

## Evolutionary Significance of the Mesozoic Toothed Birds

*Philip D. Gingerich*

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### ABSTRACT

Well-preserved fossils of the Mesozoic toothed birds *Archaeopteryx*, *Hesperornis*, and *Ichthyornis*, and of the bird-like dinosaur *Compsognathus*, discovered in the 19th century, indicated to early evolutionary biologists that dinosaurs and birds were closely related, and that birds in all probability evolved from a dinosaur similar to *Compsognathus*. The modern ratites, sharing some distinctive similarities with *Hesperornis*, were regarded as survivors of a primitive initial radiation of birds. Several workers have subsequently challenged the idea that the Cretaceous birds *Ichthyornis* and *Hesperornis* had teeth or that they bore any similarity to the ratites. After careful study of the actual fossil specimens of *Hesperornis*, it is clear that this Cretaceous bird had toothed jaws and a palaeognathous palate, the latter condition being shared with ratites and certain dinosaurs. These and other characters place *Hesperornis*, like *Archaeopteryx*, in a position morphologically, as well as temporally, intermediate between dinosaurs and typical birds. The few significant features uniting the living ratites and tinamous all appear to be primitive characteristics, suggesting that ratites and tinamous are either survivors of an early radiation of birds, or are possibly a more recently derived artificial group in which primitive characters have reappeared secondarily through neoteny.

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### Introduction

The discovery of fossil birds with teeth was one of the most dramatic events in 19th century paleontology. In 1861 a partial skeleton of the

feathered *Archaeopteryx* was discovered in the Jurassic deposits of Bavaria. In the next 16 years, skeletons of *Ichthyornis* and *Hesperornis* were discovered in the Cretaceous of North America and a more complete skeleton of *Archaeopteryx* was found in Germany. Surprisingly, the jaws of each of these birds bore reptile-like teeth. Being discovered only a few years after publication of *The Origin of Species*, toothed birds were much discussed in connection with Darwin's evolutionary hypothesis.

As spectacular as the original discoveries were, it is remarkable in retrospect how little detailed study was made of the actual specimens until relatively recently. The history of the original discoveries of toothed birds, the initial recognition of their evolutionary significance, and their subsequent fate are reviewed here. The whole provides an interesting historical comment on the treatment of intermediate forms that do not conform to preconceived archetypal categorizations.

ACKNOWLEDGMENTS.—I should like to acknowledge here the encouragement Dr. Wetmore gave to continued study of the Yale collection of Mesozoic birds when work was initiated on *Hesperornis* several years ago. My study of *Hesperornis* began, curiously enough, as a tutorial with K. S. Thomson on kinesis and jaw mechanics in fishes. Expanding the range of comparisons, the Mesozoic bird material at Yale was examined to determine the form of kinesis of primitive birds. When no simple answer was forthcoming, J. H. Ostrom authorized Peter Whybrow to undertake further preparation of the original specimens. Thus I am particularly indebted to Professors Thomson and Ostrom and to Mr. Whybrow for their assistance and encouragement.

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*Philip D. Gingerich, Museum of Paleontology, The University of Michigan, Ann Arbor, Michigan 48104.*

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### Mesozoic Birds with Teeth

It is now generally admitted by biologists who have made a study of the vertebrates, that Birds have come down to us through the Dinosaurs, and the close affinity of the latter with recent Struthious Birds will hardly be questioned. The case amounts almost to a demonstration, if we compare, with Dinosaurs, their contemporaries, the Mesozoic Birds. The classes of Birds and Reptiles, as now living, are separated by a gulf so profound that a few years since it was cited by the opponents of evolution as the most important break in the animal series, and one which that doctrine could not bridge over. Since then, as Huxley has clearly shown, this gap has been virtually filled by the discovery of bird-like Reptiles and reptilian Birds. *Compsognathus* and *Archaeopteryx* of the Old World, and *Ichthyornis* and *Hesperornis* of the New, are the stepping stones by which the evolutionist of to-day leads the doubting brother across the shallow remnant of the gulf, once thought impassable. (O. C. Marsh, 1877:352).

In 1859, perhaps the gravest deficiency of Darwin's hypothesis of evolutionary descent was the rarity of intermediate forms in the geological record. Intermediate forms linking species into graded chains or linking major groups of animals to a common ancestor were at that time poorly known. Evidence remedying this deficiency was supplied in a most spectacular way by the discovery of several intermediate forms linking birds to a reptilian origin. Interestingly, each discovery of itself was insufficient to overcome archetypical categorizations of birds and reptiles, and a truly evolutionary view of both classes was necessary in order to interpret literally the clear evidence for bird-reptile relationships offered by the skeletons of *Compsognathus*, *Archaeopteryx*, and *Ichthyornis*.

J. A. Wagner (1861) described a remarkably complete skeleton of a very small new dinosaur, *Compsognathus longipes*, from the Jurassic lithographic limestone of Solenhofen, Germany. In the same year H. von Meyer (1861) first published a notice on the skeleton of a bird from the same deposit, which he named *Archaeopteryx lithographica*. Having a dinosaurian skeleton, *Compsognathus* was clearly a variant of the "Reptile type." On the other hand, *Archaeopteryx*, with its distinct impressions of feathers, was from the beginning regarded as a variant of the "Bird type." Influenced at least in part by Darwin's dynamic view of evolution, T. H. Huxley was able to overcome his contemporaries' fixed categorizations, even of groups as large as reptiles and birds, and he found in *Compsognathus* a bird-like dinosaur, and in *Archaeopteryx* the most reptilian of birds. Thus, Huxley (1868) confirmed the Darwinian expectation of intermediate forms linking birds and reptiles in the fossil record. Although the actual common ancestor of living reptiles and birds had not been found, Huxley judged from their morphology that late Jurassic birds and reptiles were clearly much more closely related than their living descendants seemed to suggest. This closer similarity of the early forms was itself strong evidence favoring Darwin's dynamic view of evolutionary descent, as opposed to the then-prevailing view that living "reptiles" and "birds" were static groups persisting through time within some predetermined bounds.

