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THE JAWS OF THE CRETACEOUS TOOTHED BIRDS, ICHTHYORNIS AND HESPERORNIS

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The remarkable Cretaceous birds with teeth, widely cited in paleontological and biological literature as an intermediate evolutionary stage between reptiles and modern birds, are known almost exclusively from the monograph "Odontornithes" and a few preliminary publications by O. C. Marsh, their discoverer. Marsh's reconstructions have been copied extensively and formed the basis for discussions of relationships by Fürbringer, D'Arcy Thompson, Lucas, Wetmore, and others. Heilmann, Lucas, and Shufeldt have attempted revised restorations, but none of them had access to Marsh's original specimens. Recently the writer had occasion to examine the type of *Ichthyornis dispar* Marsh and was so impressed with the resemblance of the lower jaw to that of a mosasaur, that the entire collection was carefully scrutinized for evidence that might demonstrate whether the jaws really belonged to the bird skeleton or were in fact immature mosasaur jaws which had been deposited with bird bones of similar size. The results of this investigation confirm Marsh's statement (1880:124) that "the dentigerous portion of the lower jaw [of *Ichthyornis*] is so similar to that of some of the smaller Mosasauroid Reptiles, that, without other portions of the skeleton, the two could hardly be distinguished."

This conclusion is not to be lightly accepted as merely indicative of the reptilian origin of birds. Much evidence (reviewed by Heilmann, 1927) has been accumulated which indicates that birds are descended from some stock of archosaurian reptiles akin to the dinosaurs and crocodiles. Mosasaurs, on the contrary, were specialized Upper Cretaceous lizards only distantly related to the archosaurs. Their peculiar jaw structure had been recently acquired and is neither shared with other lizards nor found in any other group of reptiles. The Cretaceous diving bird *Hesperornis* possessed a transverse intramandibular joint analogous to that of the mosasaurs, a remarkable example of evolutionary convergence. The jaw assigned to *Ichthyornis,* on the contrary, is so closely similar to that of the mosasaur *Clidastes* in details of structure, that actual relationship rather than convergence is suggested. Its association with the bird skeleton seems extremely doubtful.

Mosasaurs are the most abundant fossil reptiles in the Niobrara Chalk of Kansas, the formation which yielded the remains of both *Ichthyornis* and *Hesperornis*. They were large aquatic lizards, from six to thirty-five feet long; three genera, *Clidastes, Platycarpus,* and *Tylosaurus* are abundant and well known. No small specimens have been reported, and Williston commented (1898:213) on the absence of young individuals. Although the difference in size between the "*Ichthyornis*" jaw and those of the mosasaurs seems enormous, the former is not too small to have belonged to a newly born (or hatched) mosasaur. Moreover, it seems incongruously large for the delicate bird

skeleton with which it has been associated. The possibility that these jaws are in fact those of a young mosasaur should be seriously considered.

Evaluation of the characters of the "*Ichthyornis*" jaw necessarily led to detailed comparisons with *Hesperornis* and a new reconstruction of the jaw of that bird has also been attempted. It is hoped that the additional data will be of use to future students of fossil birds. The paucity of specimens upon which these reconstructions are based should be emphasized. Only the imperfect pair of jaws associated with the type of *Ichthyornis dispar* Marsh (Yale Peabody Museum no. 1450) is sufficiently complete to yield critical information about this form. *Hesperornis regalis* Marsh (Y. P. M., no 1206) and *H. gracilis* Marsh (Kansas University Museum of Paleontology no. 2287) have relatively complete though disarticulated lower jaws, and *H. crassipes* Marsh (Y. P. M. no. 1474) includes the anterior part of an angular and a fragment of a dentary. No other jaw remains of *Hesperornis* have been recorded.

Lucas (1903:552) proposed the genus *Hargeria* for *Hesperornis gracilis*, on the basis of the form of its quadrate, short nasal processes, and proportions of the femur. Comparison of the quadrates with that of *H. regalis* fails to support his view, which was based on comparison with Marsh's illustrations. The proportions of the femora may easily have been altered by crushing.

In the course of this study I have been encouraged and aided by suggestions received in discussions with Dr. Hildegarde Howard, Prof. Glenn L. Jepsen, Dr. S. Dillon Ripley, Prof. A. S. Romer, and Dr. Alexander Wetmore. Dr. Howard kindly read the manuscript and furnished valued criticism. The illustrations have been prepared by Miss Shirley Glaser, staff artist of Yale Peabody Museum. Drs. R. W. Wilson and Frank Peabody have permitted me to examine and figure the jaw from the well preserved *Hesperornis* [*Hargeria*] *gracilis* skull in the University of Kansas Museum of Natural History.

THE JAWS OF ICHTHYORNIS

Ichthyornis dispar Marsh was described (Marsh, 1872*a*:344) in October, 1872, on the basis of biconcave vertebrae, wings and legs (Y. P. M. no. 1450). In November, 1872 (Marsh, 1872*b*:406), a lower jaw was described as *Colonosaurus mudgei* Marsh and was compared with mosasaurs. In February, 1873, Marsh (1873:161-162) stated that *Ichthyornis dispar* had well developed teeth in both jaws, and further: "When the remains of this species were first described, the portions of lower jaws found with them were regarded by the writer as reptilian [a footnote cites the description of *Colonosaurus mudgei*]: 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." In a later paper Marsh again (1880:124, *inter alia*) noted the resemblance of the jaw to that of mosasaurs.

Some years after Marsh's death the specimen of *Ichthyornis dispar* was mounted in a plaster plaque; today therefore we have only Marsh's statement of the association of the jaw with the remainder of the bird skeleton. The right jaw is mounted, median side exposed, in the plaster plaque; the left is free from matrix and lacking the articular end but preserves the joint between angular and splenial.

