Record* (1969).

At present the fossil record of birds not only throws considerable light on the history of birds, a subject of great interest in itself, but also provides evidence bearing more broadly on the principles of evolution. In what follows I shall exemplify both of those aspects of the subject.

THE EARLY BIRD

A tantalizing and perhaps incorrect reference to Jurassic birds was published by Schlotheim as early as 1820. A partial but considerable skeleton of the Jurassic *Archaeopteryx* was found in 1855, but was not recognized as avian until 1970 (see Ostrom 1972). The first specimen of a Jurassic bird to be recognized as such was a splendidly preserved, nearly complete skeleton with impressions of feathers that was found in 1861 and acquired by the British Museum (Natural History). It was named and briefly described by von Meyer (1862) and more fully described by Owen (1863). Numerous other studies of that and a second specimen similar in origin have appeared since 1863. The definitive study of the British Museum specimen, made after further preparation, was by de Beer (1954a). It is interesting that this was Sir Gavin's only excursion into paleornithology. One might say that he studied this specimen only because it was there: he was at the time director of the British Museum (Natural History).

It was at once recognized, and is obvious at first sight, that *Archaeopteryx* has resemblances both to birds and to reptiles. It was early agreed that *Archaeopteryx* had evolved from some reptilian stock, but beyond that point opinions long differed. An occasional minority view was that *Archaeopteryx* was a pseudo-bird, independently derived from reptiles with no close relationship to true birds. However, there now seems to be no dissent from the majority view that it was in or near the ancestry of some, and probably of all, later birds and should itself be classed in the Aves. As to the reptilian ancestry, it was suggested as early as 1863 (Weinland) and still maintained as late as 1950 (Petronievics) that *Archaeopteryx* was derived from some lacertilian stock. Owen (1874) hinted, although not clearly in evolutionary terms, at a pterosaur ancestry. Neither of those views is tenable in the light of later studies. Abel (1919) suggested derivation from a pseudosuchian, but possibly from some dinosaur itself evolved from a pseudosuchian (or other early thecodont). Heilmann (1926) more positively endorsed derivation from a pseudosuchian. T.H. Huxley (1868), somewhat vaguely, and Marsh (1877) and others following him, more positively, supported descent from some early dinosaurs.

There has long been a strong consensus, now virtually unanimous, that birds, including *Archaeopteryx,* evolved either from a dinosaurian (theropod) stock, or from a common ancestry with such a stock but within prior thecodonts. Ostrom (e.g., 1975), the most recent to study this question in depth, is insistent on a dinosaurian origin. He considers the skeleton of *Archaeopteryx* more dinosaur-like than bird-like, but continues to classify the genus as an ancestral, or near-ancestral, bird.

Whether birds arose from dinosaurs or from the immediate common ancestry of birds and dinosaurs is a phylogenetic detail of no great importance from a broader view of evolutionary

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Table 1. Some data on first appearances of families of birds in the fossil record, based mainly on Fisher (1967).

Geologic Period or Epoch	Number of First Known Appearances	Percent Extinct before the Holocene	Percent Surviving into the Holocene
Jurassic	1	100	0
Cretaceous	12	75	25
Paleocene	3	66.7	33.3
Eocene	41	31.7	68.3
Oligocene	18	38.9	61.1
Miocene	24	25	75
Pliocene	9	0	100
Pleistocene	38	2.6	97.4
Holocene	54	0	100

theory. In either case it is clear that *Archaeopteryx* stands in an intermediate position between the classes Reptilia and Aves. During the transition from one class to another, evolution may have been, and quite likely was, accelerated, but there was a transition, not a saltation as has from time to time been claimed for the origin of taxa at upper hierarchic levels. There are no known instances of such origins that cannot have been transitional, many known cases, of which this is only one, in which the origin was almost certainly transitional, and no known cases in which the evidence makes saltation more probable. The old saw that the first bird was born from a reptile's egg is not true.

That is the most important theoretical bearing of the early bird, but it has another also of some importance. When there is a transition from one high taxonomic category to another there are two extreme theoretical possibilities, although something between the two extremes is also quite possible. At one extreme, all characteristics of the ancestral form may evolve uniformly into the different characteristics of the descendant, so that an animal like *Archaeopteryx* would be in all respects intermediate between one high taxon, in this case the Class Reptilia, and another, here the Class Aves. As a matter of fact *Archaeopteryx* is not intermediate in that sense. Many of its characters had changed hardly at all from the reptilian grade, although I think that Ostrom, as previously cited, has somewhat overstated that case. On the other hand, some characters of that genus were already completely avian, notably the furcula, the presence of feathers, and their arrangement on the wing.