There was, however, a limit to the intermediate position even Huxley would accept for *Archaeopteryx*. Thus, of the single skeleton of *Archaeopteryx* then known, he wrote "unfortunately the skull is lost" (Huxley, 1868:70), making no mention of an earlier paper by Sir John Evans (1865) describing a premaxilla with four teeth preserved among the other bones of the specimen. Evans' note (1865:421) quotes a letter from von Meyer himself concerning the apparent association of a toothed premaxilla with *Archaeopteryx*:

Teeth of this sort I do not know in the lithographic stone . . . . From this it would appear that the jaw really belongs to the *Archaeopteryx*. An arming of the jaw with teeth would contradict the view of the *Archaeopteryx* being a bird or an embryonic form of bird. But after all, I do not believe that God formed his creatures after the systems devised by our philosophical wisdom. Of the classes of birds and reptiles as we define them, the Creator knows nothing, and just as little

of a prototype, or of a constant embryonic condition of the bird, which might be recognized in the *Archaeopteryx*. The *Archaeopteryx* is of its kind just as perfect a creature as other creatures, and if we are not able to include this fossil animal in our system, our short-sightedness is alone to blame.

The presence of teeth in the bird *Archaeopteryx* was apparently too reptilian a characteristic for even Huxley to accept.

O. C. Marsh was the first to discover the unequivocal presence of teeth in primitive birds, though he too was at the outset apparently unable to accept the evidence. In September 1872, Professor Mudge of Kansas presented Marsh with some fossils from the Cretaceous Niobrara Chalk, the formation from which Marsh had earlier described the headless skeleton of a large, flightless, diving bird as *Hesperornis regalis*. Marsh studied Mudge's new fossils and in October published a note describing the postcranial skeleton as a new form of smaller volant bird, *Ichthyornis dispar* (Marsh, 1872a). A month later he published another note (Marsh, 1872b) on the jaws of a new small "reptile," *Colonosaurus mudgei*, found in association with the remains of *Ichthyornis*. In the same month that *Colonosaurus* was described (November, 1872), Marsh's assistant T. H. Russell discovered a nearly perfect skeleton of *Hesperornis*, again in the Niobrara Chalk. This new skeleton included a skull with associated toothed jaws (Figure 1). Immediately after the discovery of this skeleton of *Hesperornis*, Marsh published a short paper in February 1873 stating that the toothed jaws of "*Colonosaurus*" actually belonged to *Ichthyornis*. Of *Ichthyornis dispar*, Marsh (1873: 162) wrote:

When the remains of this species were first described, the portions of lower jaws found with them were regarded by the writer as reptilian; the possibility of their forming part of the same skeleton, although considered at the time, was not deemed sufficiently strong to be placed on record. On subsequently removing the surrounding shale, the skull and additional portions of both jaws were brought to light, so that there cannot now be a reasonable doubt that all are parts of the same bird.

Although no mention was then made of the toothed jaws of *Hesperornis*, that discovery probably provided Marsh with the necessary corroboration for him to accept the previously evident association of toothed jaws with *Ichthyornis*. Two years after the toothed jaws of *Hesperornis* were first

described by Marsh (1875), the Berlin specimen of *Archaeopteryx* was found about 10 miles from the original Solenhofen discovery, and its feathers, reptilian skeleton, and toothed jaws left no doubt about the reptilian ancestry of birds.

Beyond their importance in dramatically filling a gap in the fossil evidence of evolution originally available to Darwin, the three early avian fossils *Archaeopteryx*, *Ichthyornis*, and *Hesperornis* are of interest for another reason. Huxley (1868:74) originally interpreted the great similarity of *Compsognathus* as indicating a dinosaurian (more specifically, coelurosaurian) origin of birds:

Surely there is nothing very wild or illegitimate in the hypothesis that the *phylum* of the Class Aves has its foot in the Dinosaurian reptiles—that these, passing through a series of such modifications as are exhibited in one of their phases by *Compsognathus*, have given rise to the *Ratitae*—while the *Carinatae* are still further modifications and differentiations of these last, . . .

Similarly, Marsh (1880:189) saw in the skull of *Hesperornis* certain resemblances to the "Ratitae," a group he regarded as being survivors of an evolutionary stage intermediate between reptiles and the true "ornithic type."

Three principal ideas have come out of the early work of Huxley and Marsh: (1) that ratites are survivors of a primitive stock of birds, (2) that *Hesperornis* was similar to ratites, and (3) that *Hesperornis* and *Ichthyornis* actually possessed jaws with teeth. All three of these views have been challenged in the century since their first publication by Huxley and Marsh. Disagreement with these ideas has come in part from authorities urging caution in attempting any interpretation at all, but in most cases a strong contrary interpretation has been offered, usually without critical examination of even the evidence available to Huxley and Marsh. Advocating ratites as a derived group of birds, reconstructing *Hesperornis* with a "neognathous" skull, and denying the presence of teeth in *Ichthyornis* or *Hesperornis* have a common effect—to deny the primitiveness and the reptilian characters of the best known Cretaceous birds and to maintain a wide gulf between birds and reptiles. This common effect of so many studies by post-Darwinian evolutionary biologists can only be ascribed to a deep-seated typological conception of "birds" and "reptiles"—an interesting comment on the pervasiveness of typological thinking.