In addition to jaws found with the type of *Ichthyornis dispar* (Y. P. M. no. 1450), Marsh noted two other jaw fragments of similar size, Y. P. M. nos. 1749 (*I. anceps*) and 1735 (*I. victor*). The latter was an isolated specimen, not associated with any avian bones; the former bears the same number as a bird humerus, but there is no proof of

association. They include the posterior portions of dentaries and splenials which agree, so far as they go, with the jaws of *I. dispar*, no. 1450; however, the splenial articulation is missing. The anterior end of a dentary of small size, Y. P. M. no. 1775, is sup-

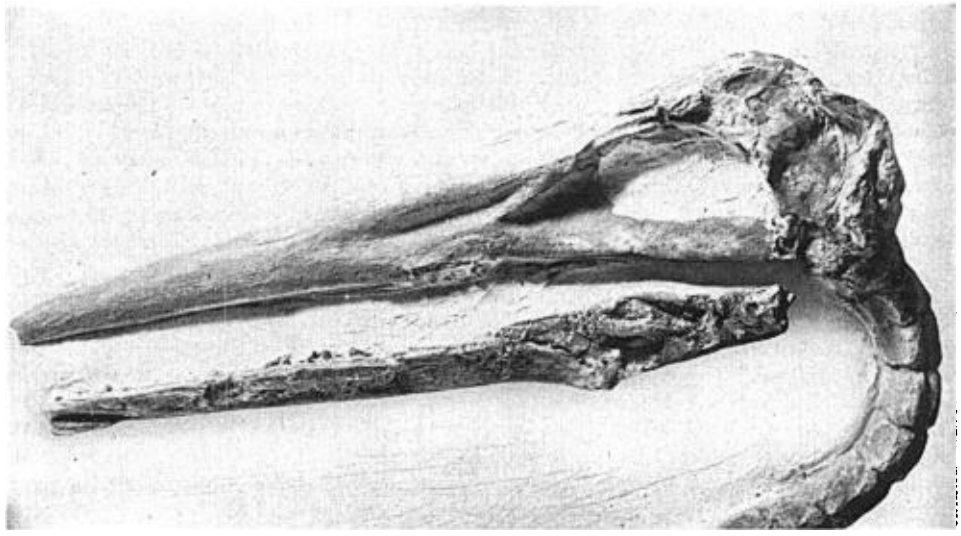


Fig. 1. Skull of *Ichthyornis dispar* Marsh as mounted and restored in Yale Peabody Museum; internal side of right mandible is shown; × 1½.

posedly associated with quadrates and other diagnostic bird bones, but again contacts and proof of association are lacking. These fragments can throw no light on the problem of the relationships of *Ichthyornis* and are not further discussed.

The lower jaw of *I. dispar* (Y. P. M. no. 1450), is 68 mm. long; of this the anterior dentigerous portion forms 50 mm. The two sides are closely similar in size. The anterior section, which consists of splenial and dentary, articulates with the posterior part, composed of angular, surangular, articular, prearticular, and coronoid. There is no symphysis between the left and right rami of the mandible.

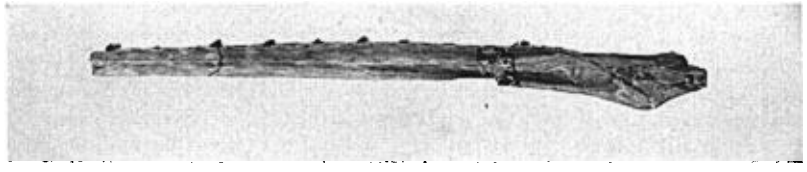


Fig. 2. Left lower jaw of "*Ichthyornis dispar* Marsh"; external side, × 1½.

Articular.—The articular is preserved only on the mounted right jaw (figs. 1, 3); its inner aspect is visible. The cotylus lies at the extreme posterior end of the dorsal surface; it is transversely elongate, concave fore and aft, and slightly constricted lateral to its center by a projection from the anterior edge. Traces of a suture separating articular from surangular may be seen; it runs from the medial surface of the jaw above and in front of the base of the medial articular expansion, upward and backward to the upper edge of the jaw and back toward the lateral posterior corner. The surangular forms the anterolateral portion of the cotylus. This is precisely the relationship in mosasaurs (see figs. 6 and 9).

Behind the cotylus the posterior end of the articular drops abruptly, at right angles to the dorsal border, forming the posterior end of the jaw. There is some crushing in this area, which bears little resemblance to any other form. It is slightly hollowed out for the insertion of the m. depressor mandibuli, with two pockets, the lateral much wider than the medial.

Angular.—Commencing beneath the articular as a thin sheath along the ventral edge of the mandible, the angular increases in size as it extends forward beneath the surangular. One and one-half centimeters ahead of the posterior end of the jaw it abruptly turns downward and terminates in the thick rim of the intramandibular articulation. The articular face is asymmetrical, projecting forward laterally into the cup at the back of the splenial; it is excavated medially to accommodate the medial projection of that bone. On the free left jaw, the articulation with the splenial is similarly developed. The lateral surface shows a faint suture between surangular and angular near the ventral edge. Thus the relations are similar to mosasaurs throughout. It must be emphasized that the anterior position of the angular, which does not reach back to form the retroarticular process, is very different from that of modern birds, of *Hesperornis,* or of any of the archosaurian reptiles from which birds originated.

Prearticular.—On the right mandible the prearticular is seen to be a flat plate of bone, wedge-shaped anteriorly, tapering to a projection which is inserted between the splenial and the dentary just behind the last tooth. Its dorsal border closely parallels the upper edge of the surangular as far back as it can be traced. The ventral edge lies close above the articular on the medial side in the region of the joint. Posteriorly it is impossible certainly to distinguish the upper edge of this bone as the coronoid(?) is crushed over the medial surface of the jaw. Ventrally it continues back beyond the angular and fuses with the articular to form the posterior end of the jaw. The relationship to the angular is identical with that found in mosasaurs and is quite unlike the condition in birds, in which the prearticular is entirely forward to the articular cotylus.

The well developed, thin, but wide prearticular that extends forward beyond the intramandibular articulation and inserts between splenial and dentary is identical to that of mosasaurs. Williston (1898: 131) emphasizes that this thin bone must have been flexible in the lateral plane and probably was instrumental in springing the jaws back into normal extension after flexion.

Surangular.—As in mosasaurs, the main element of the angular complex is the surangular, which forms nearly all the outer side of the jaw behind the dentary. Only its dorsal edge can be seen clearly in the right jaw. Between the angular cotylus and a point above the intramandibular joint it is gently convex and smoothly rounded. Directly over the joint it is concave for a short distance, beyond which it is essentially straight, in continuation with the upper border of the dentary. On the right mandible the surface of the concave section is pitted by minute vascular foramina; on the left there are fine ridges running longitudinally, slightly downward toward the front, indicating the position of the suture with the coronoid. No distinct dorsal process of the surangular rises behind the coronoid suture as in adult mosasaurs, but in such a young individual this process might easily be represented by the faint convexity of the bone in this region. Anteriorly the surangular extends well beyond the intramandibular joint and is embraced between the medial and lateral processes of the dentary.

Nothing can be said of the mandibular foramen of *Ichthyornis,* for the left jaw is broken off shortly behind the articulation with the dentary, and the area in which it might occur on the right jaw is concealed beneath another fragment of bone, mentioned beyond as a possible coronoid, for most of the distance between articular and dentary. It is obvious that there is none along the surangular-dentary suture. Marsh (1880:123) states that there was none, which is probably correct.