De Beer (1954a) did not discuss just this point in his monograph on the London specimen, but he did in an address to the British Association for the Advancement of Science (de Beer 1954b). He proposed the term "mosaic evolution" for the apparently disharmonious sort of transition exemplified in *Archaeopteryx*. He also gave other examples, and many more have been pointed out since then. In fact it had long been recognized, although not always so clearly, that different characteristics of organisms often, indeed usually, evolve at quite different rates even within a single lineage. (Although I was not the first to notice this, I did clearly state it in 1944, 10 years before the restatement by de Beer.) De Beer's term is apt and is a handy designation for this phenomenon. De Beer did not himself claim that his observation of the phenomenon was original, although some subsequent users of the term have mistakenly ascribed the principle, and not only the term, to him.

Two other points involving *Archaeopteryx* are to be mentioned here only briefly. It is fairly obvious that *Archaeopteryx* could not have been capable of long, sustained flight in the manner of most modern birds. There was, however, a clear consensus that it was capable of brief gliding or leaping flight and that its strongly feathered forelimbs were a stage in the evolution of sustained flight. Recently, however, Ostrom (1976) has maintained that the origin of those feathered forelimbs had nothing to do with flight but were adaptations of a running animal for garnering insects. If that were true, those forelimbs would be only adventitiously preadapted for flight. I do not pretend to authority on this point, but I do find Ostrom's hypothesis incredibly bizarre. (See Feduccia 1979—note added after completion of this manuscript.)

The other point is that it has several times been suggested that various birds without aerial flight (although many of them with wings) were primarily flightless either because they evolved from reptiles independently of true Aves or because the ancestral Aves were flightless (for example, Lowe 1944, and earlier papers there cited). With special reference to penguins, but incidentally to other supposedly flightless birds, I (Simpson 1946) strongly opposed that view, and I do not know of any more recent adherence to it.

BITS OF AN OUTLINE OF HISTORY

There have been several fairly recent reviews of the whole history of birds, most notably that by Brodkorb (1971b). I am not capable of writing a review in equal or greater depth and have no intention of trying. There are, however, some points bearing on evolutionary principles and on the interpretation of the fossil record that suggest brief comment here.

Some data on the first appearances of families of birds are given in Table 1. I have based these on Fisher (1967), primarily because Brodkorb's catalogue was not complete when this paper was written. Even now the earlier parts (at least Brodkorb 1963, 1964, and 1967) are out of date. The data from Fisher, more complete than Brodkorb's when this paper was written, seem to be sufficient for the general points here made.

It is not surprising that the percentage of pre-Holocene extinctions decreases, and that of survival into the Holocene increases almost regularly from Jurassic to Holocene. (A few families known only from the Holocene but now extinct are here counted as Holocene survivals.) The only somewhat evident irregularity is in the Oligocene, and this is probably a sampling error. For one thing, the Oligocene was shorter than either the Eocene or the Miocene, and so would have fewer first appearances even if the rate per annum were constant.

The very high numbers of first appearances in the Pleistocene and Holocene are a measure of the incompleteness of the record. It is highly improbable that these families actually originated in either of those epochs. Thus with no probable and few possible exceptions, their pre-Pleistocene members simply have not yet been found, to put the matter optimistically. To put it pessimistically, in many instances pre-Pleistocene representatives may not exist as accessible fossils. (Even for vertebrates it is certain that not all species or genera, probable that not all families, and possible that not all orders were fossilized and are now present in rocks accessible for exploration.)

It is a reasonable conclusion from these figures and from the more detailed data on which they are based that most and perhaps all of the families of birds that have ever existed, and hence of course those now surviving, had arisen by the end of the Miocene. That agrees with the well-informed opinion of Brodkorb (1971b:43), who wrote that, "By the end of the Miocene all of the nonpasserine families were probably established, as well as most, if not all, of the passerines." He then estimated that there were about 155 families extant in the Miocene, the number being reduced moderately to 148 in the Holocene.

