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In this paper we review the distribution of the predentary bone in Mesozoic ornithurine birds. The predentary bone, well known in ornithischian dinosaurs, has now been reported not only in hesperornithids and ichthyornithids but also in a number of Early Cretaceous basal ornithurines, such as *Yanornis*, *Yixianornis*, *Hongshanornis* and *Jianchangornis*. In many Early Cretaceous ornithurines the predentary bone is not preserved, but the anterior end of the dentary has a blunt, often inclined margin and usually shows a distinctive pit. These are characteristic features of a predentary attachment. The predentary bone is absent in extant birds, and examination of known enantiornithines and more basal avians now represented by hundreds of specimens show that none of them preserved a predentary bone, confirming that this bone was independently derived in the Ornithurae, and lost in the Neornithes. The predentary bone is found to be associated with both toothed and edentulous dentaries in basal ornithurines. In toothed birds the edentulous predentary bone always corresponds to an edentulous anterior portion of the premaxilla. Although it is possible that the presence of the predentary bone is related to a piscivorous diet in some birds, this may not be true for all the basal ornithurines with a predentary bone. It is almost certain that it was functionally very different from the predentary bone in ornithischian dinosaurs.

Keywords: predentary bone; ornithurines; Cretaceous; China

Introduction

The predentary is a small, edentulous intersymphyseal bone at the anterior end of the dentaries in almost all ornithischian dinosaurs (Bell *et al.* 2009), long believed to be unique to the Ornithischia among tetrapods. However, this view changed with the discovery of a predentary bone in some Cretaceous birds. It was first recognized in two individuals of *Hesperornis* and one of *Parahesperornis*, and presumed to be also present in *Ichthyornis* (Martin 1987). In recent years, with the discovery of several dozen avian genera represented by hundreds of nearly completely articulated skeletons from the Lower Cretaceous of China (Zhou *et al.* 2003, 2009; Zhou 2004), it has been shown that several basal ornithurines also possess a predentary bone (Zhou & Zhang 2005; Zhou *et al.* 2009), which not only confirms the presence of this structure in Mesozoic birds, but extends its temporal distribution to the Early Cretaceous. Martin (1987) and O'Connor *et al.* (2009) questioned the homology between the predentary bone in ornithischians and Mesozoic ornithurines, the latter paper calling the predentary bone in birds 'the intersymphysial ossification'.

The predentary bone is a small single cap-like edentulous bone at the tip of the lower jaw in many Mesozoic ornithurines. It seems to be relatively small compared to that in ornithischian dinosaurs of similar size. Since the predentary bone is small and very probably connected to the dentary only by loose ligaments, it is not preserved or is ignored in many specimens. Therefore a survey of the distribution of this feature in Mesozoic birds is necessary in order to gain a better understanding of its origin and evolutionary history. In addition, little is known about its function in the feeding of early birds. In this paper we will review the distribution and variation of the predentary bone in Mesozoic birds, based on published and some newly discovered avian materials, discuss how it is connected to the dentary, and provide a hypothesis about its possible role in the feeding behaviour of basal ornithurine birds.

Institutional abbreviations

KUVP: Vertebrate Paleontology Division, Natural History Museum and Biodiversity Research Center, University of Kansas; **IVPP**: Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences; **YPM**: Peabody Museum of Yale University.

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Description and distribution

In *Hesperornis regalis* the two dentaries of KUVP 71012 were found in articulation with an intersymphysial (predentary) bone articulated between them (Martin 1987; Martin & Naples 2008). The bone illustrated by Marsh (1880, pl. 2, fig. 12) as a basihyal provided an additional example in *Hesperornis regalis*. Martin (1987) also found one in the holotype specimen of *Parahesperornis alexi* (KUVP 2287), indicating that the bone was probably present throughout the Hesperonithiformes (Figs 1, 2). The unusual blunt termination of the dentary in *Hesperornis* had been remarked upon (Gregory 1952), and now could be explained as the end bears a small oval facet (predentary facet) for articulation with the predentary. The dorsal lateral surface of the dentary also bears a distinctive large pit (anterior ligamental pit) that is matched by a similar depression in the predentary (posterior ligamental pit of the predentary), presumably for a ligament that crossed the joint and tied the jaw together. The jaws are hinged anteriorly by this joint, while in modern birds the symphysis between the dentaries is fused. The toothless predentary is triangular and fits inside the slightly downturned toothless tip of the premaxillaries.