Coronoid.—A fragment of bone lies on the medial surface of the right jaw behind the intramandibular joint, below and slightly behind the position occupied by the coronoid in mosasaurs. It swells from a rounded point (directed backward as it lies) into an element of asymmetrical U-shaped cross-section which might be considered a mosasaur coronoid with undeveloped posteriomedian process were it not for its massiveness which seems excessive for a jaw of this size. Whether this bone belongs with the rest of the jaw or is an extraneous fragment cannot be positively determined. But whether it is or not, the presence of a suture on the upper edge of the surangular indicates that a coronoid was present, and in the position characteristic of mosasaurs. Inasmuch as this element is frequently detached from much larger mosasaur specimens, its loss from this jaw is not surprising.

Splenial.—As in mosasaurs, the posterior end of the splenial is thickened and forms the entire

rounded lower surface of the jaw for a short distance, projecting behind the dentary to its facet for the angular. As in mosasaurs (see fig. 3), the medial half of the facet is convex, the lateral concave. Sutures between dentary and splenial are almost impossible to distinguish in these specimens. On the left jaw a small crack 2 mm. long on the external surface just above the articular enlargement of the

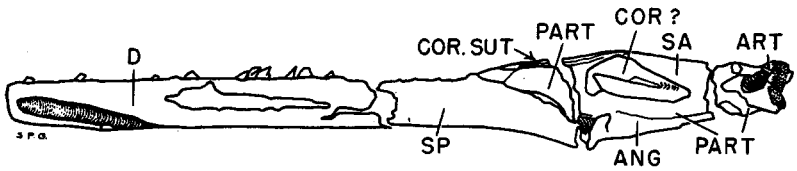
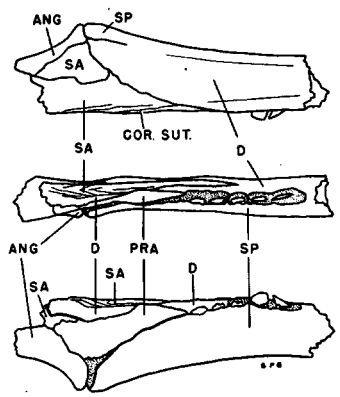


Fig. 3. Medial view of right lower jaw of "*Ichthyornis dispar* Marsh," × 1½; ANG angular, ART articular, COR? coronoid?, COR SUT coronoid suture on surangular, D dentary, PART prearticular, SA surangular, SP splenial.

splenial may indicate the beginning of the spleniodental suture; if so, the relationship is exactly as in mosasaurs. A displaced flake of bone on the right mandible just below the last tooth gives a strong suggestion of a squamous suture between the thin dorsal edge of the splenial and the inner surface of the dentary. Near the anterior end of the right splenial, along the lower edge of the jaw, further trace of the suture may be seen. On the left jaw, the suture was observed in cross-section at the more anterior of the two transverse breaks; here the splenial forms a thin plate on the inner surface of the



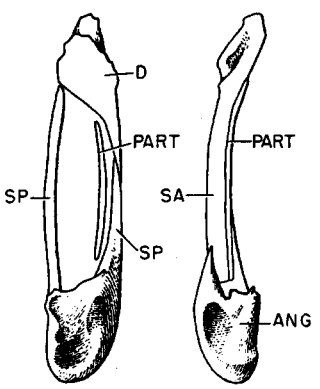


Fig. 4, left. Region of intramandibular articulation of left jaw of "*Ichthyornis dispar*" shown in external (above), superior, and internal (below) views, × 2.

Fig. 4, right. Intramandibular articulation of *Platycarpus ?coryphaeus* Cope; posterior view of dentigerous portion of mandible showing form of splenial articular surface (left), and anterior aspect of posterior portion of jaw showing articular facet on angular (right); based on Y.P.M. no. 3690, ×½.

jaw. None of the evidence conflicts with interpreting the splenial as having exactly the same relationships as those of mosasaurs. Nevertheless, the obscurity of this suture is noteworthy, especially in so young an animal.

Dentary.—Almost the entire upper edge of the slender dentary is occupied with the 22 sockets for teeth. The shape of these alveoli has been adequately described by Marsh (1880, pl. 21, fig. 3) except that the interalveolar septa are thinner than his figure shows. The dentary tapers very little compared to that of any adult mosasaur, a condition which may be reasonably attributed to immaturity. At the posterior end the dorsal margin slopes downward gradually to just above the intramandibular joint where it ends, on the lateral surface, against the rounded splenial. This portion of the dentary is bifurcated to hold the anterior end of the surangular.

A deep canal along the lateral surface of the posterior half of the dentary tapers somewhat anteriorly and then enters a foramen in the side of the bone. It is continued forward on the surface by a shallow, narrow, parallel-sided groove which extends to the tip of the jaw, and along which the series of six mental foramina open. Comparison with available mosasaur jaws suggests that the groove might be due to crushing of the internal mandibular canal, but the smooth, rounded surfaces and perfectly formed foramen by which it enters the jaw seem to oppose this hypothesis. However, farther back, there is evidence of inward crushing of the lateral face of the dentary.

On no. 1735, a portion of a mandible similar in size and character to no. 1450, the transition from groove to canal beneath the mental foramina occurs in the same region, but in it there is suggestion of crushing. There is no trace of a suture between the splenial and the dentary in this fragment.

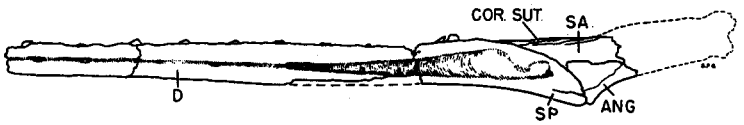


Fig. 5. External view of left lower jaw of "*Ichthyornis dispar* Marsh," × 1½.

Near the front of the right jaw, a deep groove for the anterior end of Meckel's cartilage runs upward and forward from the lower border to the symphysial region. This is exactly similar in position to the internal mandibular groove in the anterior end of mosasaur jaws. Marsh's statement (1872*b*:406) that the jaws lack the internal groove is in error but it may have been prompted by examination of the left mandible, in which the groove is much shallower. Here it runs forward from a foramen at the presumed anterior end of the splenial and becomes obsolete before reaching the symphysial area.

As in mosasaurs, there is neither suture nor symphysis between the anterior ends of the mandibular rami. Weak roughening of the medial surface of the dentary indicates a ligamentous attachment. In front, the dentary terminates quite abruptly in a nearly vertical face.