For comparison, I have given in Table 2 similar data for Mammalia, a class with a better but still quite incomplete fossil record. The figures are tentative only, because there is no recent and reliable listing of all known mammalian families and their distribution in the Cenozoic, although Lillegraven (1972) has published graphs based on a fairly recent tabulation. (There is one by Lillegraven, Lindsay, and Simpson, as yet unpublished, for the Mesozoic.) My arrangement is conservative, with fewer families than are now sometimes recognized in the Tertiary, but I believe that the pattern is significant. Even so my arrangement for mammals has many more families (259) than Fisher's for birds (200). The patterns are similar in some respects but strikingly different in others. A considerable number of bird families first known in the Cretaceous, Paleocene, and Eocene—32 families or 57 percent of those first appearing during those times—survived into the Holocene. For mammals the corresponding figures are 116 families and 26.7 percent. Both proportionately and absolutely, many more mammalian than bird families first appear in the record at those times, but fewer of them survived into the Holocene. For both classes most of the Holocene families had appeared by the end of the Miocene, but some of the mammalian families probably did become differentiated in the Pliocene whereas it is not clear that any bird families did. In both cases it is unlikely that any family emerged after the Pliocene. The much lower numbers and percentages of first appearances of mammalian than of bird families in the Pleistocene and Recent is evidence that the fossil record for mammals, although still incomplete, is better than that for birds.

As Brodkorb (1971b) has pointed out, more living families of birds appear in the record for the Eocene than at any other time. (It is understood that comparison with the higher numbers for the Pleistocene and Holocene is not valid.) For mammals there is a marked difference: the greatest number of living families appear in the record for the Miocene. There are in fact many more Miocene first appearances than Pleistocene or Holocene. As relatively few Eocene mammalian families are still living, it is clear that there has been a much more marked faunal turnover since the Eocene for mammals than for birds.

The bird record is strongly biased both taxonomically and geographically. The most striking taxonomic bias is that relatively far fewer passeriform families than nonpasseriform families are known before the Pleistocene. On Fisher's data only 22.8 percent of recognized passeriform families are known before the Pleistocene but for nonpasseriforms the figure is 67 percent. That may be a sampling bias, caused in part by nonpasseriforms (such as many shore birds) being more likely to be preserved in sediments, by a higher proportion of nonpasseriforms in regions that have been sampled, or by smaller average size of passeriforms making them harder to find and identify. However it is also evident that the differentiation of passeriform families probably occurred, on an average overall, at later dates than for nonpasseriforms.

Table 2. Some data on first appearances of families of mammals in the fossil record.

Geological Period or Epoch	Number of First Known Appearances	Percent Extinct before the Holocene	Percent Surviving into the Holocene
Rhaeto-Lias	4	100	0
Jurassic	11	100	0
Cretaceous	19	94.7	5.3
Paleocene	33	100	0
Eocene	63	82.5	17.5
Oligocene	44	56.8	43.2
Miocene	38	28.9	71.1
Pliocene	21	9.5	90.5
Pleistocene	7	0	100
Holocene	26	0	100

The geographic bias largely, although not entirely, follows the intensity of paleontological field work. Fossil birds are fairly well known in North America and Europe but less so in South America, Asia, Africa, and Australia. Yet even in Australia there is a fair sampling from the Miocene onward, as was recently tabulated by Rich (1975). The evidence suggests that by mid-Miocene, at latest, the Australian fauna was fairly modernized and largely endemic. Virtually all the known fossils are nonpasseriform. From Antarctica some fossil penguins are known, but no deposits likely to contain nonmarine birds have yet been found.

EVIDENCE FOR SUCCESSIVE RADIATIONS

Descriptions by Marsh (1872, 1880) of *Hesperornis* and *Ichthyornis,* supposedly toothed birds, created a sensation and these have been the most discussed fossil birds except *Archaeopteryx*. It was already known that *Archaeopteryx* had teeth, but Marsh's "Odontornithes" were much later, and some authorities did not consider *Archaeopteryx* wholly (or at all) a bird. More recently Gregory (1952) suggested that, although *Hesperornis* had teeth, *Ichthyornis* probably did not. Bock (1969) still later questioned whether *Hesperornis* had teeth. Brodkorb (1971b) attacked "the fable of the toothed birds." The fable was simply the claim that *all* Mesozoic birds had teeth. In fact both *Hesperornis* and *Ichthyornis* did have teeth (Gingerich 1972, 1973; Martin and Stewart 1977). Although possibly tooth-bearing parts are not known in the likewise Cretaceous genera *Baptornis* (referred by Brodkorb 1963 to the Podicipediformes), *Enaliornis* (referred by Brodkorb to the Gaviiformes), or *Neogaeornis* (referred by Brodkorb to the Podicipediformes), Martin and Tate (1976) have established that these genera, too, probably belong in the Hesperornithiformes.