The predentary bone has not been recognized in any of the specimens of *Ichthyornis*; however, Martin (1987) predicted its presence based on the shape of the termination of the dentary. Examination of the type of *Ichthyornis dispar* shows the presence of the predentary facet along with the anterior ligamental pit (Fig. 3). This would seem to confirm the presence of a predentary contrary to Clarke's (2004) observations, and the discovery of these same morphological features in the Early Cretaceous material, including predentary bones *in situ* and in articulation (Zhou & Zhang 2005; Zhou *et al.* 2009), confirms that this morphology is consistent and adequate to indicate the presence of the predentary even when it has been lost during fossilization. It should furthermore provide adequate criteria to identify an isolated predentary. The predentary bone of the ornithischians also usually has a distinct notch for a process of the dentary that is not present in the ornithurine predentary.

Hongshanornis is one of the most basal ornithurines from the Lower Cretaceous Yixian Formation (Zhou & Zhang 2005). It also represents the first Early Cretaceous bird that was recognized to have such a structure. The predentary bone is a small crescent-shaped bone near the tip of the dentaries (Fig. 4). Due to the crushed status of the bones, it is impossible to determine whether there is a ligamental pit on the dentary. However, it is noted that the terminal end of the dentary is blunt and dorsally inclined, while the premaxilla has a much more pointed end. The premaxillary bone clearly overlaps the predentary as in *Hesperornis.*

Yanornis martini is a more derived ornithurine (Zhou & Zhang 2001) than *Hongshanornis*. It is from the Jiufotang Formation, which is about 5 Ma younger than the Yixian Formation (He *et al.* 2004). Although the predentary bone has not been previously described, a referred specimen (IVPP V13358) has a triangle-shaped predentary bone anterior to the dentaries (Fig. 5A; Zhou *et al.* 2004). Although the predentary bone is not preserved, an anterior ligamental pit is visible at the end of the dentary (Fig. 5B) in the holotype of *Yanornis martini*. The blunt, anteriorly inclined and straight margin of the dentary is also identical to that of IVPP V13358. The dentary only extends anteriorly slightly past the dentitulous portion of the premaxilla. These features strongly indicate the presence of a predentary bone that was lost post-mortem. It is most likely that, the predentary corresponding to the edentulous portion of the premaxilla was only loosely connected to the dentary by ligaments that decayed rapidly after death (Bell *et al.* 2009).

Yixianornis is another derived ornithurine from the Jiufotang Formation. The predentary bone was not reported in previous descriptions of this bird (Zhou & Zhang 2001; Clarke *et al.* 2006). However, re-examination of the rostral region of the skull indicates that a predentary bone was present anterior to the dentaries in the holotype specimen, as the premaxilla extends anterior to the dentary about the

