Mandibular kinesis in *Hesperornis*

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ABSTRACT - Some aspects of mandibular morphology are known for three hesperornithiform genera: *Hesperornis*, *Parahesperornis* and *Baptornis*. All share a distinctive intramandibular joint between the angular and the splenial. A special process of the surangular extending between the splenial and the dentary bridges the joint. The symphysis appears to have been elongate and unfused, joining anteriorly with a short intersymphyseal bone. It appears that the mandibles spread posteriorly as the jaws opened, allowing the swallowing of larger prey. The closed mandible is very slender anteriorly, resembling some cetaceans, and seems highly adapted for the capture of fish. The discovery of fish remains in a preserved stomach cast of *Baptornis* gives direct support for this interpretation.

Key words: *Hesperornis, mandibular kinesis, intraramal joint, intersymphyseal bone, intramandibular joint.*

KINESIS MANDIBULAIRE DE HESPERORNIS – Quelques aspects de la morphologie mandibulaire sont connu pour les trois genres d' hesperornithiformes: *Hesperornis*, *Parahesperornis* et *Baptornis*. Tous ont en commun une articulation intramandibulaire entre l'angulaire et le splénial. Un processus spécial du surangulaire s'étend entre le splénial et le dentaire à travers l'articulation. La symphyse semble avoir été allongée et sans fusion, rejoignant antérieurement un os intersymphysial court. Il apparaît que les mandibles s'écartaient postérieurement lors de l'ouverture des mâchoires, permettant ainsi d'avaler des proies plus grandes. La mâchoire est très étroite antérieurement, ce qui rappelle certains cétacés, et paraît très bien adaptée à la capture des poissons. La découverte de débris de poissons dans un contenu stomacal de *Baptornis* apporte un soutien direct à cette interprétation.

INTRODUCTION

The cranial kinesis of *Hesperornis* is described in detail by Buhler *et al*. (1998), who conclude that it is prokinetic, but do not discuss the mandible. Kinesis in the mandible is discussed by Gregory (1951), who makes extensive comparisons with extinct giant lizards (mosasaurs), claiming that the mandibles of the two groups are similar in many respects, but especially in sharing an intramandibular joint between the splenial and the angular. This unusual joint was also found in jaws referred to *Ichthyornis*, and Gregory (1952) found the similarity between that genus and mosasaurs so great that he suggested that the putative *Ichthyornis* jaws were really those of juvenile mosasaurs. Surprisingly, this bold suggestion was quickly accepted. Swinton (1975), in a book on fossil birds, even doubted that the *Hesperornis* jaws were avian. He did accept one mandible in the University of Nebraska State Museum as evidence that *Hesperornis* was toothed and illustrated it (Swinton, 1975, Fig. 16, p. 37). Further study soon demonstrated that all of these suggestions were in error, and the toothed jaws were restored to their avian skeletons (Gingerich, 1972; Martin and Stewart, 1977). Ironically, the one exception was the only specimen that had convinced Swinton, UNSM 5363. This turned out to be a genuine juvenile mosasaur. However, the question of mandibular kinesis remained, and Gingerich suggested that a somewhat similar kinesis in theropod dinosaurs provided further support of their affinity with birds. Most of this speculation continued to be based on the original Marsh materials at Yale, and so the discovery of a more complete and better-preserved specimen of *Hesperornis regalis* (KUVP 71012) provides an opportunity to review the question of mandibular kinesis in more detail.

THE MANDIBLE OF HESPERORNIS

The two dentaries of KUVP (Kansas University Vertebrate Paleontology) 71012 were found in articulation (Fig. 1) with an intersymphyseal (predentary) bone articulated between them (Martin, 1987). This was totally unexpected, as predentary bones are otherwise only found in ornithischian dinosaurs among tetrapods (with the exception