Added indication of the archaic nature of the genera listed in the preceding paragraph is given by evidence that the skull of *Hesperornis* was in fact palaeognathous (Gingerich 1973, 1976) although faulty reconstruction had led to belief that it was neognathous. Although the skull structure of *Archaeopteryx* is not known in clear detail, Gingerich has also marshalled evidence that a palaeognathous skull was probably ancestral for birds in general, and hence probably was present in *Archaeopteryx*. (I am, however, informed that Martin and Whetstone, in a study not published when this paper went to press, deny that *Hesperornis* was palaeognathous, which would also cast doubt on the possible palaeognathy of *Archaeopteryx*.)

Thus in the Cretaceous there was a group of archaic birds apparently sharing ancestral characters, although divergent to the ordinal level in derived characters. Among the Hesperornithiformes and the Ichthyornithiformes long known, some, at least, and possibly all were palaeognathous, and some and possibly all retained teeth. To them may now be added *Gobiopteryx* from the late Cretaceous of Mongolia (Elżanowski 1977). It, too, was palaeognathous, but it was toothless. Elżanowski proposed for it a new order, Gobiopterygiformes, but it might well be put in the still living order Casuariiformes, or the Struthioniformes if, as has been defended by Bock (1963) among others, all the ratites were put in one order. (The definition of such an order becomes difficult if some palaeognathous birds are excluded from it.) Brodkorb (1978:224) has expressed his belief that *Gobiopteryx* is not a bird, but a small dinosaur.

The most economical hypothesis is that the living palaeognathous birds, the ratites (whether classified as one order or as up to six) and the tinamous, are survivors of an archaic radiation. Most of the known Mesozoic members of that radiation were aquatic or at least littoral and most were found in marine rocks. Of earlier known members of the radiation, *Archaeopteryx* and *Ichthyornis* were most likely to have been land birds, but they have been found only in definitely marine beds. The known later, Eocene to Holocene, palaeognathous birds are land birds; all but the tinamous are flightless, and the tinamous are poor fliers.

Thus we can return, with Gingerich (1976), to the essence of views already expressed by T.H. Huxley (1868) and by Marsh (1880) long ago. The palaeognathous birds are the relics ("waifs and strays" of Huxley) from an archaic (mainly Cretaceous) radiation of the Aves.

Although Brodkorb's view that almost all the known Cretaceous birds were referable to, or near the ancestry of, Cenozoic neognathous birds is an overstatement, it seems established that, near the end of the Cretaceous, some were (Brodkorb 1976). Because of the bias of sampled environments, the known Cretaceous members of probably neognathous groups are almost all aquatic, marine, or shore birds. They strongly suggest that a major radiation of neognathous nonpasseriforms was under way before the end of the Cretaceous, reaching its height in the early Cenozoic. Starting within that radiation, one basic line, that of the passeriforms, underwent its own radiation from mid-Cenozoic to Holocene and became the dominant group in later Cenozoic and Recent avifaunas.

A WORD ABOUT PENGUINS

The oldest known penguins are late Eocene in age (not early Eocene, as indicated by Fisher 1967; Fisher also errs in listing *Palaeeudyptes marplesi* as a neospecies). At that time they already had all the derived characteristics of the family Spheniscidae as a whole. Some, at least, of the known late Eocene through Miocene species had a few characters that seem to have been more primitive than recent penguins, but at the generic level they also had derived characters that make them all quite distinct from any recent genus. Some of them, even in the late Eocene, had quite specialized generic characters. It is unlikely that any of the known forms of those ages were closely related to recent penguins at the generic level, and those that are adequately known were probably not ancestral to known post-Miocene penguins. Only in the late Pliocene of New Zealand do two species occur in the known record that are close to, and have been referred to, living genera: *Pygoscelis* and *Aptenodytes*. (On those two see Simpson 1972, and on fossil penguins in general Simpson 1975, and earlier publications there cited; for a less technical discussion see also Simpson 1976.) It is curious that those two genera now live much farther south than where their known fossil species were found, although by the late Pliocene New Zealand must have been in nearly the same latitudes as now. No pre-Pleistocene fossils are known for the genera now breeding in New Zealand: *Megadyptes, Eudyptes,* and *Eudyptula*.

