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A revision of enantiornithine (Aves: Ornithothoraces) skull morphology

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Enantiornithines are the most speciose avian clade in the Mesozoic, with a fossil record that nearly spans the Cretaceous; however, with less than half of known taxa preserving skull material, our understanding of their cranial morphology remains incomplete. Here we present a comprehensive overview of the current knowledge of enantiornithine skull anatomy and discuss the range of morphologies known for each of the main cranial elements. The typical enantiornithine skull retains numerous ancestral features such as the absence of fusion among bones, the presence of a postorbital bone, a primitive quadrate with a single headed otic process, an unforked dentary, and teeth. The postorbital in at least one taxon is unreduced, suggesting the existence of a complete infratemporal fenestra and thus an unmodified diapsid skull as in confuciusornithids. The rostrum is well known and shows considerable variation, typical of theropods; however, in terms of rostral proportions, enantiornithines are extremely limited within the modern avian spectrum. Although Late Cretaceous skull material is extremely fragmentary, when compared to Early Cretaceous material it reveals a trend towards more specialized morphologies in younger taxa. The foramen magnum in all taxa points caudally, indicating that the 'flexed' type skull morphology may not have evolved in this group. Enantiornithine teeth show considerable diversity in numbers, size, morphology and placement, ranging from taxa with large teeth found throughout the jaws to taxa with small, rostrally restricted teeth, to the fully edentulous. Despite limited preservation of skull material, a number of trophic specializations can be deduced from the range of preserved morphologies, further hinting at the morphological and ecological diversity of the Cretaceous Enantiornithes.

Keywords: avian; skull; variation; Cretaceous

Introduction

Enantiornithes is a diverse group of Cretaceous birds known from deposits worldwide (Chiappe & Walker 2002). With over 50 species named in the past three decades, enantiornithines are the most speciose clade of Mesozoic birds. These small to medium sized birds are phylogenetically intermediate between basal pygostylians and modern birds, forming the sister group to Ornithuromorpha, which together make the clade Ornithothoraces (Chiappe 2002; Chiappe & Walker 2002). While their placement in the avian tree is well established, it is based primarily on postcranial synapomorphies rather than features of the skull (Chiappe 2002). A comparative study of the cranial morphology of enantiornithines has the potential to provide additional synapomorphies that can diagnose the entire group, as well as subclades, on the basis of skull morphologies, and therefore illuminate aspects of cranial evolution in basal birds. Furthermore, from the known morphology of basal bird crania, it can be inferred that the most recent ornithothoracine common ancestor retained a primitive toothed skull with an overall lack of bone fusion, and that the development of a toothless beak and an enlarged

premaxilla in several avian lineages including Enantiornithes is the result of convergent evolution (Chiappe *et al.* 1999; Zhou & Zhang 2006a). Thus studies of enantiornithine skull morphology can reveal significant information about the extent, the timing and the sequence of the evolution of modern morphologies (and their correlated ecologies) in a much older lineage, distantly related to modern birds.

For the first half of the clade's history, only very limited enantiornithine skull material had been uncovered (Elzanowski 1974, 1977; Walker 1981; Chiappe 1991) and very little information could be inferred for the clade. Subsequently, dozens of nearly complete skeletons from the Early Cretaceous Jehol Group of northern China were discovered; these have provided unprecedented information elucidating the anatomical and taxonomic diversity and the evolution of Enantiornithes (Fig. 1; Zhang & Zhou 2000; Zhang *et al.* 2000; Zhou & Zhang 2006a; Zhou *et al.* 2008). Even though almost all these largely complete specimens from the Jehol Group retain the skull, the cranial anatomy of the clade has remained largely unknown, due to the poor preservation typical of cranial bones, primarily preserved in 2D with the bones often torn between two slabs, crushed

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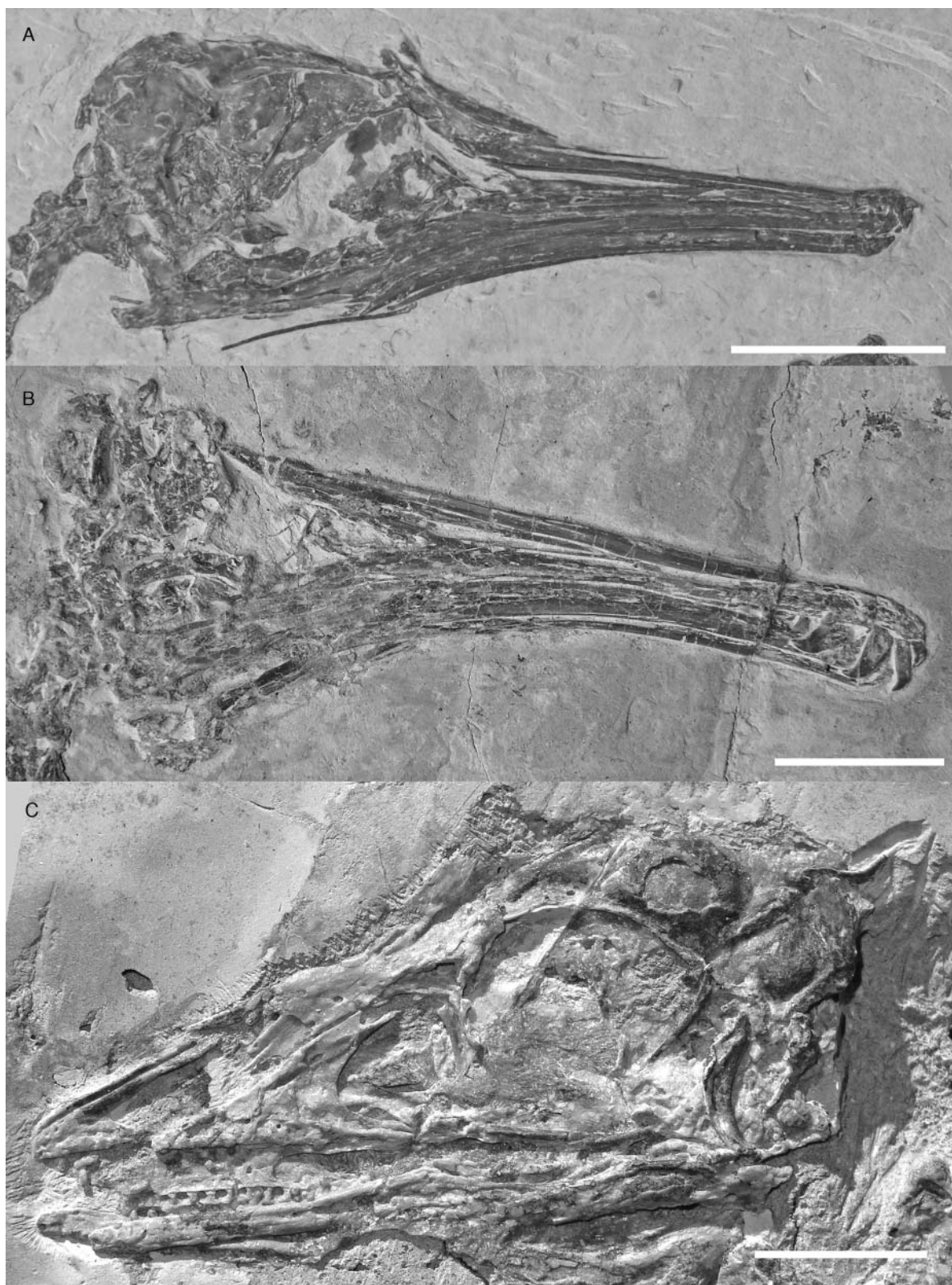


Figure 1. Photographs of well preserved enantiornithine skulls: **A**, *Rapaxavis pani*, DNHM D2522; **B**, *Longipteryx* sp., DNHM D2889; **C**, *Pengornis houi*, IVPP V15336; **D**, *Shenqiornis mengi*, DNHM D2950; **E**, *Longipteryx chaoyangensis*, IVPP V12552; **F**, *Cathayornis yandica*, IVPP V9769; **G**, juvenile *Euenantiornithes* indet, GMV 2158. All scale bars = 1 cm.