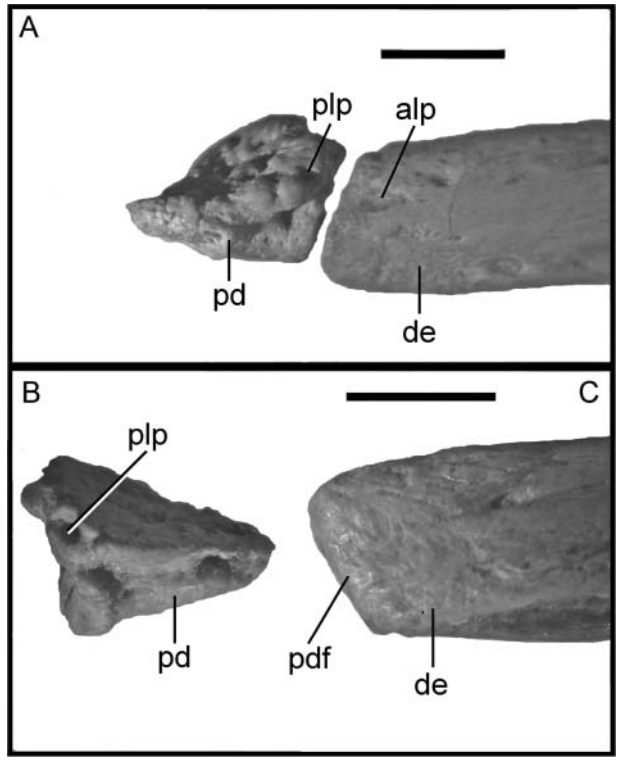

Figure 1. Photos of *Hesperornis regalis* (KUVP 71012). **A,** the predentary and tip of the left dentary in lateral view; **B,** the predentary in right view; **C,** the tip of the left dentary in medial view. Scale bar = 1 cm. Abbreviations: alp, anterior ligamental pit; de, dentary; pd, predentary; pdf, predentary facet; plp, posterior ligamental pit.

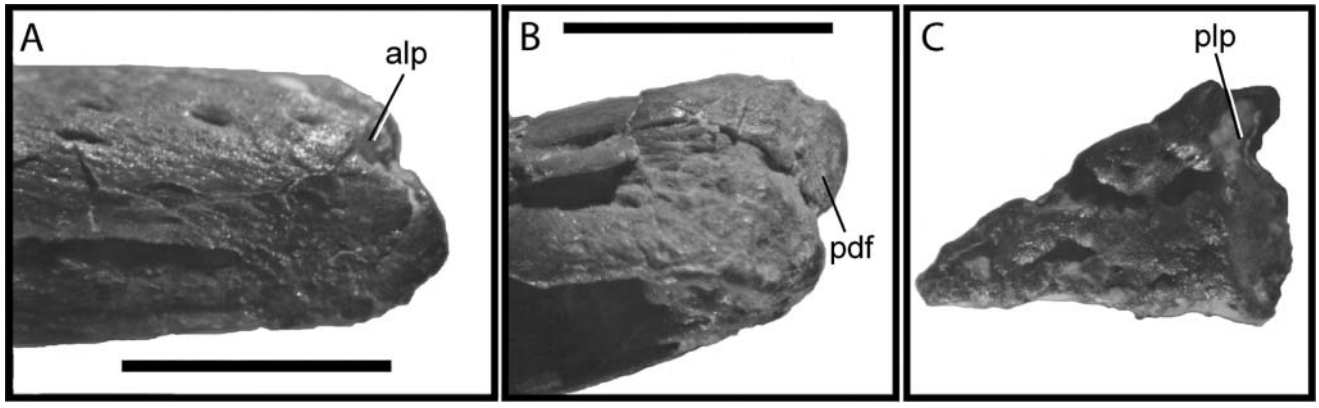

Figure 2. Photos of the holotype of *Parahesperornis alexi* (KUVP 2287). **A,** the tip of the right dentary in lateral view; **B,** the tip of the right dentary in medial view; **C,** the predentary in right view. Scale bar = 1 cm. Abbreviations as in Fig. 1.

distance to accommodate a predentary, and the anterior termination of the dentary is blunt (Fig. 6A).

Jianchangornis is a recently described basal ornithurine that preserves a distinctive predentary bone (Zhou *et al.* 2009). The anterior end of the dentary bears a strong resemblance to that of *Yanornis*. A rounded pit is also visible near the tip of the dentary (Fig. 6B). The pit is located less dorsally than in the holotype of *Yanornis*, but is more similar to that of IVPP V13358. Because the anterior portion of the premaxilla is not preserved, it is difficult to reconstruct the exact relationship between the predentary and the premaxilla.

Archaeorhynchus represents another beaked basal ornithurine bird from the Lower Cretaceous of China (Zhou & Zhang 2006). The dentary is slender and has a pointed anterior end. Examination of the holotype and two additional specimens shows no evidence of a predentary bone.