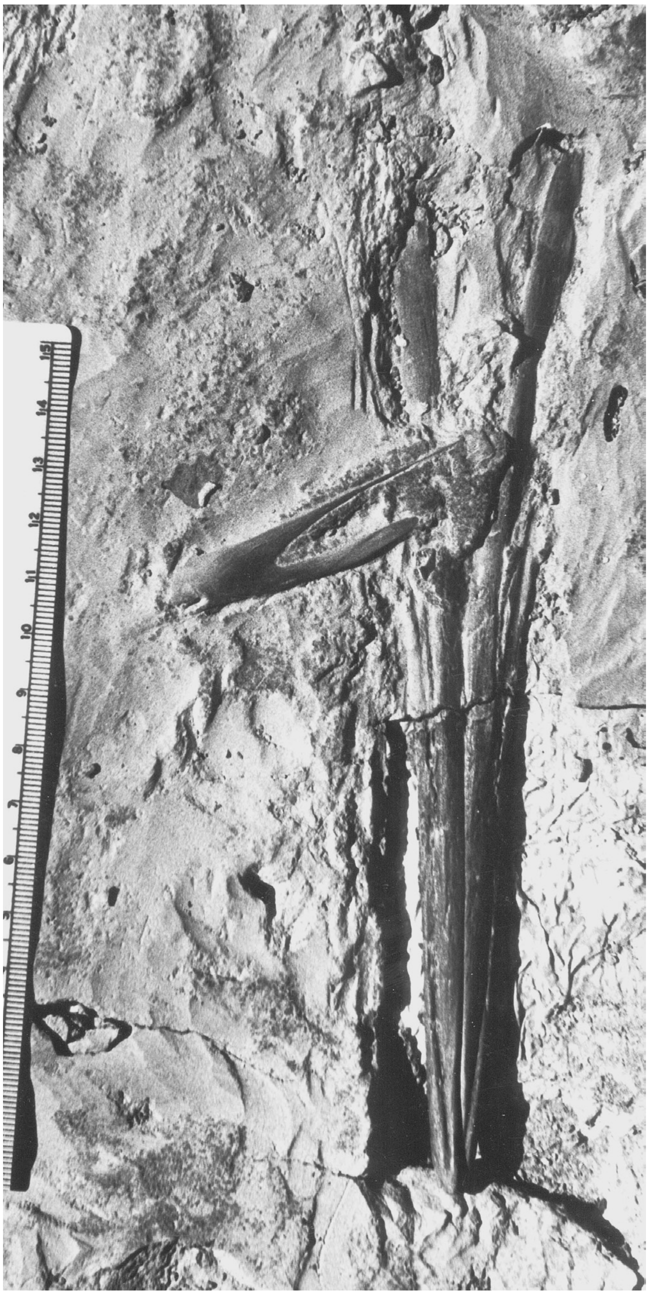

Figure 1 - Dentaries of KUVP 71012, *Hesperornis regalis* as found *in situ.*

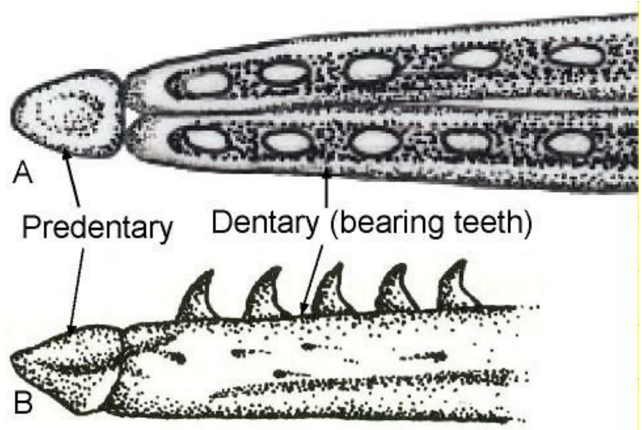

Figure 2 - Lateral view of the contact between the predentary and the dentary in KUVP 71012, *Hesperornis regalis.*

of the unusual bird, *Teratornis*). A quick search revealed a second hesperornithiform example with the type mandible of *Parahesperornis alexi* and the bone illustrated by Marsh (1880, Pl. II., fig. 12) as a basihyal provides an additional occurrence in *Hesperornis regalis*. The unusual blunt anterior termination of the dentary in *Hesperornis* had been remarked upon (Gregory, 1951), and now could be explained, as the end bears a small oval facet for the articulation with the predentary. The dorsal lateral surface of the dentary also bears a distinctive large pit that is matched by a similar depression in the predentary, presumably for a ligament that crossed the joint and tied the jaw together (Fig. 2). The jaws are hinged anteriorly by this joint, while in modern birds the symphysis between the dentaries is fused. The predentary is triangular and fits inside the down turned tip of the premaxillaries. The premaxillaries are toothless, as is the predentary bone.