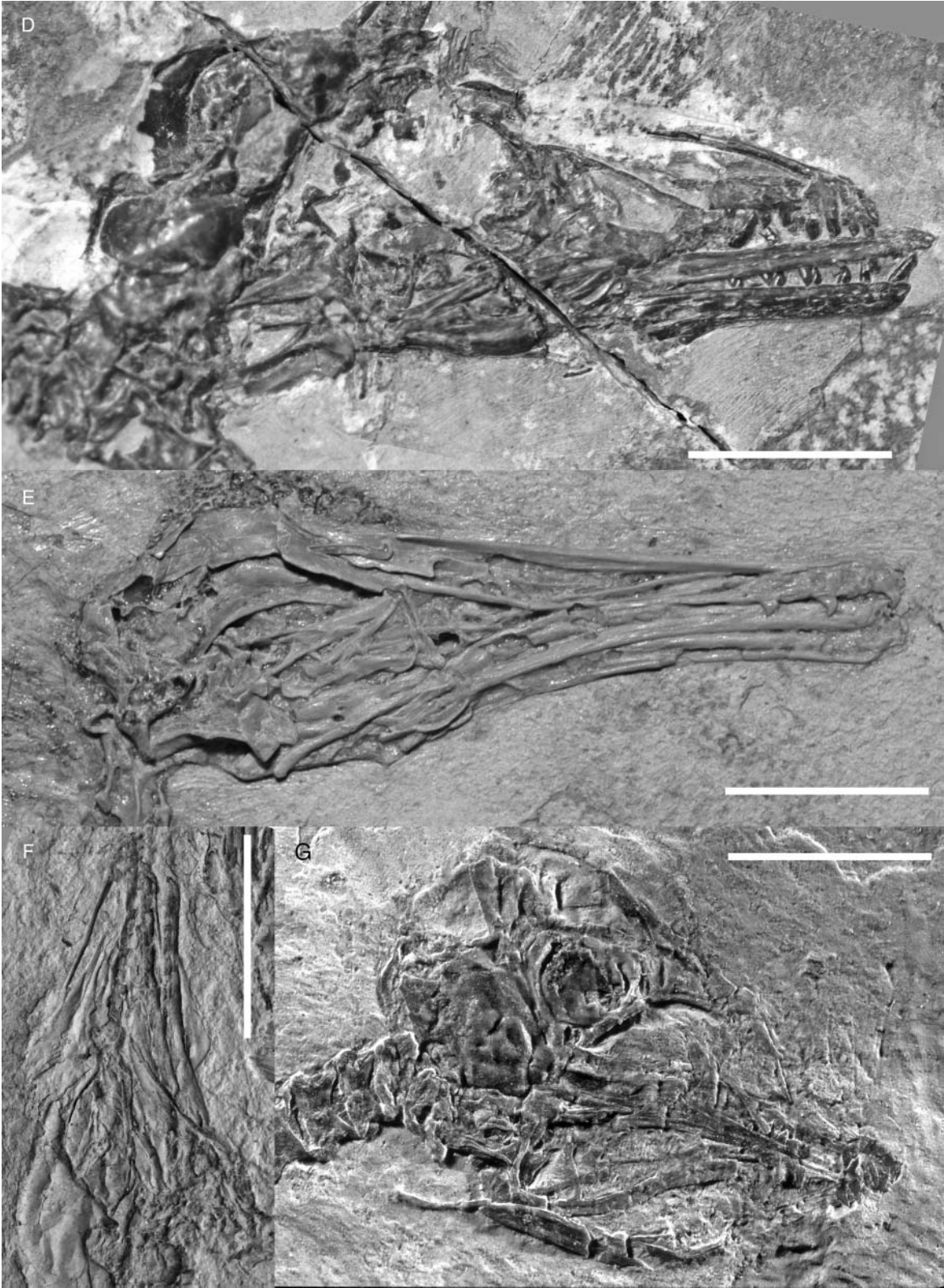


Figure 1. Continued.