Dentition.—Marsh correctly noted the presence of 21 alveoli in the dentary of "*Ichthyornis dispar*," and claimed 22 in "*I. anceps*," no. 1749 (1880:124-125). The teeth remaining in the jaw show compressed, recurved tips with sharp anterior and posterior cutting edges. An alternating tooth succession typical of many reptiles is indicated, for partly erupted crowns protrude from alternate alveoli, commencing with the first. Careful excavation of some of the empty intervening alveoli has revealed tips of unerupted teeth. No fully erupted teeth are present, which may account for the absence of the swollen bony bases so characteristic of mosasaur teeth. It has long been known that these bases, which unite the tooth to the jaw bone, were resorbed as teeth were shed and are not found in empty alveoli. It seems probable that the partly erupted teeth may be the first successional dentition. This would account for the absence of bony bases and for any trace of predecessors to the even-numbered tooth rudiments.

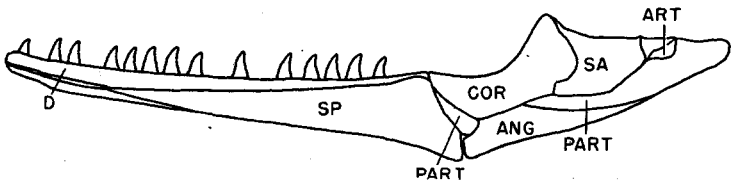


Fig. 6. Medial view of lower jaw of *Clidastes tortor* Cope, after Williston, × ⅛; COR coronoid, other abbreviations as in Fig. 3.

The number of teeth, 21 or 22, is significant for determining the relationships of this jaw fragment. Among the American mosasaurs the numbers of mandibular teeth reported are as follows: *Clidastes* 18, sometimes 17; *Platycarpus* 10 to 12, most frequently 11; *Tylosaurus* 13. Little information is available concerning variability of tooth number among mosasaurs. However, among recent thecodont reptiles there is some variation in tooth number. It is not unreasonable to suppose that

some individuals of *Clidastes* had 21 or 22 mandibular teeth. The resemblance of the "*Ichthyornis*" jaw is unquestionably closer to *Clidastes* than to any other known mosasaur genus in this respect.

In view of the antiquity of *Ichthyornis,* and the retention of such primitive features as biconcave vertebrae in its skeleton, an interpretation of its jaw morphology requires more than merely weighing its resemblances to modern birds and reptiles, for the retention of some reptilian features in an archaic bird is easily conceivable.

Accordingly, it will now be shown that the "*Ichthyornis*" jaw is not only more reptilian than avian in its morphology, but also differs from the jaws of archosaurian reptiles in most of the features which distinguish it from birds. A detailed analysis of the jaw of *Hesperornis,* another Cretaceous bird, shows that definitive avian characteristics were already present, despite the retention of teeth.

Finally, the complete agreement of the "*Ichthyornis*" jaw with that of mosasaurs in a number of distinctive features conclusively shows its relationship.

Evaluation of the unusual features of the "*Ichthyornis*" jaws requires an analysis of the jaw structure of both recent birds and of the archosaurian reptiles which gave rise to birds. As the reptilian jaw is the more complex, it will be convenient to describe it first and then attempt to show how birds differ. The rami of an alligator's jaws are united by an interlocking suture between the anterior ends of the dentaries, and in most genera also of the splenials. Each ramus consists of seven ossifications which normally are separated by sutures throughout most of the life of the animal. The large external mandibular foramen lies between the angular, surangular, and dentary. The coronoid is small, forming part of the inner wall of the large Meckelian canal. The angular forms an extensive suture with the posterior end of the dentary, extending forward between it and the splenial for some distance. The latter bone is confined to the medial surface of the jaw. There is no coronoid process (except in *Ornithischia*), the closure of the jaws being accomplished largely by the pterygoideus muscles which enter the mandibular canal.

Modern birds have a mandible whose two rami are indistinguishably fused in the anterior symphysis. Dentary, splenial, surangular, angular, prearticular, and articular elements develop in the embryo but are largely fused together in the adult. There is no separately ossified coronoid. The jaw is laterally compressed so that Meckel's canal is almost obliterated.

The articulation between dentary and splenial in the anterior part of the jaw, and the articular-angular complex at the rear, is essentially a squamous suture, the dentary overlapping the surangular and angular laterally and the splenial at least clasping the ventral point of the angular medially. A notch is sometimes present in the upper border of the dentary to clasp the anterior end of the surangular. The prearticular lies ahead of the articular cotylus and behind the splenial, medial to the surangular, and is variously developed; in loons it extends far forward so that its anteroventral border closely follows the posterodorsal edge of the splenial without actually forming a suture with it. More generally the prearticular is reduced and may not approach the splenial closely. As in archosaurs, the splenial is confined to the medial surface of the jaw.

The external mandibular foramina are variable in development and may lie either along the suture between the dentary, angular, and surangular, as in the crocodile, or entirely within the surangular; both openings are present in some, but many birds have lost these foramina completely.

A further character for distinguishing the jaws of birds and reptiles is the shape of the articular facet. In birds this tends to be double, or at least to include a ridge separating the two cotyli for the double condyle of the quadrate. In reptiles it generally is a

single transverse cylindrical surface, although in genera with pronounced propalinal jaw movements, such as *Sphenodon* and *Diadectes,* it may have an anteroposterior median ridge on its surface. These exceptions bear no resemblance to the double cotylus of birds.

In summary, the available criteria appear to be:

Archosaurian Reptile	Bird
1. Rami suturally united.	1. Rami with fused symphysis.
2. Coronoid bone present.	2. No ossified coronoid.
3. Sutures tend to remain visible.	3. Considerable fusion of jaw elements.
4. Meckel's canal open.	4. Meckel's canal obliterated.
5. Mandibular foramen well developed.	5. Mandibular foramen small or absent.
6. Cotylus simple, transverse.	6. Cotylus double, often oblique.

Exceptions to most of these points may be found; for example, the symphysis is fused in predentate dinosaurs. But confusion is not likely from these; in any case they do not apply to the *Ichthyornis* problem.

Neither of these sets of criteria is satisfied by the "*Ichthyornis*" jaw. Reptilian affinities are seen in the fairly open sutures, but not all of these are discernible. The indication of a separate coronoid bone is more significant. Meckel's canal is fairly well developed. The simple form of the articular cotylus is reptilian. But the jaw differs markedly from those of archosaurs in the absence of a mandibular foramen and of any trace of symphysis of the jaws. Moreover, the relation of the angular and prearticular are unlike those of either birds or archosaurs, in both of which the angular forms the retroarticular process and the prearticular is anterior to the quadrate cotylus.