The family Spheniscidae and order Sphenisciformes must have evolved before the late Eocene when they first appear in the record, and some, if not all, Holocene genera must have had distinguishable ancestors before the late Pliocene. As penguins are marine and littoral, they would seem well-suited for preservation as fossils. Nevertheless two special circumstances make the almost complete lack of ancestral or transitional sequences explicable. First, penguins are predominantly insular. One genus each now occurs on the coasts of three continents: Africa and South America (*Spheniscus*), and Australia (*Eudyptula*). Only two genera (*Aptenodytes* and *Pygoscelis*) occur in continental Antarctica, where, furthermore, no appropriate fossil-bearing post-Eocene rocks are known. All six living genera are now much more common on islands than on continents, and twelve of the (nominally) sixteen to eighteen living species are almost or quite confined to islands when ashore anywhere. The prolific polytypy of the group now, and even more its speciation in the past, are evidently the result of the isolation of island populations, with some subsequent dispersal. The islands on which ancestral speciation leading to later genera occurred probably no longer exist for the older part of the record, at least, and for the later part those that exist are not known to have fossiliferous rocks of appropriate ages. A second point is that all known fossil penguins are well within the geographic ranges of Recent penguins, and the whole order has probably always been almost entirely restricted to areas now in the Southern Hemisphere. But the known fossil record of birds in general in that hemisphere is exceptionally poor. It is surprising that so many, rather than so few, fossil penguins are known.

Until recently penguins were usually considered particularly primitive birds. That view is evident even in the the fairly recent compendious summary by Fisher previously cited. Penguins are there listed in the heart of orders belonging to the earliest radiation, between the Ichthyornithiformes and the Struthioniformes. That and similar arrangements may be a not wholly conscious hangover from the speculation that penguins are primitively (ancestrally) flightless. In fact they are carinate and neognathous and they fly with great power, but in water rather than in air. They quite surely had ancestors that did fly in air. The picture of avian evolution here adopted is a succession of three radiations of differing character and scope: ancient and largely or wholly palaeognathous, neognathous nonpasseriform, and neognathous passeriform. It is clear where penguins belong in that scheme: in the neognathous nonpasseriform radiation. Within that group their derived characters are unique in detail and association. They make the penguins among the most specialized birds. Only in some of the Alcidae (including Mancallinae), another branch of the neognathous nonpasseriform radiation, did some similar derived characters evolve (but see Olson and Hasegawa 1979; Olson this vol.—Ed.). That development was clearly independent and convergent on the part of sea birds that were geographic, Northern Hemisphere, vicars of the Southern Hemisphere penguins.

NOTE

The manuscript was written early in 1978. Although a few changes have been made since that time, it has not been possible to update fully.

LITERATURE CITED

ABEL, O. 1919. Die Stämme der Wirbeltiere. Verein. Wissensch. Verleger, Berlin and Leipzig. 914 pp.

BEER, G. DE. 1954a. *Archaeopteryx lithographica*. A study based upon the British Museum specimen. British Museum (Nat. Hist.), London. 68 pp.

———. 1954b. *Archaeopteryx* and evolution. The Advancement of Science, 11:160–170.

BOCK, W.J. 1963. The cranial evidence for ratite affinities. Proc. XIII Internat. Ornith. Cong. 1:39–54.

———. 1969. Origin and adaptive radiation of birds. Ann. New York Acad. Sci. 169:147–155.

BRODKORB, P. 1963. Catalogue of fossil birds. Part 1 (Archaeopterygiformes through Ardeiformes). Bull. Florida State Mus., Biol. Sci. 7:179–293.

———. 1964. Catalogue of fossil birds. Part 2 (Anseriformes through Galliformes). Bull. Florida State Mus., Biol. Sci. 8:195–335.

———. 1967. Catalogue of fossil birds. Part 3 (Ralliformes, Ichthyornithiformes, Charadriiformes). Bull. Florida State Mus., Biol. Sci. 11:99–220.

———. 1971a. Catalogue of fossil birds. Part 4 (Columbiformes through Piciformes). Bull. Florida State Mus., Biol. Sci. 15:163–266.

———. 1971b. Origin and evolution of birds. Pp. 19–55 *in* Avian Biology (Farner, D.S., and J.R. King, Eds.). Academic Press, New York and London.