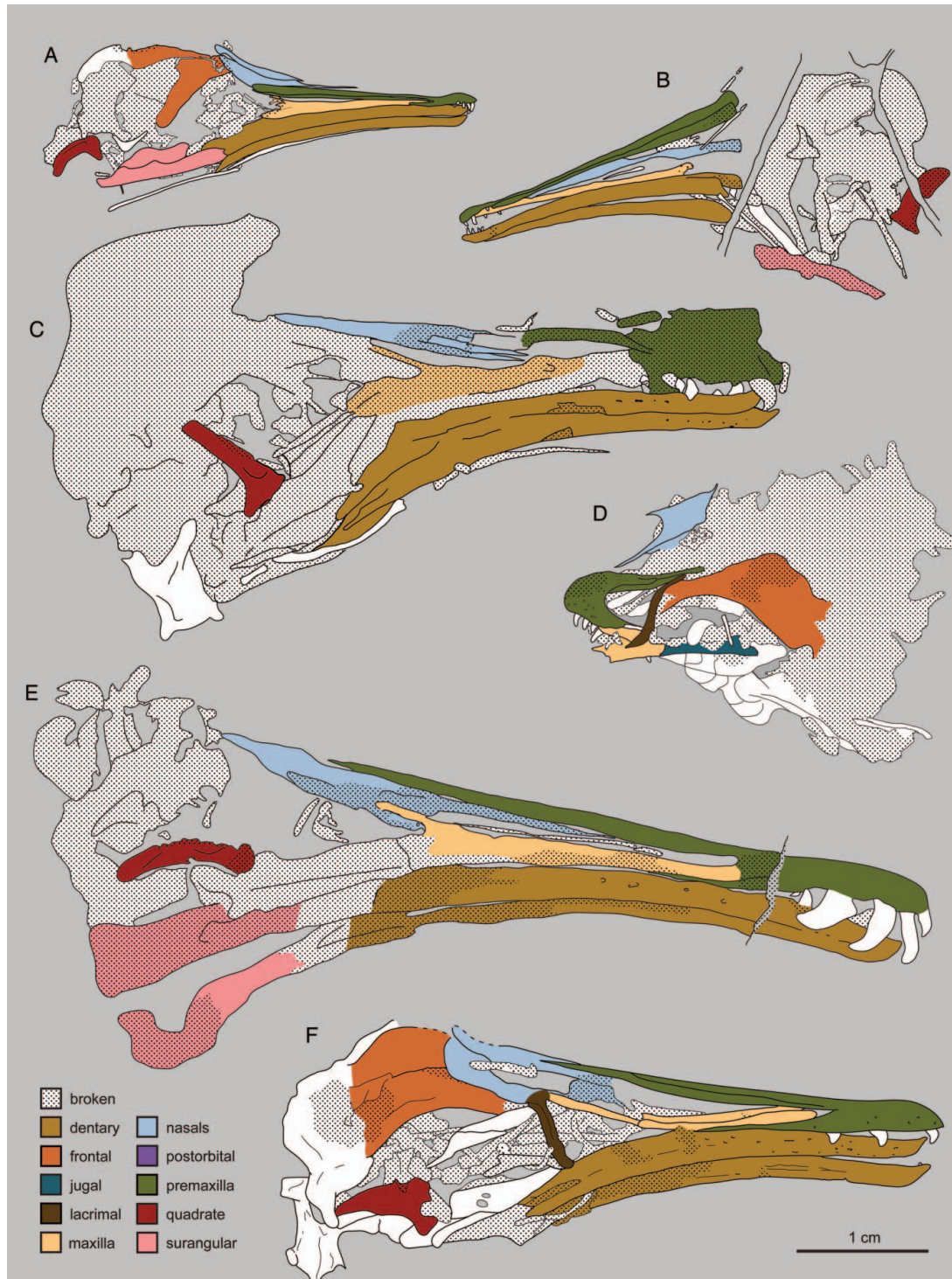


Figure 2. Camera lucida drawings of select enantiornithine skulls: **A**, *Rapaxavis pani*, DNHM D2522; **B**, *Longirostravis hani*, IVPP V11309; **C**, *Longipteryx chaoyangensis*, IVPP V12325; **D**, *Eoenantiornis buhleri*, IVPP 11537; **E**, *Longipteryx* sp., DNHM D2889; **F**, *Longipteryx chaoyangensis*, IVPP V12552; **G**, *Shenqiornis mengi*, DNHM D2951; **H**, *Pengornis houi*, IVPP 15336; **I**, *Alethoalaornis agitornis*, LPM 00009; **J**, *Cathayornis yandica*, IVPP V9769; **K**, *Dapingfangornis sentisorhinus*, LPM 00039; **L**, **M**, *Gobipteryx minuta*, IGM-100/1011, right and left lateral views.



Figure 2. Continued.

and/or disarticulated (Sereno & Rao 1992; Zhou *et al.* 1992; Hou 1997).

Reconstructions of the enantiornithine skull are few, which can be attributed to preservational limitations. The

only major attempts to construct the enantiornithine skull are those of Martin & Zhou (1997) and Sanz *et al.* (1997). The reconstruction of Martin & Zhou (1997) based on *Cathayornis yandica* (IVPP V9769, IVPP V10896 and

IVPP V10916—the latter now the holotype of *Eocathayornis walkeri* Zhou, 2002) lacks a postorbital and possesses unsubstantiated lacrimal and premaxilla morphology. The second reconstruction, that of the Montsec hatchling (LP 4450), is more accurate. However, both reconstructions are based on single taxa, and little has been done to find common morphological ground between all members of the clade.

The recent discovery of exceptionally preserved specimens, such as *Eoenantiornis buhleri*, *Longipteryx chaoyangensis*, *Pengornis houi* and new specimens of *Gobipteryx minuta*, provides new insights into how the enantiornithine skull was constructed and the degree of variation among taxa (Hou *et al.* 1999; Zhang *et al.* 2000; Zhou *et al.* 2008; Chiappe *et al.* 2001). Together with data extracted from the nearly 30 skulls used in this study, including every published taxon that preserves cranial material, we can begin to reveal the anatomy of the enantiornithine skull. Common morphologies emerge and a better understanding of enantiornithine skull morphology offers an interesting case study in diversity and evolution. By focusing on an aspect of the skeleton other than morphologies directly related to flight, we may be able to understand evolutionary pressures acting on early avifaunas that are less influenced by aerodynamic constraints.

Material

Approximately 60 species of enantiornithines have been named (including several potential synonyms); of these, 25 preserve skull material (Table 1). An additional four unnamed juveniles (Sanz *et al.* 1997; Chiappe *et al.* 2007) preserve crania and will be discussed in this review. This study relies almost entirely on Asian material and this should be recognized as a major bias of any enantiornithine study; more than 90% of the specimens come from the Jehol Group, which records a time interval spanning approximately 11 Ma (c. 131–120 Ma) and representing a single geographical area (He *et al.* 2006; Zhou 2006; Yang *et al.* 2007).

The best skull material belongs to *Gobipteryx*, specimen IGM-100/1011 from the Campanian Barun Goyot and Djadokhta formations (Fig. 2L, M; Chiappe *et al.* 2001). Though only preserving the rostral half of the skull, IGM-100/1011 boasts three-dimensional preservation and provides the most reliable information on the enantiornithine palate. Additional *Gobipteryx* skulls (ZPAL-MgR-I/12, ZPAL-MgR-I/32, PIN 4492; Elzanowski 1976, 1977; Kurochkin 1996) are known but the material is either compromised (diagenetically recrystallized), crushed, or largely incomplete. The Jehol Group has produced six specimens with well-preserved skulls: IVPP V11537—the holotype of *Pengornis houi* (Figs 1C, 2H; Zhou *et al.* 2008),

IVPP V15336—the holotype of *Eoenantiornis buhleri* (Fig. 2D; Hou *et al.* 1999; Zhou *et al.* 2005), DNHM D2522—the holotype of *Rapaxavis pani* (Figs 1A, 2A; Morschhauser *et al.* 2009), DNHM D2950/1—the holotype of *Shenqiornis mengi* (Figs 1D, 2G; Wang *et al.* 2010), LPM 00039—the holotype of *Dapingfangornis sentisorhinus* (Fig. 2K; Li *et al.* 2006—unfortunately, this specimen is poorly prepared and glue obscures most features), and two referred specimens of *Longipteryx chaoyangensis*, IVPP V12552 (Figs 1E, 2F; Zhang *et al.* 2000; Chiappe *et al.* 2007) and DNHM D2889 (Figs 1B, 2E). Other largely complete though poorly preserved skulls include: IVPP V12325—the holotype of *L. chaoyangensis* (Fig. 2C; Zhang *et al.* 2000), IVPP V11309—the holotype of *Longirostravis hani* (Fig. 2B; Hou *et al.* 2004), NIGP-CAS 130722—the holotype of *Hebeiornis fengningensis* (Xu *et al.* 1999; Zhang *et al.* 2004), IVPP V11665—the holotype of *Protopteryx fengningensis* (Zhang & Zhou 2000), IVPP V9769—the holotype of *Cathayornis yandica* (Figs 1F, 2J; Zhou *et al.* 1992), DNHM D1878—the holotype of *Shanweiniao cooperorum* (O'Connor *et al.* 2009), and LPM 00009, LPM 00038 and LPM B00017 (Fig. 2I; published as LPM 00040)—three specimens of *Alethoalaornis agitor-nis* (Li *et al.* 2007). Juvenile *Euenantiornithes* indet. (GMV 2158, GMV 2159—Fig. 3A, and NIGPAS 130723/GMV 2156) were also included in this study (Chiappe *et al.* 2007). This study relies primarily on the morphology from these specimens but includes details discerned from two-dozen other enantiornithine fossils (Table 1), including several that are undescribed (DNHM D2836, DNHM D2510/1, DNHM D2567/8, DNHM D2952/3, DNHM D2884–1/2, DNHM D2130, DNHM D2566). The holotype of *Dalingheornis liwei* (CNU VB2005001; Zhang *et al.* 2006) is in a private collection (Z.-H. Zhang pers. comm.) and the skull of the holotype of *Paraptopteryx gracilis* (STM V001) does not belong to the main slab (Zheng *et al.* 2007; Z.-H. Zhang pers. comm.). Thus these taxa are listed in Table 1 as published with skull material but not included in this morphological review. Most birds from the Jehol Group (with the exception of *Cathayornis*, *Longipteryx*, *Yanornis*, and *Alethoalaornis*) are known from a single specimen; unless specified, if the generic name is used, it refers to the holotype specimen.