The "*Ichthyornis*" jaw lacks any of the features which distinguish birds from archosaurian reptiles, and also differs from both of these in important features which they hold in common. On the basis of mandibular osteology alone, the jaw appears to be neither avian nor proavian.

COMPARISON WITH HESPERORNIS

The validity of the distinctions just made between bird and reptile jaws can be illustrated by examination of the jaws of *Hesperornis,* a large, specialized diving bird of the Upper Cretaceous which retained reptilian teeth.

Hesperornis jaws are indisputably associated with the remainder of the bird skeleton, and show unquestionable avian characteristics in their articular region. At the same time, they are convergent toward those of the mosasaurs in the lack of an intermandibular symphysis and in the presence of a transverse intramandibular joint. A comparison between *Hesperornis* and *Ichthyornis* is thus in order.

Marsh's description (1880:11) of the lower jaws of *Hesperornis* is very brief:

> "The lower jaws are long and slender, and were thickly set with teeth. The rami were united at the symphysis in front only by ligament, a feature unknown in modern adult birds. There is an imperfect articulation between the splenial and angular elements, which probably admitted of some motion; and all the other sutures are open, or distinguishable. There was apparently a mandibular foramen. There is a well marked shallow groove on the outer superior margin of each dentary bone, for the reception of the maxillary teeth, when the jaws were closed. (Plate I, figure 3b). The angle of the mandible extends backward but a short distance beyond the articular face for the quadrate, and the extremity is obliquely truncated."

Except for the allusion to a mandibular foramen, which is shown to be absent by the left jaw of *H. regalis* in Marsh's collection as well as by the excellent specimen of *Hesperornis gracilis* at the University of Kansas, and the characterization of the retro-

articular process as short, the description is essentially correct. Additional details afford a better basis for assessing the relationships of this bird.

As restored by Marsh, the mandible of *H. regalis* was 257 mm. (10 inches) long; that of *H. gracilis* as restored here from the disarticulated specimen in the University of Kansas Museum is 208 mm. (8¼ inches). A check on this reconstruction is provided by measurements (kindly furnished me by Dr. R. W. Wilson) of the skull of that individual, which is intact although somewhat distorted. The distance from the quadrate facet on the squamosal to the tip of the beak, corrected for distortion, is 190 mm., which corresponds well with the length 187 mm. from articular cotylus to the tip of the dentaries on the jaw. Perhaps the dentaries are too short; the material did not permit direct measurement of their length which was inferred by comparison with *H. regalis*.

Articular.—This small element is confined largely to the region of the cotylus, which resembles that of modern birds in its division into anterolateral and posteromedial sections, but is simpler in form. A somewhat oblique, elongate, concave facet for the inner condyle of the quadrate, its lateral end posterior to and higher than the medial end, is separated by a ridge from the lateral facet, which extends onto the surangular bone. A small basin lies just in front of the articular surface. The form of the articulation differs from that of reptiles in its oblique rather than transverse axis and in its tendency to division into two parts. Among modern birds, it most closely resembles that of loons (*Gavia*) in this region, but it differs in the absence of any separation of the posterior cotylar facet into two parts by a deep concavity for the condyle of the quadrate.

Angular.—Sutures are not determinable between the articular and angular. The latter bone presumably forms the retroarticular process. This structure is produced posteriorly far more than in modern birds (aside from the Anseriformes and Galliformes which differ radically from *Hesperornis* in the shape and position of the process). Perhaps its closest approach is to the angle of penguin (Sphenisciformes) jaws, but it exceeds these in length. In form it is more like the Ardeidae than the Gaviidae, but even more drawn out than in that family. The angular process proper is an oblique plate of bone sloping downward and slightly outward to the rear of the articular cotylus; its posterior end is thickened and rounded. It is supported externally by a vertical lamina continuous with the outer wall of the mandible, but displaced to beneath the center of the articular. An interdigitating suture between the surangular and angular on the lateral surface of the mandible just below and in front of the cotylus may be seen on all specimens. The angular continues forward along the lower edge of the mandible, its dorsal border lying medial to the lower edge of the surangular. Its thickened anterior end is rounded and slopes upward and forward at an angle of 40° to 55° with the axis of the jaw, forming an inclined, cylindrical articular surface which matches a corresponding concavity in the splenial.

Surangular.—Neither the left jaw of *H. regalis* (Y. P. M. no. 1206) nor that of *H. gracilis* (K. U. M. V. P., no. 2287) has complete surangulars, although all but the anterior end can be reconstructed from the parts available. It is a deep, thin bone, rounded above and bearing a low coronoid process about midway along its dorsal margin. Ventrally it reaches almost to the bottom of the jaw for part of its length, but forward of this the angular is again well exposed laterally. Its medial surface is somewhat excavated posteriorly below the thickened upper margin and above the descending portion of the angular ahead of the articular cotylus, most noticeably in *H. regalis*, but there clearly is no mandibular foramen. The right jaw of *H. regalis* has an oval perforation at this point, but the edges are rough and it is clearly a post-mortem fracture; there is none to correspond with it on the left jaw of the same specimen. In general form the surangular resembles that of the herons (Ardeidae) and cormorants (Phalacrocoracidae) save that the coronoid process is a bit more anterior than in either of these.

Prearticular.—No remains of this bone have been identified with certainty. However, in the type of *H. regalis* are two thin blades of bone, rounded at one end, whose size would fit well within the surangular to form the interior wall of the mandibular canal. They lie in the matrix above and behind the posterior end of the right mandible and might well be the prearticulars of the dissociated jaws. This bone is evidently the basis for the portion of the prearticular shown in Marsh's plate I, figure 4 (1880). The shape of the rounded end is not unlike the anterior end of the prearticular of *Gavia* or *Ardea*, and in figure 7 it has been restored in analogous position. In recent birds the posterior end of the prearticular is fused to the dorsal edge of the angular; all *Hesperornis* specimens lack a section

of the angular in this region so the relationship cannot be determined. However, evidence is afforded by the rugosity on the inner surface of the surangular about two centimeters in front of the articular cotylus which suggests the contact between surangular and prearticular along the posterior edge of the latter bone. If this is correctly interpreted, the prearticular ascended abruptly from the angular as in *Ardea* or *Phalocrocorax* rather than gradually as in *Gavia*. Its anterior end undoubtedly spanned the intramandibular articulation and was in contact with the dentary and the splenial.