### The Skull of *Hesperornis*

Our knowledge of the structure of the skull in *Hesperornis* is based almost entirely on three specimens: (1) that found by Marsh and Russell in 1872, now in the Yale Peabody Museum (YPM 1206) (Figure 1); (2) the premaxillae and mandibles of a skull in the National Museum of Natural History, Smithsonian Institution (USNM 4978); and (3) a nearly complete but crushed skull in the collections of the University of Kansas (KU 2287) (Figures 2 and 3). The first of these skulls was described and illustrated in some detail by Marsh (1880:5-12, plates 1,2), and a brief description of the last two was published by Lucas (1903), who illustrated the quadrate and pterygoid of the Kansas specimen and the lacrimal of the National Museum specimen. The Yale and National Museum specimens are very nearly the same size and both have been identified as *Hesperornis regalis* by virtually all workers. The Kansas specimen, on the other hand, is slightly smaller than the other two and was placed by Lucas (1903) in a new ge-

nus, *Hargeria*, having as its type the species *Hesperornis gracilis* Marsh. After extensive comparison of the three skulls, I agree with Gregory (1952) that all three are of the same genus, *Hesperornis*. It remains an open question whether more than a single species should be recognized.

The Yale skull was only partly removed from the enclosing rock by Marsh, and those portions that were freed for study were subsequently remounted on the original slab for display purposes. Consequently, the specimen was not really available for examination until relatively recently, when it was removed from public exhibition.

The Yale skull is in many respects the best one for study, because its components were scattered before fossilization and are now disarticulated and very little crushed (except for the braincase). The major portion of the Yale skull is illustrated here as it was mounted for exhibition (Figure 1). The braincase and some smaller fragments were completely removed from the rock by Marsh and it is not certain that their positions as shown in Figure 1 are those in which they were found. The pre-

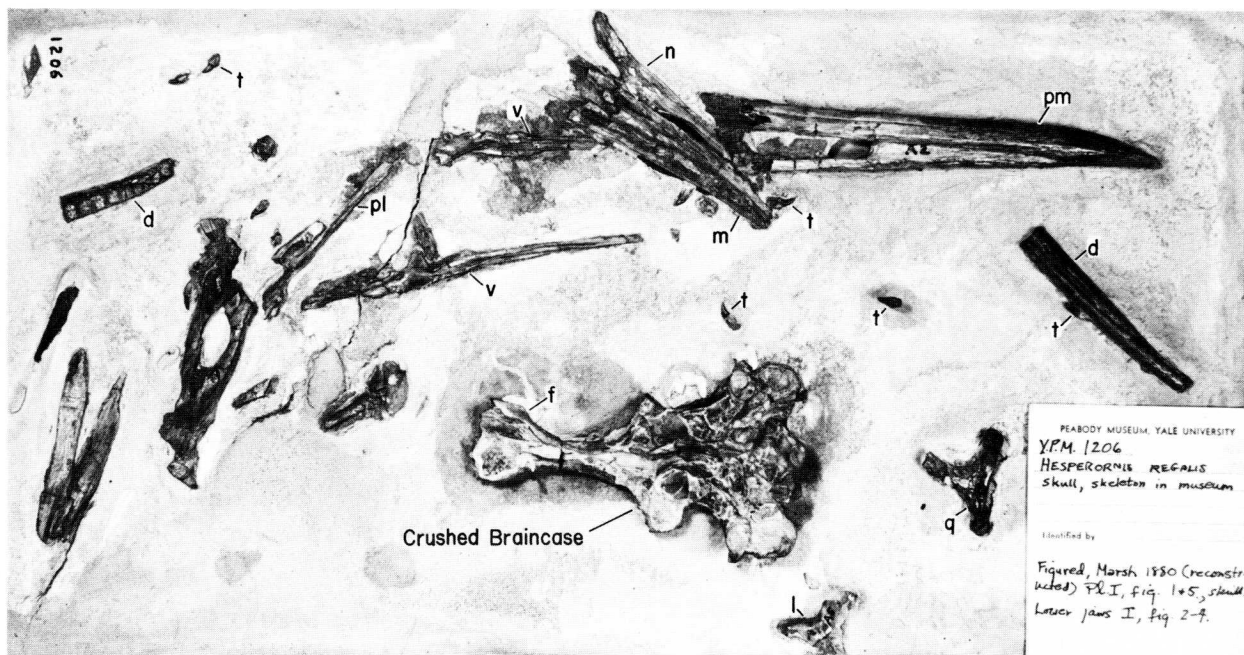


FIGURE 1.—The Yale skull of *Hesperornis regalis* Marsh (YPM 1206), showing the individual disarticulated bones well preserved. Premaxilla, nasal, maxilla, and vomers are illustrated in the position in which they were found—all have subsequently been removed and cleaned for study. (d = dentary, f = frontal, l = lacrimal, m = maxilla, n = nasal, pl = palatine, pm = premaxilla, q = quadrate, t = tooth, v = vomer.) Note presence of teeth in dentary, as illustrated by Marsh (1880, pl. 1). (Approximately one-half natural size.)

maxilla, maxilla, nasal, vomers, and palatine, however, were never removed and thus retain their original orientation as buried. It should be noted that Marsh had the nasal and maxilla exposed from both sides of the slab, but they were never completely removed. All of the important pieces of the Yale skull were carefully removed from their matrix in 1971 by Mr. Peter Whybrow, and they can now be studied freely and articulated.

The cranium of the University of Kansas skull of *Hesperornis* is also in a slab of Niobrara chalk, but unlike the Yale specimen, it was preserved in articulation and both the braincase and the maxillary portion of the skull have suffered considerable crushing. Furthermore, Lucas (1903) reported that the specimen was preserved with the skull doubled backwards against the pelvis, and that portions of both the dorsal and the sternal ribs were crushed into the palate. It is possible to identify most of the bones preserved in this specimen, but the maxillae are conspicuously lacking—whether they are crushed beyond recognition into the palate or lost entirely cannot be determined.