Outside Asia, the published record of enantiornithine skull material is limited to a nearly complete juvenile specimen from the Lower Cretaceous La Pedrera de Rubies Lithographic Limestones Formation, Lleida, Spain (Fig. 3B, C; LP 4450—Sanz *et al.* 1997), and a partial braincase belonging to the holotype of *Neuquenornis volans* from the Upper Cretaceous (Campanian) Río Colorado Formation of Neuquén, Argentina (Fig. 5B; MUCPv-142—Chiappe & Calvo 1994). A partial mandible from the Upper Cretaceous (Maastrichtian) Lecho Formation, El Brete, Argentina (PVL 4698) has been suggested to be enantiornithine based on the absence of any other

Table 1. A list of known enantiornithine specimens that preserve skull material; grey indicates unpublished material.

Taxon	Collection #		Skull material	Preservation
Early Cretaceous				
<i>Alethoalaornis agitornis</i>	LPM 00009	N China	partial skull, ventrolateral view	poor; disarticulated & crushed
<i>Alethoalaornis agitornis</i>	LPM 00038	N China	nearly complete, lateral view	good; crushed
<i>Alethoalaornis agitornis</i>	LPM 00040	N China	partial skull, dorsal view	poor; disarticulated & crushed
<i>Boluochia zhengi</i>	IVPP V9770	N China	premaxilla, maxilla, nasal, dentary	poor; voids
<i>Cathayornis aberransis</i>	IVPP V12352	N China	nearly complete; dorsal view	poor; crushed
<i>Cathayornis caudatus</i>	IVPP V10917	N China	nearly complete; dorsolateral view	poor; crushed
<i>Cathayornis indet.</i>	IVPP V10896	N China	dentary and premaxilla	poor; disarticulated
<i>Cathayornis yandica</i>	IVPP V9769	N China	nearly complete; lateral view	good; disarticulated
<i>Cuspirostrisornis houi</i>	IVPP V10897	N China	premaxilla, nasal, maxilla, dentary	poor; disarticulated
<i>Dalingheornis liwei (private)</i>	CNU VB2005001	N China	nearly complete; lateral view	poor; crushed
<i>Dapingfangornis sentisorhinus</i>	LPM 00039	N China	nearly complete; ventrolateral view	good; poorly prepared
<i>Eocathayornis walkeri</i>	IVPP V10916	N China	partial skull; premaxilla, maxilla,	poor; disarticulated voids
<i>Eoenantiornis buhlerei</i>	IVPP V11537	N China	nearly complete; dorsal view	excellent; disarticulated
<i>Liaoxiornis deicatus</i>	NIGPAS 130723	N China	nearly complete; dorsal view	poor; crushed
<i>Euenantiornithes indet.</i>	LP 4450	Spain	nearly complete; lateral view	good; crushed
<i>Euenantiornithes indet.</i>	GMV 2158	N China	nearly complete; lateral view	good; crushed
<i>Euenantiornithes indet.</i>	GMV 2159	N China	nearly complete; lateral view	poor; crushed
<i>Euenantiornithes indet.</i>	DNHM D2510/1	N China	nearly complete, ventrolateral view	poor; crushed
<i>Euenantiornithes indet.</i>	DNHM D2836	N China	nearly complete; dorsolateral view	poor; crushed
<i>Euenantiornithes indet.</i>	DNHM D2567/8	N China	nearly complete; lateral view	poor; crushed
<i>Euenantiornithes indet.</i>	DNHM D2884	N China	nearly complete; lateral view	poor; crushed
<i>Euenantiornithes indet.</i>	DNHM D2130	N China	nearly complete; lateral view	poor; crushed
<i>Euenantiornithes indet.</i>	DNHM D2952/3	N China	nearly complete; lateral view	poor; crushed
<i>Hebeiornis fengningensis</i>	NIGPAS 130722	N China	nearly complete; ventral view	good; voids
<i>Largirostrornis sexdentornis</i>	IVPP V10531	N China	partial skull; premaxilla, dentary	poor; disarticulated & crushed
<i>Longchengornis sanyanensis</i>	IVPP V10530	N China	dentary	poor; disarticulated voids
<i>Longipteryx chaoyangensis</i>	IVPP V12325	N China	nearly complete; lateral view	good, crushed
<i>Longipteryx chaoyangensis</i>	IVPP V12552	N China	nearly complete; lateral view	good, crushed; juvenile
<i>Longipteryx sp.</i>	DNHM D2889	N China	nearly complete; lateral view	good; crushed
<i>Longipteryx sp.</i>	DNHM D2566	N China	nearly complete; lateral view	good; crushed
<i>Longirostravis hani</i>	IVPP V11309	N China	nearly complete, lateral view	poor; crushed and broken
<i>Paraprotapteryx gracilis</i>	STM V001	N China	nearly complete; lateral view	poor; crushed -chimera?
<i>Pengornis houi</i>	IVPP V15336	N China	complete; lateral view	excellent; flattened
<i>Protopteryx fengningensis</i>	IVPP V11665	N China	nearly complete; lateral view	poor; crushed
<i>Rapaxavis pani</i>	DNHM D2522	N China	nearly complete; lateral view	good; crushed
<i>Shanweiniao cooperorum</i>	DNHM D1878	N China	nearly complete; lateral view	poor; crushed
<i>Shenqiornis mengi</i>	DNHM D2950/1	N China	nearly complete, lateral view	good; crushed
<i>Sinornis santensis</i>	BNHM BPV538a	N China	partial skull; dentary	poor; disarticulated
Late Cretaceous				
<i>Incertae sedis</i>	PVL 4698	Argentina	partial mandible	excellent; 3D
<i>Gobipteryx minuta</i>	ZPAL-MgR-I/12	Mongolia	partial skull (holotype)	poor; 3D
<i>Gobipteryx minuta</i>	ZPAL-MgR-I/32	Mongolia	partial skull	poor; 3D
<i>Gobipteryx minuta</i>	ZPAL-MgR-I/88	Mongolia	partial skull	good; 3D
<i>Gobipteryx minuta</i>	ZPAL-MgR-I/33	Mongolia	partial skull	poor, recrystallized; 3D
<i>Gobipteryx minuta</i>	ZPAL-MgR-I/34	Mongolia	partial skull	poor; crushed
<i>Gobipteryx minuta</i>	IGM-100/1011	Mongolia	partial skull; rostral half	excellent; 3D
<i>Gobipteryx minuta</i>	PIN 4492	Mongolia	partial skull; rostrum, pterygoids, mandible	excellent; 3D
<i>Neuquenornis volans</i>	MUCPv 142	Argentina	braincase	good; incomplete

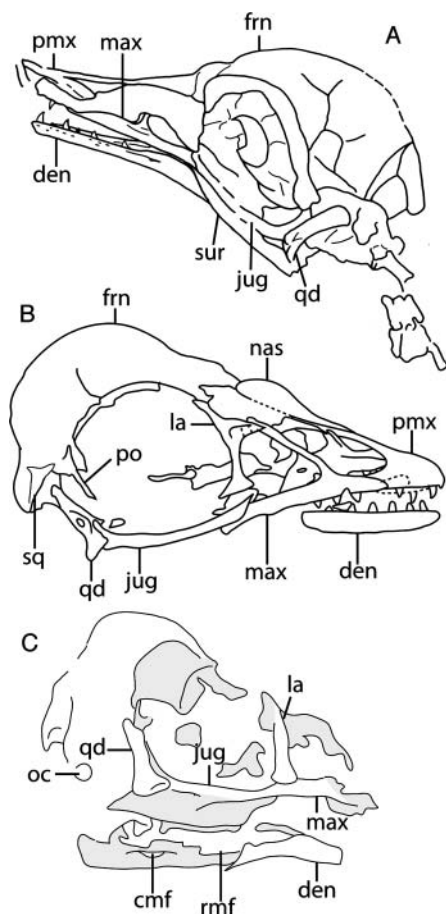


Figure 3. Interpretive drawings of select juvenile enantiornithine skulls: **A**, GMV 2159; **B**, **C**, LP 4450 slab and counterslab. Anatomical abbreviations: cmf, caudal mandibular fenestra; den, dentary; frn, frontal; jug, jugal; la, lacrimal; max, maxilla; nas, nasal; oc, occipital condyle; pmx, premaxilla; po, postorbital; qd, quadrate; rmf, rostral mandibular fenestra; sq, squamosal; sur, surangular.

avian material from the locality (Chiappe & Walker 2002). Currently there are no synapomorphies that support the placement of this specimen within the group, thus it will not be included in this review. The entire Late Cretaceous record of enantiornithine skull material is limited to the *Neuquenornis* and *Gobipteryx* material.