The articulated dentaries showed another feature of the hesperornithiform mandible that had been overlooked. The dentaries lie directly against each other for most of their length (Fig. 1). This resulted in an extremely narrow mandible. The validity of this arrangement is easily demonstrated by placing the mandible into the premaxilla, demonstrating a perfect and unique fit. This arrangement, seen in a wide variety of animals that catch fish (cetaceans, gavials and gars), displaces very little water as the mouth is closed. The mandibles were toothed, with the teeth set into an open groove. These tooth crowns were inserted tightly on the inside margin of the premaxillaries, where slight indentations leave a record of their presence. There is an open Meckel's groove on the inside of the dentary covered by an elongate, triangular splenial bone (Fig. 3b, d). The splenial has an inclined facet for the angular (Fig. 3b). The dentary develops a lateral grooved shelf to accommodate the teeth from the maxilla (Fig. 3b). Just above the intramandibular joint, the dentary sends back a thin ventral-lateral flange overlapping the surangular. he medial surface of this flange has a groove extending onto the ventral medial margin of the dentary that is covered by the splenial, forming an elongated pocket. The surangular has an elongated slender anterior projection extending forwards across the intramandibular joint and into the pocket formed by the splenial and the dentary. Gregory (1951) incorrectly suggested that the surangular ended where it met the dentary and might have interdigitated with that bone, a relationship that Clarke (2004) also suggested for *Ichthyornis*. The articular is fused to the surangular. The angular fits posteriorly against a shallow indentation on the ventral lateral side of the surangular (Fig. 3) and does not extend posteriorly to form the retroarticular process as stated by Gregory (1951,