In addition to the portions illustrated in Figure 2, the Kansas specimen includes most of the lower jaws, a complete left quadrate, and a complete left pterygoid, which have been fully prepared and can be articulated with each other and also with the left palatine preserved with the main part of the cranium. The quadrate and pterygoid were illustrated by Lucas (1903, figs. 1,2; the left pterygoid is incorrectly identified as a right pterygoid), and they are illustrated here in articulation (Figure 3). The complicated S-shaped surface of the left pterygoid ("Apl" in Figure 3) articulates with the S-shaped proximal end of the palatine ("Apt" in Figure 2).

The principal contribution of the USNM specimen to our understanding of the skull morphology of *Hesperornis* is furnished by the nearly complete left lacrimal (illustrated by Lucas, 1903, fig. 3).

By studying all three specimens it is possible to reconstruct the major features of the morphology of the rostrum, the palate, and the mandible (Figure 4). The reconstruction has been discussed elsewhere (Gingerich, 1973), but some additional notes are added here. These notes and the illustrations of the Yale and Kansas specimens (Figures 1–3) are preliminary to a more definitive description of this important material. They are intended

to provide additional documentation of the remarkable completeness of the preserved specimens and to answer, in part, some questions raised by several skeptical colleagues.

The length of the reconstructed skull was determined from the Yale specimen (YPM 1206). The dorsal surface of the braincase in this specimen is crushed forward, but without affecting the length from the occipital condyle to the anterior end of the frontals. The overlapping articulation between the nasal and the frontal is outlined on the surface of the frontal, and the two can be fitted together as in life. The nasal-premaxillary articulation is preserved in both of the elements and these too can be fitted together accurately. As neither frontals, nasals, premaxillae, nor the base of the braincase appear in any way distorted in length, a total length of 26–27 cm is estimated for this skull.

Regarding the possibilities of cranial kinesis, little can be added to my previous discussion (Gingerich, 1973) except perhaps to add a more cautionary note. Rhynchokinesis in *Hesperornis* is almost certainly ruled out by the complete ring of bone formed by the premaxillae and nasals around the external narial opening. Some slight prokinetic movement might have been possible if the premaxillae and nasals were capable of being lifted off the frontals, although I know of no modern bird with such thick bone in the region of bending, and the complex interdigitation of the nasal and lacrimal in *Hesperornis* would likewise limit prokinetic movement. The quadrates were clearly streptostylic, which appears to have been correlated with a unique form of maxillokinesis whereby the maxillae were able to slide anteroposteriorly on rails formed by the nasal-premaxillary subnarial bars (Gingerich, 1973). While I am reluctant to postulate a form of kinetic motion so distinctive from that of any other animal, the preserved osteology of the rostrum in *Hesperornis* is unique and its adaptations were clearly different from those of any known vertebrate. Maxillokinesis appears to explain several unique features of the known fossil material.

One of the most curious features of the upper jaw of *Hesperornis* is the fact that the premaxilla bore a horny sheath as in modern birds (indicated by the vascular nature of the underlying bone), while the teeth were confined to the maxillae