Despite the serious limitations of material in terms of temporal and geographical distribution, even the few known specimens record a large range of morphologies and specializations, and some major evolutionary patterns can be discerned.

Institutional abbreviations

CNU: Capital Normal University, Beijing, China; **DNHM**: Dalian Natural History Museum, Dalian, Liaoning China; **GMV**: Geological Museum of China, Beijing, China; **IGM**: Geological Institute, Mongolian Academy of Sciences,

Ulaan Bataar, Mongolia; **IVPP**: Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **LP**: Institut d'Estudis Ilerdencs, Lleida, Spain; **LPM**: Liaoning Paleontological Museum, Shenyang, Liaoning, China; **MUCPv**: Museo de Ciencias Naturales, Universidad Nacional del Comahue, Neuquén, Argentina; **NIGP-CAS**: Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences, Nanjing, Jiangsu, China; **PIN**: Paleontological Institute, Moscow, Russia; **PVL**: Paleontología de Vertebrados, Fundación-Instituto Miguel Lillo, Universidad Nacional de Tucumán, Tucumán, Argentina; **STM**: Shandong Tianyu Museum, Tianyu, Shandong, China; **ZPAL-MgR**: Zoological Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Morphology

Anatomical nomenclature mainly follows Baumel & Witmer (1993); certain structures not cited therein follow Howard (1929). While the Latin terminology used by Baumel & Witmer (1993) is retained for muscles and ligaments, osteological structures are described using English equivalents of the Latin terms.

Cranium

The rostrum, orbit and braincase in all enantiornithine taxa appear aligned in the same plane in lateral view (Figs 1, 2). All known foramina magna are directed caudally, indicating that these birds had 'extended' type skull morphology (Fig. 5; Marinelli 1928; Van der Klaauw 1948). Well-preserved skulls indicate enantiornithines were typically mesorostrine (*sensu* Busbey 1995) with the rostrum contributing to around 50% of the total skull length. Longipterygid enantiornithines (e.g. *Longirostravis*, *Longipteryx* and others), though not truly longirostrine (*sensu* Busbey 1995), represent a significant departure from other enantiornithines and an excursion into new morphospace, with the average rostrum being 65% of the skull length (Fig. 6).

Premaxilla. This element varies considerably throughout the clade in degree of fusion, relative lengths of the nasal and maxillary processes, degree of facial contribution, morphology of the articulations with the nasal and maxilla, and dentition. The premaxillae range from completely free from one another (unfused) (e.g. *Pengornis*; Figs 1C, 2H) to rostrally fused (nasal processes remain unfused) (e.g. *Eoenantiornis*, *Longipteryx*, *Gobipteryx*), and in some cases (e.g. IVPP V10897—the holotype of *Cuspirostrisornis*) these bones even appear fused along their entire length.

The prenasal portion of the premaxilla ranges from low, with the dorsal and ventral margins nearly parallel (e.g. *Boluochia*, *Longipteryx*), to high, with the dorsal margin strongly angled caudodorsally forming a skull with a more

robust rostrum (e.g. *Shenqiornis*). The prenasal region is usually short and thus small (e.g. *Longirostravis*, *Eoenantiornis*), but in some taxa it is long (e.g. *Longipteryx*) and massive (e.g. *Gobipteryx*). The premaxilla typically bears four teeth, as in most non-avian theropods and other basal birds (e.g. *Archaeopteryx*, *Sapeornis*). Teeth are absent in *Gobipteryx*, thus far the only known edentulous enantiornithine (Elzanowski 1976, 1977). The nasal (frontal) processes of the premaxilla are shorter than those of modern birds, typically extending only to the level of the caudal margin of the nares (e.g. *Shenqiornis*) and not reaching the frontals. Although the morphology is not limited to this group (present also in *Gobipteryx*), the longipterygids all possess elongate nasal processes that extend nearly to the level of the caudal margin of the antorbital fenestra (e.g. *Rapaxavis*, *Longirostravis*, *Shanweiniao*).

The articulation of the premaxillae with the nasals is typically wedge-like, extending for approximately 50% of the length of the nasal (e.g. *Shenqiornis*, *C. yandica*, *Rapaxavis*).

The premaxilla is often perforated with small nutrient foramina along the facial margin (e.g. *Longirostravis*, *Pengornis*, *Eoenantiornis*, *Longipteryx*). In the presumably beaked *Gobipteryx*, the premaxilla bears a pair of dorsal grooves in which the nutrient foramina are located (Elzanowski 1977; Chiappe *et al.* 2001). This distribution differs from foramina associated with sensory organs in modern birds, which have been suggested for the beaked bird *Confuciusornis* (Zinoviev 2009), in which the foramina have a greater distribution and are more densely packed (Piersma *et al.* 1998). The maxillary process of the premaxilla is typically short so that the facial contribution of this bone is restricted rostrally in most taxa (e.g. *Pengornis*, *Eoenantiornis*, *Gobipteryx*). However, the three-dimensionally preserved skulls of *Gobipteryx* (Chiappe *et al.* 2001) show that the maxillary process of this taxon extends for approximately half the length of the rostrum, but a portion of this is laterally obscured by the overlapping premaxillary process of the maxilla. While the condition in *Gobipteryx* suggests that the visible portion of the maxillary process of taxa preserved in two dimensions such as *Eoenantiornis* may extend farther caudally, the disarticulated premaxilla of IVPP V10897 (i.e. *Cuspirostrisornis*) indicates that, in at least some taxa, the maxillary process of this bone was short. In *Longipteryx*, a long and tapering maxillary process fully exposed laterally shows that the premaxilla of this taxon also contributed to nearly half the facial margin (IVPP V12552). Unsurprisingly, the taxa with a more extensive contribution of the premaxilla to the facial margin (e.g. *Longipteryx* and *Gobipteryx*) also possess a larger prenasal region. Very little is known about the details of the premaxilla–maxilla contact. In *Gobipteryx* it is complex; the maxillary process of the premaxilla tightly fits into a dorsal groove defined by the premaxillary process of the maxilla (Chiappe *et al.* 2001).

Nasal. The nasal varies in relative length, width, and morphology of the maxillary process. The nasals are typically elongate bones that contact each other; however, the long nasal processes of the premaxilla of *Longipteryx* may have separated both nasals for most of their length (Fig. 2C, E, F). The premaxillary (internarial) process of the nasal is sharply tapered. The maxillary process of the nasal is not present in all taxa. The maxillary process, when present, is typically short—shorter than the premaxillary process—and also sharply tapered (e.g. *Eoenantiornis*, *C. yandica*). The maxillary process is longer than the premaxillary process in at least *Gobipteryx* (Fig. 2L, M). In *Longipteryx*, the maxillary process is reduced so that it does not extend ventrally beyond the caudodorsal margin of the nares, while in other taxa (e.g. *Shenqiornis*, *Rapaxavis*, *Shanweiniao*), the process is completely absent (Fig. 2).