Gansus is a relatively derived ornithurine from the Lower Cretaceous. Although more materials are now known (You *et al.* 2006), unfortunately no skull is available to examine to determine if it also possesses a predentary bone.

To date, the avian predentary bone is only known in Mesozoic ornithurine birds. None of the enantiornithine taxa from the Lower Cretaceous preserve a predentary bone despite the discovery of several hundred specimens. Examination of the morphology of the anterior end of the dentary shows that most enantiornithines have a pointed end. For instance, the dentary of *Longirostravis* (Hou *et al.* 2004) has a pointed anterior end, and no pit is visible at the anteromost end of the medial dentary. *Longipteryx* also has a pointed anterior dentary, showing no evidence for the presence of a predentary bone (Zhang *et al.* 2001). In both *Longirostravis* and *Longipteryx*, the dentary extends anteriorly to the anteriormost end of the premaxilla, and the premaxilla lacks a distinctive edentulous portion as in those basal ornithurines with a predentary bone. Another long snouted enantiornithine, *Shanweiniao,* also seems to lack a predentary bone for similar reasons to *Longirostravis* and *Longipteryx* (O'Connor *et al.* 2009). Other Early Cretaceous enantiornithines with known skulls, such as *Sinornis* (Sereno & Rao 1992; Sereno *et al*. 2002), *Cathayornis* (Zhou *et al.* 1992), *Eocathayornis* (Zhou 2002), *Vescornis* (Zhang *et al.* 2004) and a hatchling from Spain (Sanz *et al.* 1997; Chiappe & Walker 2002), possess a dentary with a pointed anterior end, and the premaxilla does not have a distinctive edentulous portion. The dentary of the Late Cretaceous edentulous enantiornithine *Gobipteryx* also has a pointed anterior end, and shows no evidence for the presence of the predentary bone (Chiappe *et al.* 2001).

The predentary bone has not been recognized in any of the most basal birds from the Upper Jurassic or Early Cretaceous. None of the specimens of *Archaeopteryx* (Mayr *et al.* 2005), *Sapeonis* (Zhou & Zhang 2003), *Jeholornis* (Zhou & Zhang 2002), *Zhongjianornis* (Zhou *et al.* 2009), *Zhongornis* (Gao *et al.* 2008) or confuciusornithids (Hou *et al.* 1995; Martin & Zhou 1997; Chiappe *et al.* 1999; Zhang *et al.* 2008) preserve a predentary bone or show evidence in the shape of the termination of the dentary that a predentary bone might have been present. Considering the great sampling size of specimens, we are confident the predentary bone did not exist in any of these birds.

Discussion

While the predentary bone was first described in hesperornithids and ichthyornithids, it was suggested that this feature might be primitive for the Class Aves, a derived feature for the Ornithurae that was lost in all modern birds, or a feature associating the Ichthyornithiformes with the Hesperornithiformes (Martin 1997). Because the predentary bone is now known in a number of Early Cretaceous basal ornithurine birds, including *Hongshanornis*,