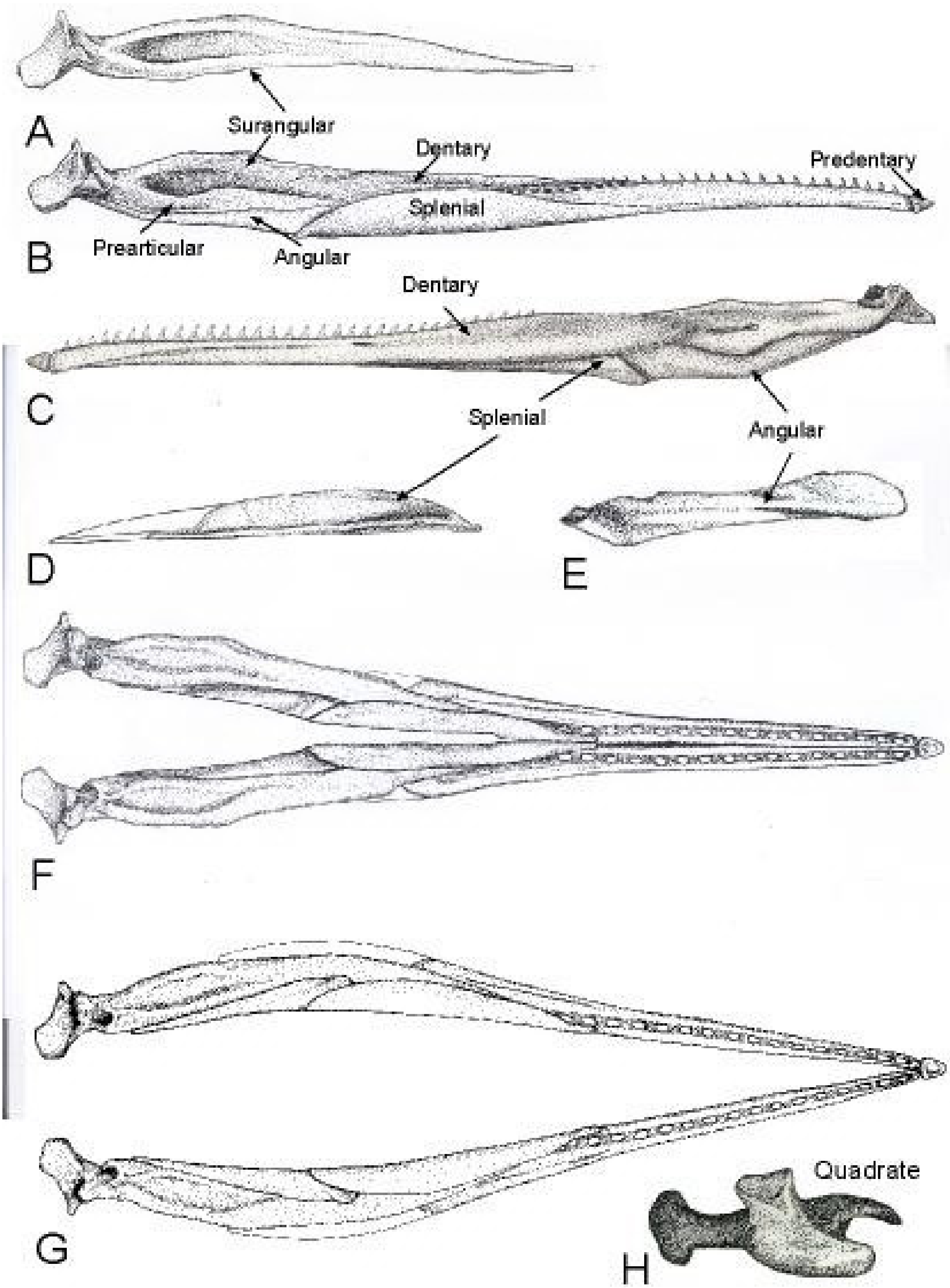

Figure 3 - Mandible of KUVP 71012, *Hesperornis regalis*: A. medial view of the left surangular with the articular and prearticular fused to it; B. medial view of the left mandible; C. lateral view of the left mandible; D. medial view of the left splenial; E. medial view of the right angular; F. dorsal view of the mandible when the jaws are closed; G. dorsal view of the mandible when the jaws are open, showing separation at the interdentary joint and bending at the intramandibular joints; H. ventral view of the right quadrate showing the articular surfaces.

p. 348). The surangular runs forward above the angular's dorsal medial surface extending to where the angular articulates with the splenial. At that junction, it fits into a shallow groove on the dorsal surface of the angular that locks the angular to the surangular. The angular is distinctly curved (convex labially), as compared to the surangular, and this curvature may help guide the bending of the surangular. The surangular is thin, flat, and presumably, bendable above the joint between the angular and the splenial. The thinner the bone, the greater the flexibility should be, but thinner bones are less strong; therefore three thin bones, each of which can flex independently, participating in the intraramal joint, allow this jaw region to bow laterally, while maintaining strength.

The surangular, articular and prearticular are tightly fused and hard to distinguish. The prearticular is not fused to the angular, a possibility suggested by Gregory (1951). It also does not extend across the intraramal joint, as suggested by Gregory (1951), as it does in mosasaurs. Because the coronoid and surangular end at the intramandibular joint and the prearticular crosses it in mosasaurs, Gregory's 1951 misinterpretation of the Yale *Hesperornis* material might have resulted from his use of mosasaurs to interpret it.

The quadrate has an exceptionally large and upwardly turned orbital process. The ventral articulation has a large inwardly inclined medial trochlea and a small lateral one (Fig. 3h). This causes the jaws to spread as they open, bending them at the intramandibular joint. The dentaries then spread at the intersymphyseal joint, causing a significant increase in gape (fig. 3g). The posterior flange of the dentary and the surangular form an overlapping structure that facilitates bending at the interramal joint. As Gregory (1951) suggested, there is a slight rotation of the dentaries outward as the jaws open. This would dislodge the maxillary teeth and permit the captured prey to be rotated into the headfirst swallowing position favored by piscivores. The loss of teeth in the premaxilla may have facilitated this rotation, while the maxillary and dentary teeth could assist with holding the prey for manipulation. Because of the incorporation of the arm into a wing (extremely reduced in *Hesperornis*), birds cannot use their manus to assist with the manipulation of food held in the mouth. This is not much of a problem when the food is small, as is the case with most insects, but larger prey may be caught sideways and have to be rotated for swallowing. A system of rotation not involving release of the prey is provided by movement (kinesis) within the jaw and may have been a major impetus for the evolution of the jaw kinesis characteristic of birds.