Splenial.—Marsh's figures show the outline of this element correctly; its ventral edge is thickened posteriorly and formed the lower edge of the jaw for some distance anterior to the angular bone. Above this thickened portion the medial lamina rises nearly the full depth of the jaw one centimeter in front of the posterior end and then tapers very gradually downward to the anterior point about two centimeters behind the tip of the dentary. A thin low ridge rises laterally from the base, forming a slight groove for the Meckelian canal. The posterior end of the lower thickened part of the splenial

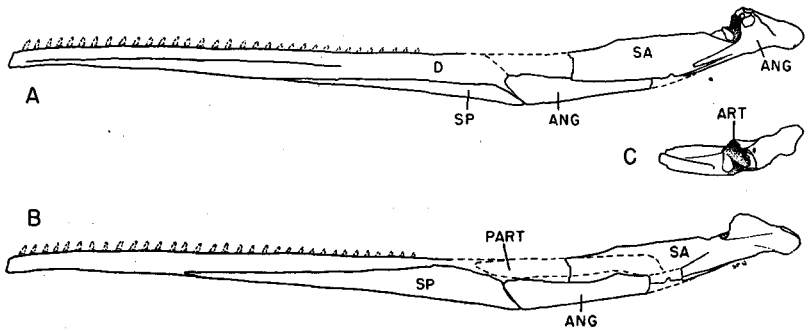


Fig. 7. Reconstruction of lower jaw of *Hesperornis gracilis* Marsh, based on K.U.M.V.P. no. 2287, × ½; A, lateral view, B, medial view, and C, superior view of articular region.

extends far backward, and has a sloping, somewhat rugose, concave upper surface. This formed an inclined transverse hinge with the anterior end of the angular. Presumably this joint was spanned by the prearticular and the posterior lamina of the dentary, which limited the movement on it and also acted as spring leaves to restore the jaw after distortion.

Dentary.—Marsh pointed out the lack of fusion or even of a suture between the two dentaries and also the groove in which teeth were inserted. A lateral groove which he described as for the points of the upper teeth might also be interpreted as analogous to grooves for insertion of the horny beak on the jaws of modern birds. The bone is relatively stout, somewhat deeper behind than in front, and bears a series of mental foramina along a longitudinal groove on the exterior surface. None of the preserved specimens shows its posterior termination, but the left jaw of *H. gracilis* (K. U. M. V. P., no. 2287) becomes extremely thin and deep in the region just anterior to the angular-splenial joint; it is broken off and hence must have projected somewhat farther back, overlapping the surangular.

To summarize, the jaws of *Hesperornis* resemble those of mosasaurs and the "*Ichthyornis*" jaw in the lack of an intermandibular symphysis, the presence of a transverse joint, and the presence of teeth. Here the resemblances stop. The jaw of *Hesperornis* is distinctly avian in its complex articular cotylus, the relations of its angular and prearticular bones, and in the absence of a coronoid bone. Also the form of the angular-splenial articulation is very different from that of mosasaurs and "*Ichthyornis*." Thus the jaw of *Hesperornis* differs from the supposed "*Ichthyornis*" jaw in the very features which set the latter apart from birds and show its affinity to mosasaurs.

FUNCTION OF THE JAWS IN HESPERORNIS

Hesperornis was a large aquatic bird about five feet in length from beak to tail. It shows convergence in structure toward the specialized marine mosasaurs in general

aquatic modifications and in the piscivorous adaptations of its jaws. Details of the convergence have been discussed elsewhere (Gregory, 1952).

Both *Hesperornis* and the mosasaurs are reasonably inferred to have been fish-eaters; their bones are found in a marine limestone which abounds in fossil fish remains, and their sharp, pointed teeth are well suited to catching fish and are comparable to those of other piscivorous animals. The transverse mandibular joint permits outward

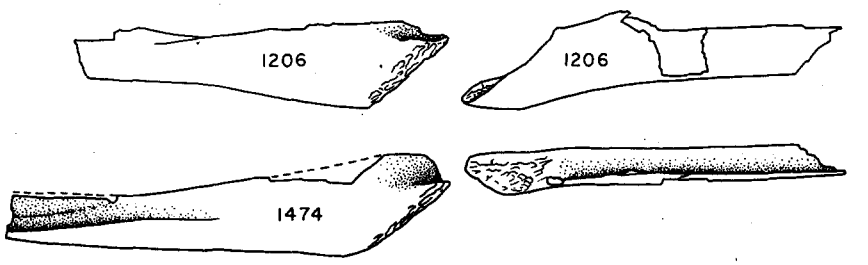


Fig. 8. Intramandibular articulation of *Hesperornis*; left, medial aspect of anterior ends of angulars of Y.P.M. no. 1206 (*H. regalis*) and Y.P.M. no. 1474 (*H. crassipes*); right, medial and superior views of posterior portion of splenial of *H. regalis*; all × 1.

bowing of the jaws to a greater extent than is otherwise possible without dislocation. This device allows the swallowing of much larger prey than would otherwise be possible. It may be noted that the jaws of cormorants have a zone of weakness in the region of the sutures between the anterior (spleniodentary) and posterior (angular-surangular-prearticular) parts of the jaw which permits flexibility in this region.

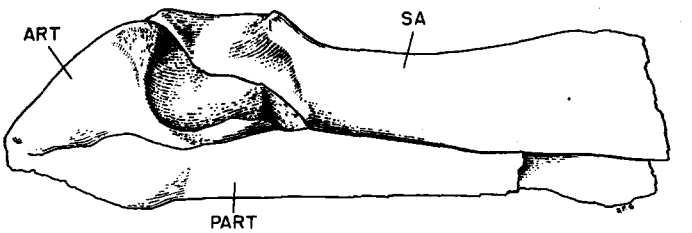


Fig. 9. Dorsomedial view of posterior end of jaw of a mosasaur (*Platycarpus*?) showing simple articular surface, × ½.

Williston (1898:212-213) pointed out a further possible significance to the intramandibular joint of mosasaurs which may well apply equally to *Hesperornis*. Instead of forcing food down the throat by alternate anteroposterior movements of the two mandibles as do snakes, the jaws were pulled backward together by bending outward at the articulation; after the palatal teeth had engaged the prey the jaws both disengaged and sprang forward together for a new hold. The hypothesis of alternate jaw movements, suggested by Cope (1869:216) must be rejected because of the limited possible movement of the quadrate, which is fixed with the pterygoid. Movement of the avian quadrates is likewise limited by the quadratojugal connection, so the same restriction doubtless applies.

Recurved palatal teeth, which are well developed in both snakes and mosasaurs, are an important adjunct to such a feeding mechanism. *Hesperornis* lacks palatal teeth, but the posterior maxillary teeth and recurved tip of the beak would have served the same function of holding the prey while the jaws were being extended.

The similarities of the lower jaws of *Hesperornis* and the mosasaurs are thus seen to be adaptations to swallowing large and slippery prey, specifically fish.

