# Teeth in *Ichthyornis* (Class: Aves)

Abstract. *Both* Hesperornis *and* Ichthyornis *are toothed birds; they and* Archaeopteryx *share broad flattened teeth with highly expanded roots. The teeth of* Ichthyornis *have been reported to have been set in sockets as were those of* Archaeopteryx, *but new specimens of* Ichthyornis *show the teeth set in a groove as in* Hesperornis. *These new fossils are from an adult but not old bird; thus, the presence or absence of tooth sockets in birds may be dependent on age.*

In 1872, Marsh described the Cretaceous flying bird *Ichthyornis dispar* on the basis of vertebrae, wings, and legs associated on a slab of Niobrara Chalk (*1*). Later that year he described an extinct reptile, *Colonosaurus mudgei* (*2*), from a toothed ramus on the same slab. In 1873, Marsh reassigned the ramus to *I. dispar* and placed the species in a new subclass, the Odontornithes (*3*).

In 1875 Marsh described the toothed lower jaw of *Hesperornis regalis* (*4*). These discoveries were the first toothed birds known from North America, and they popularized a concept that Mesozoic birds were toothed, although teeth were already known (*5*) in *Archaeopteryx* from the Old World Jurassic. These birds were the only Mesozoic birds known to have jaws, but most later workers assumed that teeth must also have been present in other Mesozoic birds (*6*). In 1952, Gregory challenged Marsh's assignment of the toothed jaws to *Ichthyornis* and suggested that, on the basis of morphology, they should be regarded as the jaws of a small mosasaur (*7*). This view has met with widespread acceptance and is still the predominant interpretation in recent texts (*8*). However, Russell, in his 1967 review of the mosasaurs, rejected the mosasaur affinities of the jaws assigned to *Ichthyornis* (*9*), and Walker (*10*) also doubted that Gregory was correct in his identification.

Since then, Gingerich (*11*) has pointed out many avian features in the posterior mandible of *Ichthyornis*, and few specialists now doubt that *Ichthyornis* was toothed. Until recently only Marsh's collection, which is now part of the Yale Peabody Museum (YPM) collection, could be used to resolve this controversy. However, during the summer of 1970, one of us (J.D.S.) found a large portion of an *Ichthyornis* skeleton [Sternberg Memorial Museum (SMM) 13520] including parts of both mandibles, much of the vertebral column, and most of the skeleton of both wings. The wing elements preserved include complete humeri and definitely establish the specimen as a large *Ichthyornis*. The mandibles are essentially the same as those described by Marsh but are uncrushed and relatively free of matrix. They indicate that *Ichthyornis* mandibles and teeth are similar to those of the hesperornithids in nearly all respects. The mandibular teeth of both groups are laterally flattened and are recurved posteriorly. The lingual sides of hesperornithid teeth are nearly planar, but the labial sides are strongly convex. The teeth of *Ichthyornis*, however, are convex on both sides. The teeth of both groups are also slightly recurved lingually. The anterior edge of the teeth of both have a distinct shoulder, which increases the angle of inclination and gives the teeth their posteriorly recurved appearance. This effect is more pronounced in the anterior part of the dentition than in the posterior part. The crowns of the teeth of both groups have unserrated enamel edges on their anterior and posterior margins, those of *Ichthyornis* being more strongly pronounced. The enamel stops at the base of the crown, and the teeth rapidly expand as they enter the jaw. The broken edges and our x-rays indicate that the expanded bases of the teeth may be inclined posteriorly in the dentaries. The inclination is more pronounced in the anterior half of the dentition. In contrast, the teeth of mosasaurs are conical, and their edges are not so well defined as in their avian contemporaries.