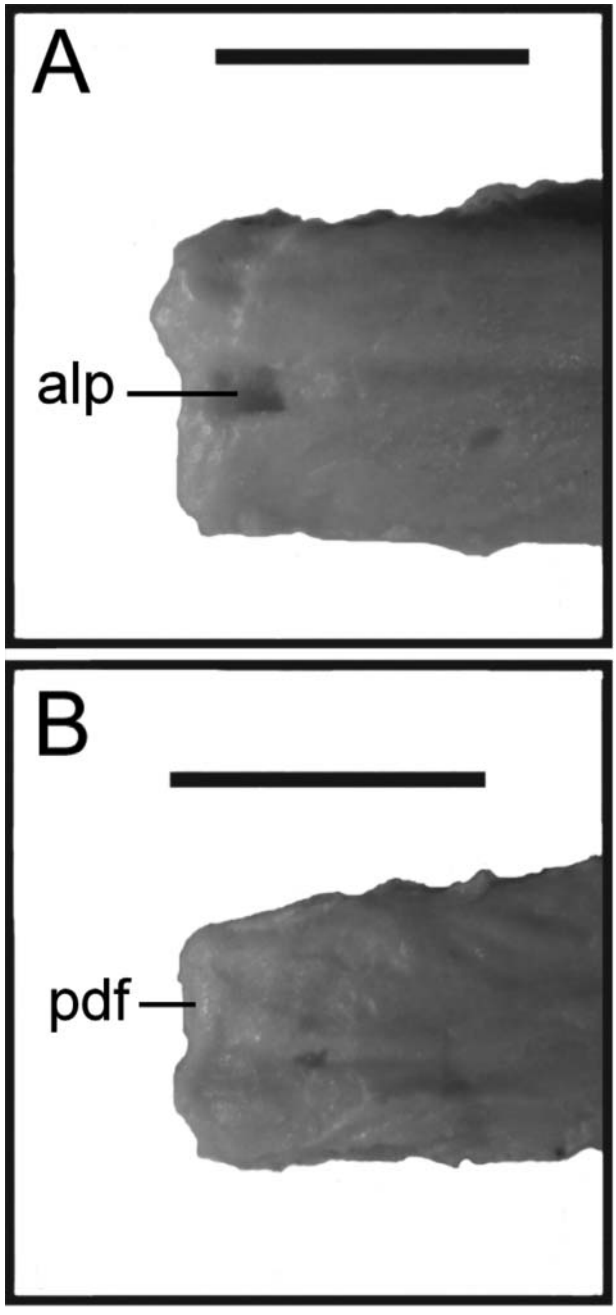

Figure 3. Photos of the cast of the tip of the left dentary of *Ichthyornis dispar* (YPM **1450**). **A,** lateral view; **B,** medial view. Scale bar = 1 cm. Abbreviations as in Fig. 1.

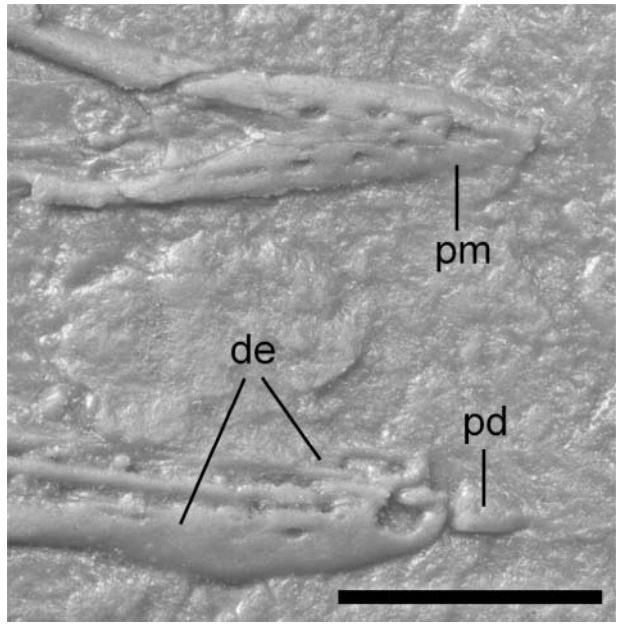

Figure 4. Photo of the cast of anterior jaws of the holotype of *Hongshanornis longicresta* (IVPP 14533) in right view, showing that the predentary bone lies anterior to the dentaries and corresponds to the anteromost portion of the premaxilla. Scale bar = 5 mm. Abbreviations: pm, premaxilla. See Fig. 1 for other abbreviations.

Yanornis, *Jianchangornis* and *Yixianornis*, but is obviously absent in enantiornithines or the basalmost birds of the Late Jurassic to Early Cretaceous, we conclude that it represents a common feature of early ornithurines and was subsequently lost in extant birds (Zhou & Zhang 2005). On the other hand, according to a current phylogeny (Zhou *et al.* 2009), one of the basalmost ornithurines *Archaeorhynchus* lacks a predentary bone, and it is unclear if the structure occurred only in more derived clades or was secondarily lost in this taxon.