RELATIONSHIPS OF HESPERORNIS

Three principal views have been advanced concerning the relationships of this toothed diving bird. Marsh (1880) considered it a member of a distinct order of primitive toothed birds, related to the flightless ground birds, or ratites; Fürbringer (1888: 1473) accepted the ratite relationship of *Hesperornis* although rejecting the grouping of toothed birds into one order. D'Arcy W. Thompson (1890:14) showed the incorrectness of this view, and considered it an early branch of the same stock as the grebes and loons. Lucas, Stolpe, and other recent students have voiced caution against accepting the aquatic modifications of the skeleton as evidence of affinity, for such characters may arise repeatedly by convergence. The present study, confined to a single portion of the skeleton, cannot hope to solve the problem of relationships. Nevertheless the distinctive features of the jaw of *Hesperornis* which have been described may be said to support the isolated position of *Hesperornis,* which may well have developed its resemblances to the grebes and loons independently.

COMPARISON WITH ARCHAEORNIS

Dames (1884:129) described the lower jaw of the Jurassic bird *Archaeornis* as a long narrow bone with weakly concave ventral border, somewhat higher posteriorly than anteriorly. It has a retroarticular process 4 mm. long. The shattered condition of the specimen renders identification of the irregular hole in the jaw as a mandibular foramen uncertain. Heilmann, however (1927:6), states definitely that there is a vacuity between the surangular and the dentary, although his figure of the specimen fails to show this. A small portion of the splenial is visible on the external surface of the lower edge of the jaw, as in primitive archosaurs and unlike modern birds. Heilmann (1927:5) shows an elongate angular extending to the posterior end of the jaw. The coronoid region is concealed. There is no evidence of a mosasauroid intramandibular joint. This is important evidence that this peculiar structure was not a heritage from reptilian ancestors of birds.

About the only feature in which the "*Ichthyornis*" jaw shows more resemblance to that of *Archaeornis* than to those of modern birds (aside from the presence of teeth) is the lateral exposure of the splenial. But as this itself is a reptilian character, it does not aid in solving the problem of relationships.

COMPARISON WITH MOSASAURS

Throughout the preceeding discussions comparisons have repeatedly been made with mosasaurs. This family of marine lizards is abundantly represented in the Niobrara formation of Kansas. Specimens of *Platycarpus* cf. *coryphaeus* (Cope) have been used for illustration of certain features of mosasaur anatomy, but these features do not vary greatly among the various genera. Because of its slenderness and the large number of teeth, it seems most probable that the "*Ichthyornis*" jaw actually pertains to the genus *Clidastes*.

In all mosasaurs, the angular arises along the lower edge of the rear of the jaw well forward of the retroarticular process, and expands anteriorly. It bears an articular facet for the correspondingly enlarged posteroventral end of the splenial on the lower edge of its anterior end. The form of the articulation is shown in figure 3. The splenial projects slightly behind the dentary and forms the entire ventral edge of the mandible just

anterior to the articulation. The surangular projects slightly forward of the angular, and may in life have had slight contact with the inner edge of the dentary. It is capped by a short coronoid which overhangs the upper edge of the dentary laterally. The prearticular forms the retroarticular process and extends forward on the median wall of the jaw above the joint between angular and splenial and passes between splenial and dentary (see Williston, 1898: pl. 22; also fig. 4).

The "*Ichthyornis*" jaw resembles that of *Clidastes* and other mosasaurs in the following:

1. The presence of a conspicuous articulation between the dentigerous and articular portions of the jaw, and in the exact form and position of the articular surfaces on the angular and splenial bones.

2. The lack of a suture or bony symphysis between the two halves of the jaw anteriorly.

3. The presence of thecodont, recurved, sharp-edged teeth.

4. The position and nature of the coronoid suture on the surangular.

5. The form of the articular cotylus.

6. The posterior prolongation of the prearticular to form the retroarticular process of the jaw and the anterior position of the angular bone.

This combination of characters is known in no other group of animals.

Possible objections to considering the "*Ichthyornis*" jaw that of a young mosasaur include:

1. The obliteration of much of the suture between the splenial and the dentary, which suggests maturity. In far larger mosasaur jaws the sutures all remain open and distinct. Possibly the small size of the specimen may account in part for the obscurity of this suture; other sutures are well defined. Nevertheless one expects all sutures to be visible in newly hatched reptile skeletons.

2. The posterior ends of the splenial and the dentary slope forward at a much smaller angle with the axis of the jaw than in adult mosasaurs. Possibly this is a feature which changes with growth. Although it gives the "*Ichthyornis*" jaw a more bird-like appearance than would otherwise be the case, its significance does not approach that of any one of the mosasauroid resemblances mentioned above.

3. The anterior end of the surangular is embraced between the posterior ends of the splenial and the dentary exactly as in birds. This feature is not found in adult mosasaurs in which the ends of the surangular and the dentary abut against one another in a loose interlocking suture. I am inclined to attribute the difference to growth. The interdigitations at the ends of the dentary and the surangular of a large *Platycarpus* are many times the depth of this interleaving between the elements of the small "*Ichthyornis*" jaw.

In correspondence about this problem, Dr. Hildegarde Howard raised the question of the presence of vertebrae and limb bones of mosasaurs of a size comparable to the "*Ichthyornis*" jaw. To my knowledge no such specimens have been found. Small mosasaur vertebrae, belonging to individuals two feet or less in length, are known; limb and paddle bones are far less abundant than vertebrae or skull fragments in the extensive collections of mosasaurs at Yale; this ratio of occurrence together with the greater probability of collectors overlooking such small specimens in the field might easily account for the lack of such material.

These objections are trivial and in no way modify the conclusion that the jaw is that of a mosasaur and not a bird.