In the mandibles of our specimen, all of the teeth are implanted in an open groove with only slight constrictions of the dentary, as in the hesperornithids (Fig. 1). This is contrary to previously published observations. Marsh (*12*) shows distinct sockets for *Ichthyornis*; because of doubts raised by our specimen, we reexamined the Yale specimen. This examination confirmed the presence of distinct sockets in *I. dispar* (YPM 1450), except for the last two teeth, which are set in an open groove (Fig. 1). Thus, there are *Ichthyornis* mandibles in which all the teeth are in an open groove and those in which all of the teeth except for a few posterior ones are in distinct sockets. The sockets become better defined as one progresses anteriorly on the tooth row. Edmund (*13*) has reported that crocodilians have thecodont teeth as adults but that in the young, the posterior teeth are set in a deep relatively unrestricted groove, which becomes divided by interdental septa as the individual ages. The process begins anteriorly and progresses posteriorly. We suggest that a similar ontogenetic process occurred in *Ichthyornis*. Indeed, the sutures on our mandibular fragments are more distinct than on Marsh's specimen, which has distinct sockets. However, SMM 13520 is clearly from an adult, so the development of sockets must have been somewhat delayed. All specimens of *Hesperornis* have been reported (*7*) to have their teeth implanted in an open groove. Because the jaw fragments available are few, we cannot be certain that this finding is not due to a biased sampling of only young individuals. It is also possible that the Hesperornithiformes are to some degree neotenic, which would explain the persistence of the groove in the jaws as well as other morphological characteristics, including the presence of unfused clavicles. Sockets of the sort found in *Ichthyornis* do

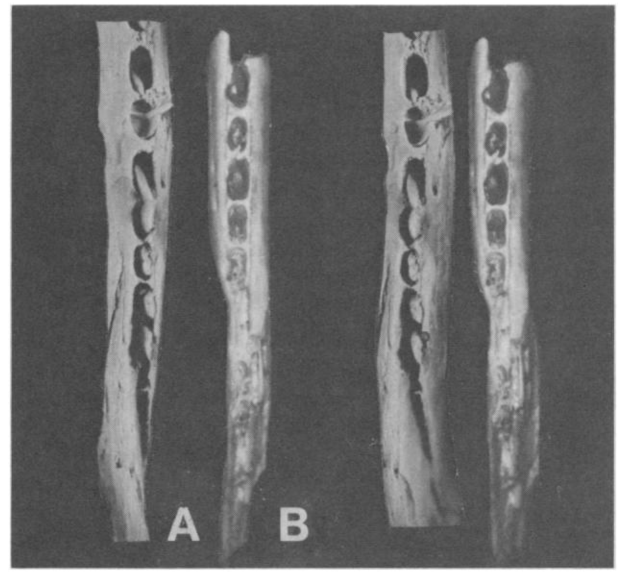


Fig. 1. Stereophotographs of the dorsal side of posterior segments of right dentaries of *Ichthyornis*. (A) *Ichthyornis dispar* (holotype), YPM 1450. (B) *Ichthyornis* sp., SMM 13520.

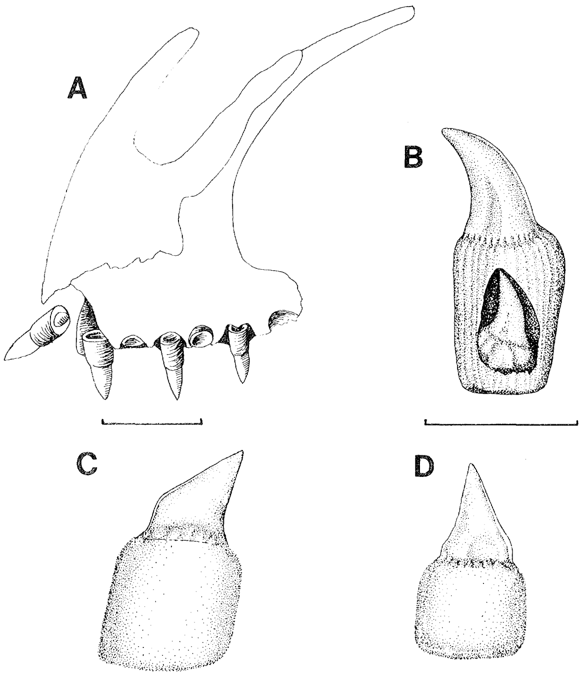


Fig. 2. Teeth of birds. (A) Reconstruction of the premaxilla of *Archaeopteryx lithographica* [after Edmund (*13*)]. (B) Lingual view of a tooth from the maxilla of *Hesperornis regalis* [after Marsh (*12*)]. C and D) Lingual views of teeth from the dentary of *Ichthyornis* sp., SMM 13520 (roots restored on the basis of radiographs). (C) Right anterior tooth. (D) Left posterior tooth. Scale equals 5 mm.

not occur in mosasaurs, in which the teeth are fused to the labial side of the dentary.