The predentary bone in the herbivorous ornithischian dinosaurs forms part of a beak-like apparatus that provided an efficient mechanism for nipping and acquiring plant material (Horner & Goodwin 2008). What was the function of a predentary bone in Mesozoic ornithurines? Known ornithurines with a predentary bone are toothed with one exception, the edentulous *Hongshanornis*. The functional explanation for the independent development of a predentary bone in ornithurines is difficult to find. However, it might be related to a piscivorous dietary adaptation, as both *Yanornis* and *Jianchangornis* have preserved direct evidence of fish eating which is also confirmed by their dentitions (Zhou *et al.* 2004, 2009; Yuan 2007) despite the preservation of gizzard stones in one *Yanornis* specimen that possibly indicated seasonal diet change (Zhou *et al.* 2004). Furthermore, it is generally believed that both ichthyornithids and hesperornithids were piscivorous. However, there is as yet no evidence for the diet of either *Hongshanornis* or *Yixianornis*, although the toe proportions and pedal ungual morphology indicate that they are terrestrial birds like *Yanornis* and *Jianchangornis* (Zhou & Zhang 2001, 2006), suggesting at least the possibility of piscivorous diet. It is also interesting to note that *Archaeorhynchus*, which lacks a predentary bone, is believed to be herbivorous, based on the preservation of gizzard stones within the holotype (Zhou & Zhang 2006),

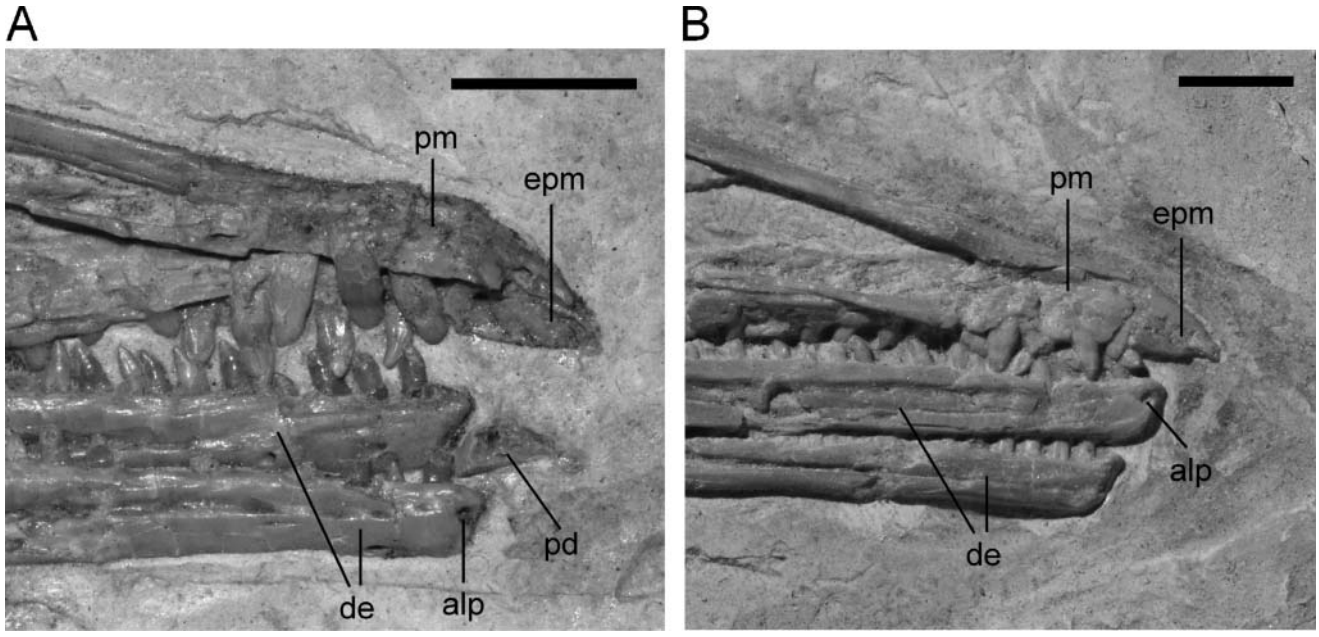

Figure 5. Photos of the anterior jaws of various specimens of *Yanornis*, showing the predentary and/or anterior dentaries. **A,** *Y. martini* (IVPP 13358) in right view; **B,** holotype of *Y. martini* (IVPP 12558) in right view. Scale bar = 5 mm. Abbreviations: epm, edentulous portion of the premaxilla. See Figs 1 and 4 for other abbreviations.

and two additional specimens also contain gizzard stones, further confirming this hypothesis.