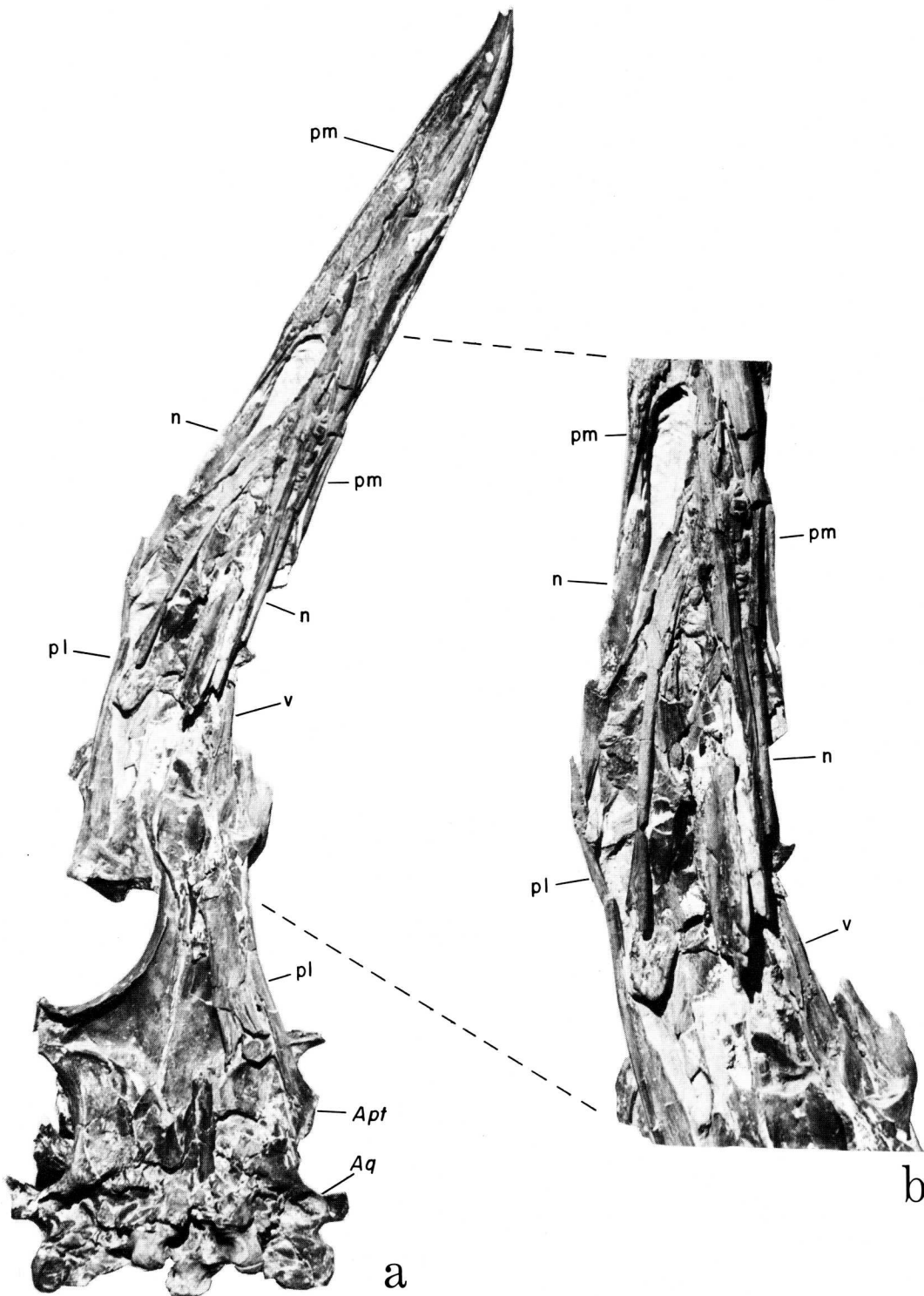


FIGURE 2.—The Kansas skull of *Hesperornis* (KU 2287), ventral view as preserved, articulated on a slab of Niobrara Chalk. Note particularly the little-disturbed contact between the premaxillae and nasals, while the maxillae are completely missing. (Apt = pterygoid articulation of palatine, Aq = quadrate articulation of squamosal, n = nasal, pl = palatine, pm = premaxilla, v = vomer; approximately two-thirds natural size.)

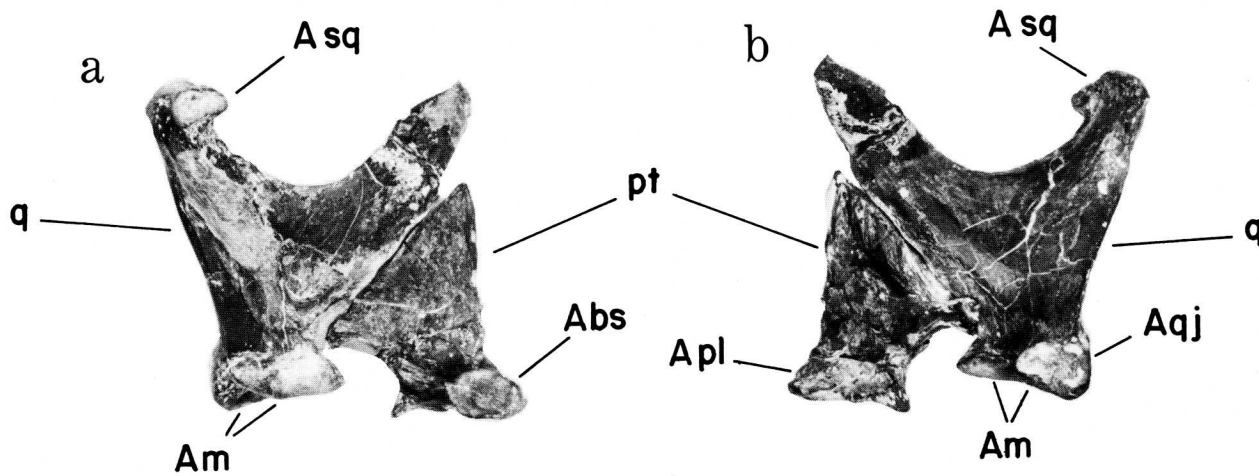


FIGURE 3.—Articulated left pterygoid (pt) and quadrate (q) of Kansas specimen of *Hesperornis* (KU 2287): a, medial view; b, lateral view. Note particularly the complicated articulation between quadrate and pterygoid, the broad basisphenoid articulation of the pterygoid, and the complicated S-shaped articulation of the pterygoid with the palatine. (Abs = basisphenoid articulation of pterygoid, Am = mandibular articulation of quadrate, Apl = palatine articulation of pterygoid, Aqj = quadratojugal articulation of quadrate, Asq = squamosal articulation of quadrate; twice natural size.)

proper. The lower jaw bore teeth throughout the length of the dentary. Secondly, in both the Yale and Kansas specimens, the maxillae have clearly separated from the nasal-premaxillary subnarial bars while, at least in the Kansas specimen, the subnarial bars were little disturbed by crushing. It should be noted also that the anterior end of each maxilla was grooved to fit over anteroposteriorly aligned keys or ridges of bone on the ventral surface of the premaxilla. This system of locking would keep the anterior ends of the maxillae from dropping away from the subnarial bars, while permitting anteroposterior motion of the maxillae relative to the subnarial bars. Finally, it now seems unlikely that the left and right vomers were fused to each other at their anterior ends. Such fusion would have prevented independent motion of the left and right maxillary segments of the palate relative to each other. The only possible functional advantage of having the kind of maxillary kinesis postulated here would be in moving each side independently. As evidenced by the unfused mandibular symphysis, such independent movement of the lower jaws was clearly possible. Independent movement of the maxillae would further expand

the range of possible movements used in ingesting prey, which in this case was almost certainly fish.

A new specimen of *Archaeopteryx*, described recently by Wellnhofer (1974), fortunately has a relatively well-preserved skull. Wellnhofer (1974: 185) interprets the skull as being definitely kinetic, but in *Archaeopteryx*, as in *Hesperornis*, it is difficult to see where bending that would lift a significant portion of the rostrum could have taken place. Wellnhofer favors bending in the dorsal processes of the premaxillae, but at most this would lift only the tip of the upper jaw. Kinesis approaching that of modern birds seems not to have been present in either *Archaeopteryx* or *Hesperornis*.