In SMM 13520, tooth replacement took place in posterior to anterior waves in alternating alveoli, as Edmund (*13*) has also reported for YPM 1450. Considering the nature of the root and the mode of implantation, it seems likely that the germinal replacement tooth developed in association with the resorption of the root of its predecessor from the lingual side and ultimately expelled it. This is the same method of replacement observed in *Archaeopteryx* (Fig. 2a), the hesperornithids (Fig. 2B), mosasaurs, theropod dinosaurs, and numerous other reptilian groups. Marsh stated, "The young teeth are much inclined when they appear above the jaw, after the old teeth have been expelled" (*12*). To some extent, this is due to the curve of the upper part of the crown. But our x-rays show that the newly erupted teeth are inclined in proportion to the size of the cavity allotted them between the adjoining teeth until their bases fully develop.

Marsh (*12*) recorded 21 alveoli in the mandible of *Ichthyornis dispar* and 22 in *Ichthyornis anceps*. By reconstructing a complete jaw from the two left and two right fragments at our disposal, we believe that our specimen possessed at least 26 teeth in each mandible. The alveolar length would have been approximately 44 mm, slightly larger than Marsh's 41 mm. The total length of the dentigerous portion of our mandible would have been 48 mm.

As stated, the sutures on our specimen are more apparent than on Marsh's fossil. On the lateral side of the right mandible, the splenial is broken just behind the posterior end of the tooth row. Gregory's interpretation of the position of the splenial in this area (*7*) was correct. The ventral spleniodental suture runs forward from the intermandibular joint just above and nearly parallel to the ventral margins of the mandible. It is soon nearly obliterated, but it is marked by a series of microscopic foramina. The suture gradually crosses the midpoint of the ventral margin about one-third of the distance to the tip of the mandible. From here it gradually ascends the lingual side. It terminates just behind a foramen 19 mm from the anterior end of the mandible, where it meets the dorsal suture. The dorsal spleniodental suture begins at the posterior end of the tooth row. The lingual alveolar wall of at least the four posteriormost teeth is formed entirely of the splenial. The suture gradually descends to meet the ventral spleniodental suture at the foramen located in the lower third of the width of the mandible. This foramen marks the posterior border of Meckel's canal, which terminates only a few millimeters farther forward.

As Gregory (*7*) and Marsh (*12*) have observed, the dentaries were joined at the symphysis by ligaments. Marsh's figure (*12*) fails to indicate the presence of seven mental foramina along the lateral surface, although Gregory noted them (*7*). Near the middle of the dentigerous portion of the mandible the last of these foramina gives rise to a fairly deep canal, which widens posteriorly. Our specimen clearly shows that this canal was not caused by the crushing of the internal mandibular canal, as Gregory (*7*) suggested. There is a well-defined upward arc in the ventral margin of the dentary between the second and fourth mental foramina.

Study of the mandibles and teeth of *Ichthyornis* shows that their mode of tooth implantation is not radically different from that of *Hesperornis* and that the teeth of Mesozoic birds resemble each other in shape and manner of tooth replacement. *Ichthyornis* is not especially similar to mosasaurs in these features; no reason now exists to confuse the dentaries of mosasaurs and birds or to doubt the presence of teeth in *Ichthyornis*.

The presence of teeth set in a groove in the hesperornithids may be due to the age of the individuals sampled, or it may be a neotenic character state. The distribution of teeth among Cretaceous birds is currently unclear, and the avian status of those taxa that lack teeth has been questioned (*14*). However, we do not really know how widespread teeth were among Late Cretaceous birds. The Hesperornithiformes are an archaic group that diverged from the mainstream of bird evolution early in the avian radiation, and a similarly distant relationship has been argued for the Ichthyornithiformes (*15*). It is possible that the birds that gave rise to the Cenozoic radiation were already edentulous in the Late Cretaceous.

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