COMPARISONS

In modern birds the symphysis is fused, but there may be a bending zone just behind it that acts in a similar way to the joint between the dentaries and the intersymphyseal bone. Such a joint would be difficult to develop within the relatively thick and inflexible dentaries of the toothed birds, and this may have promoted the development of a synovial joint in the same position, resulting in a separate predentary ossification. The intraramal joint in *Hesperornis* is a combination of a synovial joint between the surangular and the splenial and a bending zone across the posterior flange of the dentary and the surangular. In either case, extinct toothed and modern piscivorous birds use intraramal bending to facilitate gape. Intraramal bending is also characteristic of the extinct bony-toothed birds, Odontopterygia (Zusi and Warheit, 1992). An intersymphyseal bone also occurs in the giant vulture-like *Teratornis* (Campbell and Tonni, 1982), representing independent evolution of a similar gape mechanism.

The intraramal joint of mosasaurs and some dinosaurs is unlike that of *Hesperornis* in that they lack the posterior dentary flange and the anterior process of the surangular. *Hesperornis* also lacks a coronoid bone, a prominent feature in mosasaurs and most dinosaurs. In many animals the coronoid would lie across and interfere with an intraramal joint (it lies behind the joint in mosasaurs). The supposed similarity between mosasaur and bird mandibles is overdrawn and the two are easily separated. These differences extend to the pleurodont implantation of the teeth in mosasaurs and the thecodont implantation in birds.

Parahesperornis has the same mandibular kinesis as *Hesperornis*, and an anterior part of a *Baptornis* angular shows the characteristic intraramal joint, so we might suppose that it occurs throughout Hesperornithiformes. The intraramal joint also occurs in *Ichthyornis*, and examination of the anterior tip of the dentary in a number of specimens of that genus reveals the characteristic facet for the predentary bone. This combination of features is unique enough to raise the possibility that it arose before foot-propelled diving developed in Hesperornithiformes and represents a complex synapomorphy uniting an early ornithurine clade, the Odontornithes of Marsh (1880). In contrast, Clarke's (2004) description of *Ichthyornis* would suggest a very isolated position for that genus.

Gregory (1952) described a large coronoid bone in *Ichthyornis,* and Clarke (2004) a smaller one. Gingerich (1972) was unable to find a coronoid. All of the birds, living and fossil that we are aware of, lack the coronoid, so its presence would be of considerable interest. According to Clarke (2004, Fig. 30), the surangular in *Ichthyornis* turns labially and inserts into a slot on the medial side of the dentary, while the coronoid is a small sliver inserted between it and the prearticular. The prearticular extends across the joint between the angular and the splenial and inserts between the splenial and the dentary, the same position occupied by the surangular in *Hesperornis* (Clarke, 2004). The prearticular ends behind the intraramal joint in *Hesperornis*; there is no coronoid, and the surangular turns medially when it reaches the dentary rather than laterally. The dentary in *Hesperornis* extends across the intraramal joint rather than ending at the joint as described for *Ichthyornis* by Clarke (2004). This would indicate very different intraramal joints in hesperornithiforms and *Ichthyornis*. However, the *Ichthyornis* material is so broken and crushed that it could easily be misinterpreted, and probably a re-examination in light of the new hesperornithiform material is warranted.

Hesperornis has a mandible that is not similar in detail to either mosasaurs or dinosaurs. Nor is it close to modern birds, which have rhamphotheca-covered dentaries that permit different opportunities for bending. The predentary bone occupies the same position as a bending zone in modern birds with intraramal joints, and the resistance to bending of the thicker tooth-bearing dentary may have forced the development of a synovial joint. A similar joint and predentary bone is suggested for *Ichthyornis* on the basis of a similar articular facet on the tip of the dentary to that for the predentary in *Hesperornis*.

CONCLUSIONS

We do not presently know the distribution of predentary bones among early birds. They are absent from *Archaeopteryx* and other known members of the Sauriurae. Presumably, predentaries define a clade within the early Ornithurae. It seems certain, on the basis of anterior dentary morphology, that they occur in the Ichthyornithiformes, as well as the Hesperornithiformes, thus uniting these two groups into what may be considered a superorder (Odontornithes of Marsh, 1880). They occur at the same position as a well-recognized bending zone in the dentary of modern birds that have an intramandibular joint, and this provides an analogue for their origin. Almost all known Mesozoic ornithurines are aquatic or water marginal, and many undoubtedly ate fish. The combination of a narrow mandible with a wide posterior gape has obvious advantages for a piscivore. The kinetic system in *Hesperornis* is unique and not really comparable to that of either mosasaurs or theropod dinosaurs.

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