———. 1976. Discovery of a Cretaceous bird apparently ancestral to the orders Coraciiformes and Piciformes (Aves Carinatae). Smithsonian Contrib. Paleobiol. No. 27:67–73.

———. 1978. Catalogue of fossil birds. Part 5 (Passeriformes). Bull. Florida State Mus., Biol. Sci. 23(3):139–228. Dec. 15, 1978. (I had not received this publication when the present manuscript was completed.)

ELŻANOWSKI, A. 1977. Skulls of *Gobiopteryx* (Aves) from the upper Cretaceous of Mongolia. Palaeontologia Polonica No. 37:153–165.

FEDUCCIA, A. 1979. Feathers of *Archaeopteryx*: asymmetric vanes indicate aerodynamic function. Science 203:1021–1022. (Received after this manuscript was completed.)

FISHER, J. 1967. Aves. Pp. 733–762 *in* The Fossil Record (Harland, W.B. et al., Eds.) Geol. Soc. London.

GINGERICH, P.D. 1972. A new partial mandible of *Ichthyornis*. Condor 74:471–473.

———. 1973. Skull of *Hesperornis* and early evolution of birds. Nature 243:70–73.

———. 1976. Evolutionary significance of the Mesozoic toothed birds. Smithsonian Contrib. Paleobiol. No. 27:23–33.

GREGORY, J.T. 1952. The jaws of the Cretaceous toothed birds, *Ichthyornis* and *Hesperornis*. Condor 54:73–88.

HEILMANN, G. 1926. The origin of birds. Witherby, London. 208 pp.

HOWARD, H. 1927. A review of the fossil bird *Parapavo californicus* (Miller) from the Pleistocene asphalt beds of Rancho La Brea. Univ. California Publ., Bull. Dept. Geol. 17:1–30.

HUXLEY, T.H. 1868. Remarks upon *Archaeopteryx lithographica*. Ann. Mag. Nat. Hist. (4)1:220–224.

LAMBRECHT, K. 1933. Handbuch der Palaeornithologie. Borntraeger, Berlin. 1024 pp.

LILLEGRAVEN, J.A. 1972. Ordinal and familial diversity of Cenozoic mammals. Taxon 1:261–274.

LOWE, P.R. 1944. Some additional remarks on the phylogeny of the Struthiones. Ibis 86:37–43.

MARSH, O.C. 1872. Discovery of a remarkable fossil bird. Amer. Jour. Sci. 3:56–57.

———. 1877. Introduction and succession of vertebrate life in America. Proc. Amer. Soc. Advan. Sci. 1877:211–258.

———. 1880. *Odontornithes*: a monograph on the extinct toothed birds of North America. Report of the geological exploration of the 40th parallel by Clarence King: i–xv, 1–201. Government Printing Office, Washington. (Also published as Yale University Peabody Museum Memoirs, No. 1.)

MARTIN, L.D., AND J.D. STEWART. 1977. Teeth in *Ichthyornis* (Class: Aves). Science 195:1331–1332. (Received after this manuscript was completed.)

MARTIN, L.D., AND J. TATE, JR. 1976. The skeleton of *Baptornis advenus* (Aves: Hesperornithiformes). Smithsonian Contrib. Paleobiol. No. 27:35–66.

MEYER, H. VON. 1862. *Archaeopteryx lithographica* aus dem lithographischen Schiefer von Solenhofen. Palaeontographica 10:53–56.

OLSON, S.L. 1980. A New Genus of Penguin-like Pelecaniform Bird from the Oligocene of Washington (Pelecaniformes: Plotopteridae). (this vol.)

OLSON, S.L., AND Y. HASEGAWA. 1979. Fossil Counterparts of Giant Penguins from the North Pacific. Science 206(4419):688–689.

OSTROM, J.H. 1972. Description of the *Archaeopteryx* specimen in the Teyler Museum, Haarlem. Proc. Konikl. Nederl. Akad. Wetensch. Amsterdam B75:289–305.

———. 1975. The origin of birds. Ann. Rev. Earth and Planetary Sci. 3:55–77.

———. 1976. Some hypothetical stages in the evolution of avian flight. Smithsonian Contrib. Paleobiol. No. 27:1–20.

OWEN, R. 1863. On the *Archaeopteryx* of von Meyer, with a description of the fossil remains of a long-tailed species