The mediolateral width of the nasal corpus varies from very narrow (e.g. *Shenqiornis*, *Longipteryx*, *Rapaxavis*) to broad (e.g. *Eoenantiornis*, *C. yandica*). Taphonomic biases notwithstanding, estimated nasal width-to-length ratios vary from 0.04 in taxa such as *Rapaxavis* (Fig. 2A), to 0.22 in *C. yandica* (IVPP V9769; Fig. 2J). Caudally, the nasal articulates with the lacrimal and the frontal. In *Pengornis* and LP 4450, the articulation with the lacrimal extends over the caudal half of the lateral margin of the nasal. While the shape of the articulation with the frontal remains unclear, the caudal margin of the nasal is typically rounded (e.g. *Longipteryx*, *C. yandica*, *Shenqiornis*).

Maxilla. The maxilla is not as well known as the premaxilla. It varies mainly in dentition, relative lengths of the premaxillary, jugal, and nasal processes, and fenestration. The typical maxilla contributes to a majority of the facial margin, has premaxillary and jugal processes (the jugal process here refers to the ramus of the maxilla that extends from the rostral margin of the antorbital fossa to the articulation with the jugal) of subequal length, and bears teeth (e.g. *Shenqiornis*, *Gobipteryx*, *Hebeiornis*, *Pengornis*). *Gobipteryx* and the longipterygids represent the only known examples in which the maxilla lacks teeth. When present, the number of teeth varies from 5–6 to 11. The longipterygid *Rapaxavis* further departs from the typical morphology, possessing a premaxillary process three times longer than the jugal process (Fig. 2A). Conversely, in some taxa (e.g. LP 4450) the premaxillary process is shorter than the jugal process (Fig. 3B), although there are no known taxa in which the latter is considerably longer than the former.

The nasal process (ramus) is typically thin and caudally directed, separating the nares from the antorbital fenestra. The rostral portion of the nasal process of *Pengornis* forms a fenestrated recessed bony wall that medially lines the rostral third of the antorbital fossa (Figs 1C, 2H).

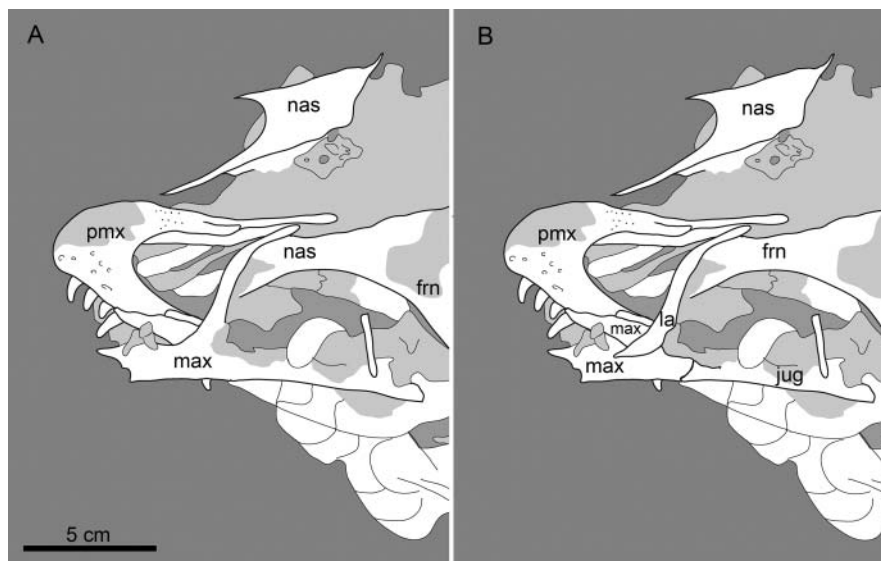


Figure 4. Close-up of the skull of *Eoenantiornis buhleri* IVPP showing the two alternate interpretations of the specimen: **A**, the S-shaped bone fragment is inferred to be part of the maxilla as in Zhou *et al.* (2005); **B**, the S-shaped bone as the lacrimal. See Fig. 3 for anatomical abbreviations.

The recessed nasal process and accessory antorbital fenestra, less clearly preserved in DNHM D2889 (Figs 1B, 2E) and suggested to be present in *C. yandica* (Martin & Zhou 1997), may have a broader distribution but preservational biases in two-dimensional specimens make this difficult to determine (including the presence of this condition in *C. yandica*). The nasal process of the maxilla is reduced in *Gobipteryx*, only contributing to the caudoventral margin of the nares, and thus clearly lacked the above-mentioned recessed bony wall (Fig. 2L, M). In *Pengornis*, the caudodorsal end of its well developed nasal process forms a fork (unforked in LP 4450), presumably for the articulation with the lacrimal, in which the ventral ramus projects considerably beyond the dorsal ramus (Fig. 2H). Whether the nasal process of the maxilla articulated with the lacrimal in other taxa is not clear due to the poor preservation of the latter bone in most specimens, yet the elongate nasal process of some taxa (e.g. *Shenqiornis*, LP 4450, *Longipteryx*) suggests that this condition may have had a wider distribution.

Lacrimal. The morphology of this bone is definitively clear in only two specimens: *Pengornis* (IVPP V15336) and LP 4450 (Fig. 3B). In these specimens, the lacrimal is T-shaped as in most non-avian maniraptorans (e.g. *Velociraptor*, *Jinfengopteryx*, *Tsaagan*). The dorsal rami are tapered and angled so that the rostral ramus is rostroventrally directed and the caudal ramus is oriented caudodorsally. In *Pengornis*, the dorsal margin is strongly concave between the two rami defining a small foramen between the lacrimal and the nasal (Fig. 2H). The dorsal margin of the nasal also

appears slightly concave in LP 4450; however, the nasal is broken along the lacrimal contact, making it impossible to determine if a foramen was present. In LP 4450, the descending (ventral) ramus of the lacrimal appears to form a mediolaterally broad sheet descending perpendicularly to the long axis of the skull; the distal end, not preserved in *Pengornis*, expands into a broad articulation with the jugal. *Eoenantiornis* may exhibit a unique lacrimal morphology, depending on the reinterpretation of the structure identified as the nasal process of the maxilla by Zhou *et al.* (2005; Fig. 4A). In this alternative view, the caudal half of the skull is interpreted as pushed forward, covering most of the left maxilla so that only the caudal end of this bone is visible in lateral view (Fig. 4B). The nasal process of the maxilla of Zhou *et al.* (2005) is thus regarded as the lacrimal (Fig. 4). If this is the case, the lacrimal of *Eoenantiornis* is a thin, rostroventrally angled S-shaped bone with an expanded ventral ramus and a caudally tapering dorsal ramus, a design significantly different from the T-shaped bone described above.

Jugal. In most taxa the jugal appears to be a simple rod-like element lacking a postorbital process (e.g. *C. yandica*, *Pengornis*, *Rapaxavis*). This bone is best preserved in LP 4450 (Fig. 3B). In this specimen, the rostral end articulates with both the maxilla and lacrimal, contributing to the caudoventral corner of the antorbital fenestra. The caudal end is forked, with the dorsal ramus longer and more robust than the ventral ramus, a condition similar to that in *Archaeopteryx*. This morphology also appears to be present in *Shenqiornis* (Wang *et al.* 2010).