It might be argued that inasmuch as jaws unquestionably associated with *Hesper-*

Table 1

Summary of Differences and Similarities

Ichthyornis	Platycarpus	Alligator	Archaeornis	Hesperornis	Gavia
Coronoid					
Prominent.	Prominent.	Small, internal.	Unknown.	Absent.	Absent.
Articular cotylus					
Single, transverse.	Single, transverse.	Single, transverse.	?	Double, oblique.	Triple, oblique.
Angular					
Confined to ventral edge jaw, tapering to point below art. cotylus.	Confined to ventral edge jaw, tapering to point anterior to art. cotylus.	Large, forming retroarticular process.	Angular elongate, extending to end of retroarticular process.	Angular large, extending back to fuse with articular to form retroarticular process.	Angular large, forming retroarticular process.
Anterior end of angular					
With facet near lower edge to articulate with splenial.	With facet near lower edge to articulate with splenial.	Interdigitating suture between angular and dentary and splenial.	In sutural contact with splenial.	Deep, inclined forward, cylindrical surface for articulation with splenial.	Inserted between dentary and splenial with squamous overlap.
Prearticular					
Large, extending back to form retroarticular process—anteriorly inserted between splenial and dentary.	Large, extending back to form retroarticular process—anteriorly inserted between splenial and dentary.	Small, on inner edge Meckel's fossa.	Unknown.	Apparently like birds.	Arises in front of articular and extends forward to posterior end of splenial.
Splenial					
Visible posteriorly on external edge of jaw where it has small facet for articular.	Visible posteriorly on external edge of jaw where it has small facet for articular.	Confined to interior jaw. Squamous suture with coronoid and prearticular.	Said by Heilmann to have slight external exposure.	Exposed laterally, bearing oblique concave facet for angular.	Confined to interior jaw; squamous overlap of angular, little or none with prearticular.
Anterior ends of dentaries					
Without symphysis.	Without symphysis.	With sutural symphyses.	Symphysis present.	Without symphysis.	Fused anteriorly.
Teeth					
Thecodont (= in sockets)	Thecodont.	Thecodont.	Thecodont.	With swollen bases, in groove.	None.

ornis show indications of an intramandibular articulation, *Ichthyornis* could also have possessed such jaws. Consideration of the following facts, however, will show that this is extremely unlikely.

1. As shown by other portions of their skeletons, *Hesperornis* and *Ichthyornis* are only remotely related, and also were birds of entirely dissimilar adaptations and habits.

2. The intramandibular joint is not part of the common heritage of Mesozoic birds, hence if such a jaw was present in *Ichthyornis*, it must have evolved independently of the jaw of *Hesperornis*.

3. It is most improbable that two birds so dissimilar as *Hesperornis* and *Ichthyornis* would have identical feeding habits and thus evolve functionally similar jaw mechanisms.

4. Even if *Ichthyornis* had developed a jaw mechanism closely similar to *Hesperornis*, it seems beyond probability that it should agree with mosasaurs in those details of jaw structure in which it differs from *Hesperornis* and which distinguish that genus from the mosasaurs.

5. Finally, it must be borne in mind that the "*Ichthyornis*" jaw lacks those features which distinguish the jaws of birds from those of reptiles.

Hence it must be concluded that the lower jaws attributed by Marsh to *Ichthyornis* are in all probability not correctly associated with that bird but represent an extremely small individual of the mosasaur *Clidastes*.

SUMMARY AND CONCLUSIONS

Detailed descriptions and illustrations of the lower jaws attributed to the Cretaceous birds *Hesperornis* and *Ichthyornis* have been given. Important anatomical relations of the jaws of these forms are compared with those of loons (*Gavia*), the earliest known bird (*Archaeornis*), *Alligator* (representing the archosaurian reptiles), and *Platycarpus* (a mosasaur) in table 1.

From these comparisons, *Hesperornis* is found to show remarkable convergence toward the aquatic reptiles known as mosasaurs in the presence of an intramandibular articulation between angular and splenial bones. The details of this articulation are quite different, and *Hesperornis* shows definitely avian characteristics in the morphology of the articular, angular, and coronoid regions of its jaw.

The jaw of *Ichthyornis*, on the contrary, agrees with mosasaurs in minute details of form and relationship of the jaw elements. It lacks every feature by which bird jaws may be distinguished from those of reptiles and differs considerably from the archosaurian prototype from which birds were derived. There is no proof of association with the remainder of the bird skeleton with which the jaw was found, and its occurrence with the bird may easily have been a depositional effect of currents washing objects of the same size together. No quadrate is known in *Ichthyornis* and no contact can be established between the jaw and the remainder of the skull.

Finally, it should be pointed out that the lower jaws attributed to *Ichthyornis* are extremely long and massive in comparison to the rest of the lightly built skeleton of that form. Hawks, owls, and other predatory birds have far shorter beaks in comparison to body size, and have relatively large skulls for birds; but their skull-body ratio is much less than in Marsh's restoration of *Ichthyornis*.

The small fragments of bone containing alveoli which were described as portions of the upper jaw of *Ichthyornis* are quite indeterminate as to what bone was represented as well as what animal.

Therefore, it is concluded that the toothed jaws attributed to *Ichthyornis* are not those of a bird but belong to a small mosasaur.

LITERATURE CITED

Cope, E. D.
1869. Synopsis of the extinct Batrachia and Reptilia of North America. Trans. Am. Phil. Soc., 14, pt. 1: 1-104, pls. 2-12; pt. 2, pp. 105-235.

Dames, W.
1884. Ueber Archaeopteryx. Paleontologische Abhandlungen, 2, Heft 3:119-196.

Fürbringer, M.
1888. Untersuchungen zur Morphologie und Systematik der Vögel, zugleich ein Beitrag zur Anatomie der Stütz- und Bewegungsorgane. Amsterdam and Jena, i-xlix, 1-1713 pp., 30 pls.

Gregory, J. T.
1951. Convergent evolution: the jaws of *Hesperornis* and the mosasaurs. Evol., 5:345-354.

Heilmann, G.
1927. The origin of birds (London), 208 pp., 2 pls.

Lucas, F. A.
1903. Notes on the osteology and relationships of the fossil birds of the genera *Hesperornis, Hargeria, Baptornis,* and *Diatryma*. Proc. U. S. Nat. Mus., 26:545-556.

Marsh, O. C.
1872*a*. Notice of a new and remarkable fossil bird. Am. Jour. Sci., 4:344.
1872*b*. Notice of a new reptile from the Cretaceous. Am. Jour. Sci., 4:406.
1873. On a new sub-class of fossil birds (Odontornithes). Am. Jour. Sci., 5:161-162.
1880. Odontornithes, a monograph of the extinct toothed birds of North America. Rept. Geol. Expl. 40th parallel, 7:i-xv, 1-201, 34 pls., 40 figs.

Shufeldt, R. W.
1915. On a restoration of the base of the cranium of *Hesperornis regalis*. Bull. Am. Paleo., 5: 75-84, 2 pls.

Stolpe, M.
1935. *Colymbus, Hesperornis, Podiceps*: ein Vergleich ihrer hinteren Extremitat. Jour. für Ornithologie, 83:115-128.

Thompson, D.
1890. On the systematic position of *Hesperornis*. Studies Mus. of Zool. Univ. College, Dundee, 1, no. 10.

Williston, S. W.
1898. Mosasaurs. Univ. Kan. Geol. Survey, 4:81-411, 62 pls.

Peabody Museum, Yale University, New Haven, Connecticut, July 12, 1951.