Although we can argue that the presence of the predentary bone was an adaptation to piscivorous diet in some birds, such as *Ichthyornis*, *Yanornis* and *Jianchangornis*, there is inadequate evidence showing that this was true for all the basal ornithurines with a predentary bone. Furthermore, we propose that the predentary bone in basal ornithurines played a much different role in feeding from that of the herbivorous ornithischians.

In modern birds (Martin & Naples 2008) the symphysis between the dentaries 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 predentary 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

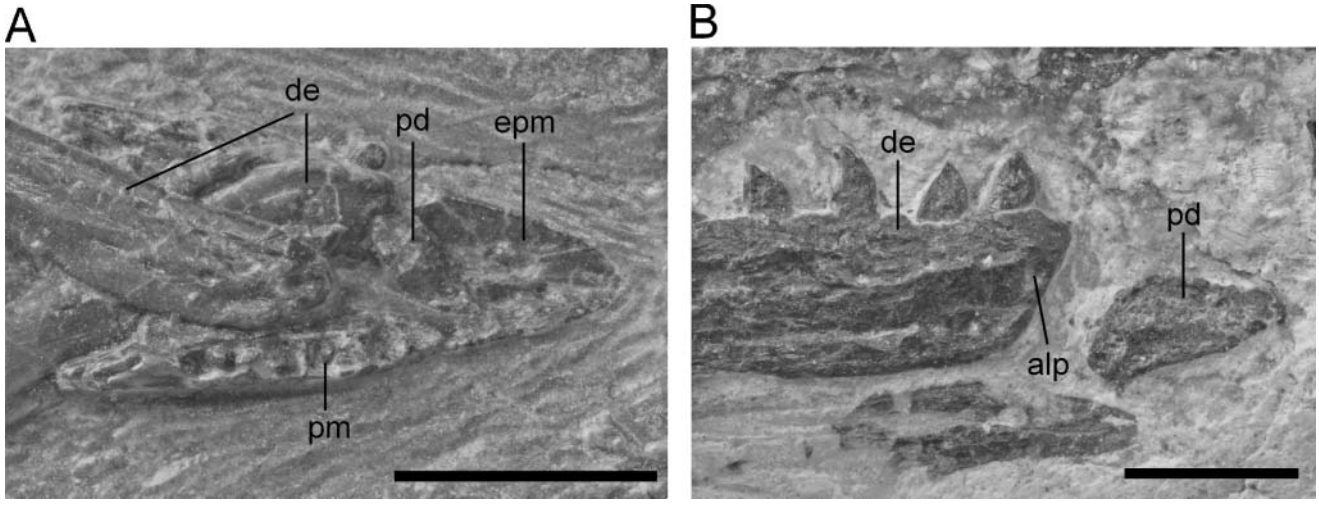

Figure 6. Photos of anterior portion of the skull of the holotypes of: **A,** *Yixianornis grabaui* (IVPP 12631) in ventral view; **B,** *Jianchangornis microdonta* (IVPP 15708) in right view, showing the predentary and anterior dentaries. Scale bar = 5 mm. Abbreviations as in Figs 1,5.

a bending zone across the posterior flange of the dentary and the surangular. In either the extinct toothed birds or in modern examples, intraramal bending facilitates gape and this is characteristic of forms that eat fish, such as gannets and the albatross. It is also characteristic of *Ichthyornis* and the extinct bony-toothed birds, Odontopterygia (Zusi & Warheit 1992). We suggest that the distribution of an intraramal joint in early birds should be investigated in terms of the distribution of the predentary.

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