The present evidence bearing on Huxley's and Marsh's conclusions regarding the evolutionary position of the ratites, the relationship of *Hesperornis* to the ratites, and the presence of teeth in *Hesperornis* and *Ichthyornis* can now be considered. The skeleton of *Archaeopteryx* is more reptilian than avian, and the uncontested fact that its jaws bear teeth is easy to believe. The skeletons of *Hesperornis* and *Ichthyornis*, on the other hand, are more typically avian. That a bird with an avian postcranial skeleton should have jaws with

teeth has proved more difficult for some ornithologists to accept. The quadrate is not preserved in the original specimen of *Ichthyornis* and the toothed jaws that Marsh found associated with this skeleton thus cannot be articulated with the remainder of the cranium. The articular regions of the original jaws are also badly distorted. Gregory (1952) made a careful study of the lower jaws of *Ichthyornis* and concluded that they belonged to a small mosasaur. Therefore *Hesperornis* alone was left with the combination of toothed jaws and a nearly typically avian skeleton. Inevitably, the association of teeth with the skull of *Hesperornis* was also questioned. Bock (1969) claimed that the teeth found with *Hesperornis* were not in place in the jaws, but scattered and cemented with matrix onto the skull. However, one need only examine the Yale specimen to see that teeth are preserved in the jaws as well as being scattered through the matrix (Figure 1). Discovery of a new, uncrushed posterior portion of a mandible of *Ichthyornis* (Gingerich, 1972), and its comparison with the mandibles of the original specimen and with those of *Hesperornis* and modern birds, leaves little doubt that Marsh was correct in associating toothed jaws with *Ichthyornis*.

Interpretation of the structure of the palate in *Hesperornis* has had an interesting history. Marsh (1880:6) originally determined that the palate resembled most closely that of "Struthious" birds, but he confused the vomers with the palatines of his specimen of *Hesperornis* and gave no figure or reconstruction of the palate. Thompson (1890), followed by Lucas (1903), Shufeldt (1915), and Heilmann (1926), challenged Marsh's interpretation of *Hesperornis* as indicating any relationship to the ratites. In the course of the 36 years from 1890 to 1926, the palatal structure of *Hesperornis* "evolved" rapidly in the literature, ultimately "converging" toward the neognathous palatal type of the modern loon (*Gavia*), a fish-eating, diving bird with certain similar locomotor adaptations.

Fortunately, the Yale and Kansas specimens of *Hesperornis* (Figures 1-3) preserve virtually intact at least one example of each of the palatal bones. The quadrate and pterygoid are complete in the Kansas specimen, portions of both vomers are present in the Yale specimen (Figure 1), a crushed left vomer remains in the Kansas specimen (Figure 2), and virtually complete palatines

are preserved in both. About midway along their length, a rounded surface is present on the medial side of the vomers, which apparently articulated with the parasphenoid rostrum. The left maxilla is preserved in the Yale specimen (Figure 1) and it fits together with, and is overlapped by, the left vomer, as shown in Figure 4. There appears to be an articular facet on a ventrolateral expansion of the vomer for the narrow anterior end of the palatine (Figure 4). It is possible, but unlikely, that the palatines articulated directly with posterior projections of the maxillae (not preserved) rather than with the vomers. As noted above, the maxillae articulated with the subnarial bars formed by the premaxillae and nasals. Returning to the pterygoid-quadrate complex, it should be noted that each pterygoid bears a large, round, flat surface that articulates with a "basipterygoid" process of the basisphenoid (Figure 3, "Abs").

The entire reassembled palate is illustrated in Figure 4c. Compared with that of living ratites, the palate of *Hesperornis* is obviously different from an emu or an ostrich in being much longer and narrower. This lengthening has clearly been accomplished by elongation of the premaxillae, maxillae, vomers, and palatines relative to the more posterior elements of the skull. Although having adaptations quite different from those of any living palaeognathous bird, *Hesperornis* shares with palaeognathous birds all essential palatal characters that distinguish them from neognathous birds: (1) a relatively large vomer, (2) a firm pterygoid-palatine connection, (3) palatines widely separated from the sphenoid rostrum by the pterygoids, (4) strong basipterygoid processes of the sphenoid articulating with the pterygoids, and (5) a complex pterygoid-quadrate articulation including portions of the orbital process of the quadrate (Figure 3).

The structure of the palate is still unknown in *Archaeopteryx*, but the presence of a palaeognathous palate in *Hesperornis* would appear to be strong evidence favoring the view that the palaeognathous conformation is primitive in birds. Additional evidence bearing on the primitive structure of the palate of birds is offered by this structure in theropod dinosaurs. Ostrom (1973) has compared the skeleton of *Archaeopteryx* with that of reptiles and concluded that birds originated from theropod dinosaurs, more specifically, from a coelurosaurian stock of theropods. The palatal