Postorbital. This element—absent among modern birds—is retained within Enantiornithes but is only definitively preserved in three specimens: LP 4450, *Pengornis* and *Shenqiornis*. In LP 4450 and *Shenqiornis* it exhibits a typical T-shaped design but in *Pengornis* the caudodorsal (squamosal) ramus is either absent or broken. The postorbital of these specimens shows considerable variation in size and morphology. In *Shenqiornis* it is large and broad, with a straight and tapered jugal process that possibly enclosed a complete infratemporal fenestra (Figs 1D, 2G). In contrast, in *Pengornis* and LP 4450 the bone is much smaller, with a rostrally deflected, splint-like jugal process that fails to reach the jugal (Figs 2H, 3B). In LP 4450 and *Shenqiornis* the dorsal margin of the postorbital is concave, suggesting it contributed to the margin of a supratemporal fenestra. The rostradorsal (frontal) ramus is larger than the caudodorsal ramus in LP 4450; in *Shenqiornis* the disarticulated postorbital cannot be oriented unequivocally, however one ramus is much more robust than the other, and has a more dorsal position.

Squamosal. The only known squamosal is preserved in LP 4450 (Fig. 3B). It is a small triradiate bone that, unlike modern birds, is unincorporated into the braincase. In lateral view it has a broad descending process and a small caudally directed process. The third process articulated with the dorsocaudal ramus of the postorbital and contributed to the caudal margin of the supratemporal fenestra.

Quadrate. The quadrate is preserved in several taxa (e.g. *Rapaxavis*, *Pengornis*, LP 4450, *Shenqiornis*, *Eocathayornis*, *Protopteryx*, *Gobipteryx*), but unfortunately few morphological details are known (Figs 2, 3B). The mandibular process appears bicondylar in all specimens, with the medial condyle larger than the lateral condyle. As in other basal birds and non-avian theropods, the orbital ramus is broad (e.g. *Gobipteryx*), lacking the narrow and tapered morphology of ornithurines. The caudal surface is excavated. Some quadrates are pierced by a foramen, which may be an indication that the bone was pneumatic; the ‘pneumatopore’ is interpreted as piercing the bone caudally in *Shenqiornis* and *Pengornis*.

Frontal. Completely unfused in most taxa, the frontals are rostrocaudally elongate, narrow rostrally and largely expanded caudally (e.g. *C. yandica*, *Shenqiornis*, *Pengornis*, DNHM D2511; Fig. 2). They form a majority of the dorsal margin of the orbit; in *Pengornis*, this portion of the lateral margin of the frontal forms a slight laterally projecting surface. Best evidenced in *Neuquenornis*, the frontals contact on the midline forming a longitudinal suture; the caudal margin of each frontal is rounded, forming a caudally convex suture with the parietals.

Parietal. These bones are unfused to each other and the rest of the braincase (e.g. *Dapingfangornis*, *Pengornis*, *Eocathayornis*; Fig. 2). They are vaulted and oval in shape. The parietals are smaller and rostrocaudally shorter than the frontals. In *Neuquenornis*, the medial portion of both parietals contributes to a dome-like structure located between the interfrontal suture and the central occiput. The parietals of *Neuquenornis* also form a gentle nuchal crest along their margin with the occiput.

Supraoccipital. This bone is completely fused to the exoccipital bones in all known specimens (e.g. *Neuquenornis*, *Hebeiornis* and *Shenqiornis*), thus the precise lateral margin of this bone is unclear. The midline is vaulted, forming a cerebral eminence that is most prominent in *Shenqiornis* (Fig. 5A). In this taxon the dorsal margin of the supraoccipital is horizontal, forming right angles with the lateral margins. The supraoccipital forms the dorsal margin of the foramen magnum. In *Shenqiornis* this forms a ventrally obtuse angle that defines the dorsal margin of a pentagonal foramen magnum, a feature currently an autapomorphy of this taxon (Fig. 5A; Wang *et al.* 2010).

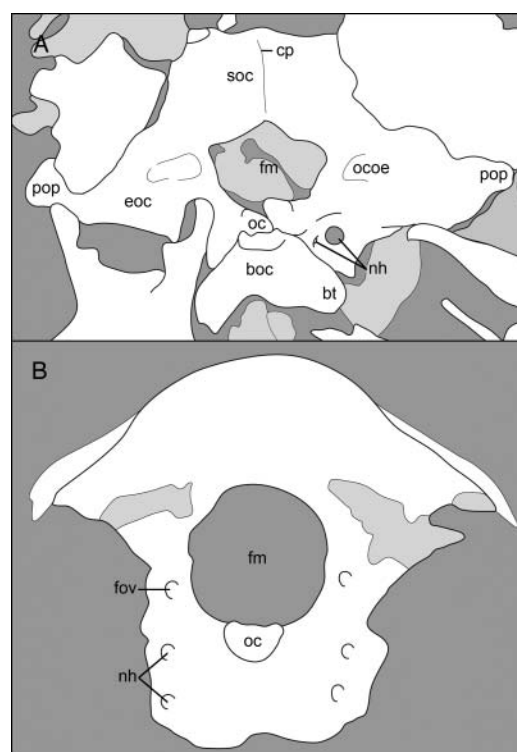


Figure 5. Basicrania: **A**, the Early Cretaceous *Shenqiornis mengi*, DNHM D2951; **B**, the Late Cretaceous *Neuquenornis volans*, MUCPv 142. Abbreviations: boc, basioccipital; bt, basal tubera; cerebral prominence; eoc, exoccipital; fm, foramen magnum; fov, foramen for the external occipital vein; nh, canals for the hypoglossus nerve; oc, occipital condyle; ocoe, *ostium canalis ophthalmici externi*; pop, paraoccipital process; soc, supraoccipital.

Exoccipital. The exoccipitals may (e.g. *Neuquenornis*) or may not (e.g. *Hebeiornis*, *Shenqiornis*) be fused to the basioccipital. In *Shenqiornis*, the exoccipitals form the lateral and complete ventral margin of the foramen magnum; the medial margins slope medioventrally, giving the foramen magnum a pentagonal shape (Fig. 5A). The exoccipitals bear mediolaterally long excavations on either side of the foramen that shallow laterally, and based on location, may possibly be homologous to the external opening of the ophthalmic canal (*ostium canalis ophthalmici externi*) of modern birds (Baumel & Witmer 1993). In the same location, *Neuquenornis* possesses a foramen interpreted as for the external occipital vein (Fig. 5B; Chiappe & Calvo 1994). In *Shenqiornis*, the exoccipitals extend laterally, forming long and slightly tapering paraoccipital processes.

The dorsal half of the occipital condyle is formed by the exoccipitals in *Shenqiornis*; they contact on the midline but remain completely unfused, each forming approximately a quarter of the condyle (Fig. 5A; Wang *et al.* 2010). In *Hebeiornis*, the basioccipital accounts for a majority of the occipital condyle; the exoccipitals each bear a small flange that contributes to a small portion of the margin of the foramen magnum and possibly the occipital condyle (Zhang *et al.* 2004).

Ventral and lateral to the occipital condyle in *Neuquenornis* there is a vertical depression that contains two foramina, one located above the other (Fig. 5B; Chiappe & Calvo 1994). Between the basioccipital and right exoccipital in *Shenqiornis* lies a bone fragment with two foramina; this bone is interpreted as a piece of the exoccipital, and defines a concave margin between the paraoccipital processes and the basioccipital (Fig. 5A). The larger of the two foramina is circular; the second, much smaller, elliptical foramen is located just medial to the former. The openings in both taxa are interpreted as the canals for the hypoglossus nerve; their position in the exoccipital is consistent with that of modern birds. A similar location for the hypoglossus nerve is reported in *Gobipteryx* (ZPAL-MgR-I/33; Elzanowski 1981).