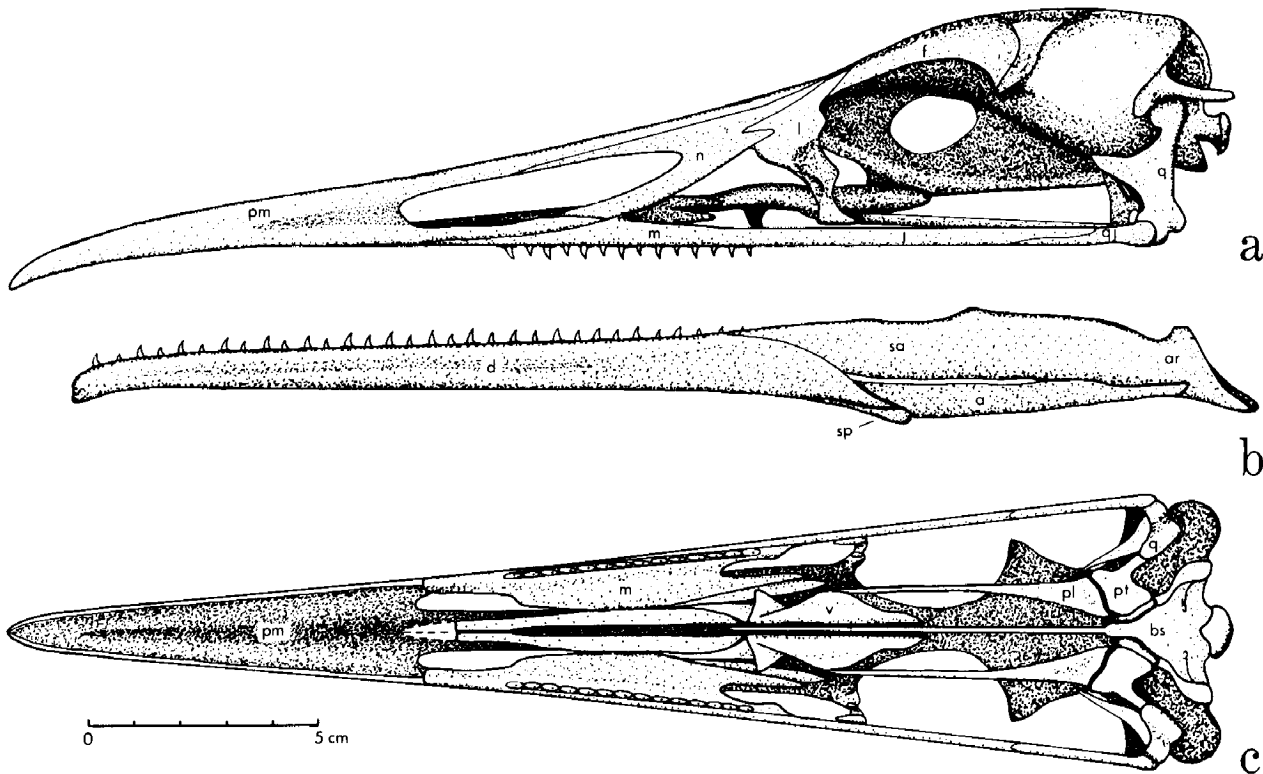


FIGURE 4.—Reconstructed skull (a) and mandible (b) of *Hesperornis regalis* in lateral view; c, reconstructed palate in ventral view. (a = angular, ar = articular, bs = basisphenoid, d = dentary, f = frontal, j = jugal, l = lacrimal, m = maxilla, n = nasal, pl = palatine, pm = premaxilla, pt = pterygoid, q = quadrate, sa = surangular, sp = splenial, v = vomer) (From Gingerich, 1973.)

structure is not known in any coelurosaur, but it is completely preserved in the large carnivorous *Tyrannosaurus* (Osborn, 1912) and less well preserved in the smaller *Dromaeosaurus* (Colbert and Russell, 1969) and *Deinonychus* (Ostrom, 1969). The structure of each of these skulls appears to meet all of the criteria listed above for the palaeognathous palate. Osborn (1912:11) noted this "analogy" implicitly in comparing the palate of *Tyrannosaurus* with that of a cassowary. The presence of a palaeognathous palate in Mesozoic theropods, the "sister group" of birds, together with the palaeognathous palate of the Cretaceous bird *Hesperornis*, should leave little doubt that this palatal conformation is truly primitive in birds.

I emphasize the strength of the evidence in this case because Cracraft (1974) has proposed that the living ratite birds are cladistically a "strictly monophyletic" group on the basis of their "de-

rived" palaeognathous palate, their unique rhamphothecal structure, and their large ilioischial fenestra. Cracraft asserts that the palaeognathous palate is a derived state in birds, not a primitive one, because "it is restricted to a small number of species within this large class" (Cracraft, 1974:497). This specious reasoning would lead one to assume that teeth in Mesozoic birds are a derived condition also, an unlikely hypothesis.

The unique rhamphothecal structure and other resemblances of ratites and tinamous were interpreted by Parkes and Clark (1966) rather less stringently than Cracraft now proposes. They (1966:469) noted that "resemblances are to be attributed to parallel evolution from a common stock . . . rather than to convergence from unrelated stocks, and thus, employing Simpson's concepts, the group may be considered monophyletic." The resemblance in rhamphothecal structure of

ratites and tinamous provides no evidence that this group is strictly monophyletic in Cracraft's sense rather than monophyletic in G. G. Simpson's sense (i.e., possibly paraphyletic, if indeed the unique rhamphothecal structure is a derived state at all—it may very well be primitive).

The third character Cracraft (1974:505) cites as evidence that ratites and tinamous are "each other's closest relatives" is their possession of a large ilioischiatic fenestra. *Archaeopteryx* has long been known to have a large ilioischiatic fenestra (see for example Petronievics and Smith Woodward, 1917), and Cracraft (1974:503) himself notes that this is the condition in *Hesperornis* and *Ichthyornis*. In short, of the three "derived" characters cited by Cracraft (1974), the first and third are almost certainly primitive and the second may be primitive as well.

Evidence that ratites are strictly monophyletic remains to be discovered and it is possible, even probable, that the groups of living ratites and the tinamous are paraphyletic. Huxley (1867:419) envisioned the living palaeognathous ratites as "waifs and strays" of an early radiation of birds, the neognathous types representing a subsequent radiation. Judging from the fossil record, successive adaptive radiations replacing older stocks by

newer ones are common in vertebrate evolution, and the class Aves is no exception. Although they are sometimes highly modified from the ancestral stock, we are fortunate to have in many groups of vertebrates surviving "waifs and strays," and still more fortunate to have well-preserved archaic fossil forms. In the absence of a more complete fossil record, some question must remain as to whether the modern ratites and tinamous are in fact survivors of a primitive radiation of birds, or whether their primitive characteristics are neotenic solutions to particular adaptive problems, since both the palaeognathous palate and the open ilioischiatic fenestra appear to be present in the developmental stages of modern nonratite birds (Jollie, 1958; Olson, 1973:35–36). To explain away the primitive morphology of *Hesperornis* and ally it with modern loons and grebes (Cracraft, 1974:497, 503), however, illustrates on the one hand the arbitrary nature of the cladistic method of reconstructing a phylogeny, and on the other hand exemplifies another typological attempt to force an archaic bird into a modern morphological category. To paraphrase von Meyer (1861), if *Hesperornis* does not fit our philosophical wisdom and if we are not able to include this fossil in our system, our shortsightedness is alone to blame.

### Literature Cited

- Bock, W. J.  
1969. The Origin and Radiation of Birds. *New York Academy of Sciences Annals*, 167:147–155.
- Colbert, E. H., and D. A. Russell  
1969. The Small Cretaceous Dinosaur *Dromaeosaurus*. *American Museum Novitates*, 2380:1–49, 15 figures.
- Cracraft, J.  
1974. Phylogeny and Evolution of the Ratite Birds. *Ibis*, 116:494–521, 10 figures.
- Evans, J.  
1865. On Portions of a Cranium and of a Jaw, in the Slab Containing the Fossil Remains of the *Archaeopteryx*. *Natural History Review*, new series, 5:415–421, 1 figure.
- Gingerich, P. D.  
1972. A New Partial Mandible of *Ichthyornis*. *Condor*, 74:471–473, 2 figures.  
1973. Skull of *Hesperornis* and the Early Evolution of Birds. *Nature*, 243:70–73, 2 figures.
- Gregory, J. T.  
1952. The Jaws of the Cretaceous Toothed Birds, *Ichthyornis* and *Hesperornis*. *Condor*, 54:73–88, 9 figures.
- Heilmann, G.  
1926. *The Origin of Birds*. 208 pages. London: H. F. and G. Witherby.
- Huxley, T. H.  
1867. On the Classification of the Birds; and on the Taxonomic Value of the Modifications of Certain of the Cranial Bones Observable in that Class. *Proceedings of the Zoological Society of London*, 1867:415–472, 36 figures.  
1868. On the Animals Which Are Most Nearly Intermediate between Birds and Reptiles. *Annals and Magazine of Natural History*, 4th series, 2:66–75.
- Jollie, M.  
1958. Comments on the Phylogeny and Skull of the Passeriformes. *Auk*, 75:26–35.
- Lucas, F. A.  
1903. Notes on the Osteology and Relationship of the Fossil Birds of the Genera *Hesperornis*, *Hargeria*, *Baptornis*, and *Diatryma*. *Proceedings of the United States National Museum*, 26:545–556, 8 figures.
- Marsh, O. C.  
1872a. Notice of a New and Remarkable Fossil Bird. *American Journal of Science*, 3rd series, 4:344.

- 1872b. Notice of a New Reptile from the Cretaceous. *American Journal of Science*, 3rd series, 4:406.
1873. On a New Subclass of Fossil Birds (Odontornithes). *American Journal of Science*, 3rd series, 5:161-162.
1875. On the Odontornithes, or Birds with Teeth. *American Journal of Science*, 3rd series, 10:402-408, plates 9-10.
1877. Introduction and Succession of Vertebrate Life in America. *American Journal of Science*, 3rd series, 14:337-378.
1880. Odontornithes: A Monograph on the Extinct Toothed Birds of North America. Volume 7 of *Report of the Geological Exploration of the 40th Parallel*. xv + 201 pages, 34 plates, 40 figures. Washington: Government Printing Office.
- von Meyer, H.
1861. *Archaeopteryx lithographica* (Vogel-Feder) und *Pterodactylus* von Solenhofen. *Neues Jahrbuch für Mineralogie, Geologie, und Palaeontologie*, 1861: 678-679.
- Olson, S. L.
1973. Evolution of the Rails of the South Atlantic Islands (Aves: Rallidae). *Smithsonian Contributions to Zoology*, 152:1-53, 11 plates, 8 figures.
- Osborn, H. F.
1912. Crania of *Tyrannosaurus* and *Allosaurus*. *Memoirs of the American Museum of Natural History*, new series, 1:1-30, plates 1-4, 27 figures.
- Ostrom, J. H.
1969. Osteology of *Deinonychus antirrhopus*, an Unusual Theropod from the Lower Cretaceous of Montana. *Yale University, Peabody Museum of Natural History Bulletin*, 30:1-165, 83 figures.
1973. The Ancestry of Birds. *Nature*, 242:136.
- Parkes, K. C., and G. A. Clark
1966. An Additional Character Linking Ratites and Tinamous, and an Interpretation of their Monophyly. *Condor*, 68:459-471, 7 figures.
- Petronievics, B., and A. Smith Woodward
1917. On the Pectoral and Pelvic Arches of the British Museum Specimen of *Archaeopteryx*. *Proceedings of the Zoological Society of London*, 1917:1-6, 1 plate.
- Shufeldt, R. W.
1915. On a Restoration of the Base of the Cranium of *Hesperornis regalis*. *Bulletins of American Paleontology*, 5:73-85, plates 1-2.
- Thompson, D'A. W.
1890. On the Systematic Position of *Hesperornis*. *University College, Dundee, Studies from the Museum of Zoology*, 10:1-15, 17 figures.
- Wagner, J. A.
1861. Neue Beiträge zur Kenntnis der urweltlichen Fauna des lithographischen Schiefers, II: Schildkröten und Saurier. *Abhandlungen der Bayerischen Akademie der Wissenschaften, München*, 9:65-124, plates 1-6.
- Wellnhofer, P.
1974. Das Fünfte Skelettexemplar von *Archaeopteryx*. *Palaeontographica*, Abteilung A, 147:169-216, plates 20-23, 13 figures.