Basioccipital. This bone varies in degree of fusion with other occipital bones and degree of contribution to the occipital condyle. The basioccipital is unfused to the exoccipitals in *Hebeiornis* and *Shenqiornis*, but fully fused in *Neuquenornis*. The dorsal-most portion of this bone contributes to the occipital condyle in all known taxa (e.g. *Hebeiornis*, *Shenqiornis*), as in modern birds (Zusi 1993). Ventral to the occipital condyle, the basioccipital expands giving this bone an overall trapezoidal appearance (e.g. *Hebeiornis*, *Shenqiornis*). The basioccipital forms ventrolaterally projecting basal tubera which define a strongly concave ventral margin (e.g. *Shenqiornis*; Fig. 5A).

Foramen magnum and occipital condyle. The foramen magnum (Fig. 5) is mediolaterally wider than it is dorsoventrally tall (e.g. *Hebeiornis*, *Shenqiornis*). Its shape ranges from round (e.g. *Neuquenornis*) to pentagonal (e.g. *Shenqiornis*). The foramen magnum is much larger than the occipital condyle (e.g. *Neuquenornis*, *Hebeiornis*, *Shenqiornis*) but the exact proportion varies widely from three (i.e. *Shenqiornis*) to eight times the size of the latter (i.e. *Neuquenornis*). Although the exact proportion cannot be measured, the Early Cretaceous holotype of *Hebeiornis* displays a relatively small foramen magnum compared to Late Cretaceous enantiornithines and modern birds.

Palatal bones. The only information available on the enantiornithine palate comes from *Gobipteryx* (Elzanowski 1995; Chiappe *et al.* 2001). In the palate, the premaxilla does not contact the rostral end of the fused vomers, which are instead contacted by the maxilla. This results in a horseshoe-shaped rostral opening that connects the palatal vault and oral cavity. Just caudal to this opening lies the choana, below the caudal margin of the nares, rostral to its position in modern birds. The fused vomers form a slender rod-like element forming the palatal midline; rostrally it contacts the maxilla and the palatine, a paddle-shaped bone. The pterygoids are robust, forked rostrally and do not contact the vomers (Chiappe *et al.* 2001). An *Archaeopteryx*-like ectopterygoid has been suggested for *Gobipteryx* by Elzanowski (1995). A possible ectethmoid has also been identified in this taxon (Chiappe *et al.* 2001).

Cranial fenestrae

The external nares are typically elliptical and longer than the antorbital fenestra, and the orbit is the largest cranial opening, as in modern birds. The antorbital fossa is filled by a large fenestra in most taxa (e.g. *Shenqiornis*, *Rapaxavis*, *Alethoalaornis*). The external nares and antorbital fenestra are not separated by a large space, so the caudal margin of the external nares usually approaches and sometimes overlaps the rostral margin of the antorbital fenestra (Figs 1, 2). Maxillary fenestrae homologous to those of non-avian theropods appear to be absent, although the homology of an accessory fenestra in the maxilla of *Pengornis* remains uncertain. An enclosed supratemporal fenestra is known in some taxa (e.g. *Shenqiornis*, LP 4450, *Pengornis*). Likewise, a fully separated infratemporal fenestra may have existed in at least one taxon (i.e. *Shenqiornis*), although this fenestra appears to be partially connected to the orbit in most (e.g. *Pengornis*, LP 4450). Additional pneumatic foramina are known to occur (e.g. *Pengornis*).

External nares. The nares vary in the bones that form them, position and shape. The nares are typically holorhinal, rostrocaudally elongate and elliptical (e.g. *Eoenantiornis*,

C. yandica). The opening is bounded rostrally, rostrodorally and typically rostroventrally by the premaxilla; in some longipterygids it appears that the majority of the ventral margin of the nares is formed by the maxilla. The nasals form the dorsal margin of the nares and, depending on the development of their maxillary process, contribute to the caudodorsal and caudal margins (e.g. *Eoenantiornis*, *Gobipteryx*, *C. yandica*, DNHM D2889). The maxilla forms the caudoventral margin and contributes to the caudal and caudodorsal (e.g. *Shenqiornis*, *Rapaxavis*) margins of the nares in varying degrees depending on the morphology of the maxilla-nasal contact. In most taxa, the nares are contained within the rostral third of the skull. An exception is represented by the longipterygids in which the nares are retracted and appear to be schizorhinal (Fig. 2A–C, E, F). The latter condition is also known outside the longipterygids (e.g. *Shenqiornis*; Fig. 2G). The proportions between length and height vary among taxa. Typically, the nares are elliptical—the length is several times the height—but in the retracted nares of the Late Cretaceous *Gobipteryx* these two dimensions are subequal (Fig. 2L, M). The shape of the longipterygid nares is difficult to ascertain due to poor preservation but it appears that these openings are very narrow and slit-like (Fig. 2A–C, E, F).

Antorbital fossa. In most taxa, the antorbital fossa appears to be entirely excavated by a large antorbital fenestra (e.g. *Shenqiornis*, LP 4450); however, in at least two specimens (e.g. *Pengornis*, DNHM D2889) the fossa is rostrally lined by a recessed medial wall of the maxilla—in *Pengornis*, the antorbital fenestra is approximately two-thirds the size of the antorbital fossa (Fig. 2). The antorbital fossa and fenestra are typically triangular with subequal length and height. The relative contribution of the maxilla, nasal and lacrimal to the antorbital fossa is unclear for most taxa. In *Pengornis* and *Shenqiornis*, the maxilla forms the rostral margin and rostral half of the dorsal margin; the lacrimal forms the remaining half of the dorsal margin, thus excluding the nasal from participating in the fossa. However, in *Gobipteryx*, the maxillary contribution is limited to a small rostroventral corner of the fossa, while most of the rostral and possibly dorsal margins are formed by the nasal (the lacrimal contribution remains unknown; Fig. 2L, M). The jugal contributes to the caudoventral corner of the antorbital fossa in LP 4450 (Fig. 3B). In *Pengornis*, the maxilla is pierced by a single accessory foramen (Fig. 2H). The foramen is small and elliptical, located in the rostradorsal corner of the fossa; its size and placement suggest it may not be homologous to either of the accessory fenestrae (maxillary and promaxillary) of *Archaeopteryx* and non-avian theropods, which are more ventrally located (Elzanowski 2002; Norell & Makovicky 2004).

Temporal fenestrae. The preservation of a T-shaped postorbital suggests the presence of a fully demarcated

supratemporal fenestra formed by the frontal, parietal, postorbital and squamosal (e.g. *Pengornis*, *Shenqiornis*, LP 4450). The elongate jugal process of the postorbital of at least one specimen (i.e. *Shenqiornis*; Fig. 2G) further suggests a completely enclosed infratemporal fenestra, and thus a fully diapsid skull, may have been present in at least one taxon. However, the reduced postorbital of other specimens indicates that in most taxa the infratemporal fenestra converged with the orbit (e.g. *Pengornis*, LP 4450). The elongate postorbital bone in *Shenqiornis* is disarticulated, making it difficult to determine with absolute certainty if this bone fully separated the infratemporal fenestra from the orbit, especially given the absence of a postorbital process on the jugal or a preserved quadratojugal (Figs 1D, 2G). The jugal process of the postorbital in this specimen is very long (more than three times the length of the proximal rami), suggesting the postorbital would have been capable of forming a completely delimited infratemporal fenestra. Based on the position of the postorbital in articulated specimens, if the postorbital were to contact a bone ventrally in *Shenqiornis*, it likely be the medial or lateral surface of the jugal, a very different articulation from the long overlapping contact between the postorbital and postorbital process of the jugal in non-avian theropods and some other basal birds (e.g. *Confuciusornis*; Chiappe *et al.* 1999).

Additional fenestrae. In *Pengornis* the nasal and lacrimal form a small fenestra (Figs 1C, 2H). This feature, not preserved in any other enantiornithine, is inferred to be pneumatic based on the extensive pneumaticity that characterizes the nasolacrimal region of birds and non-avian theropods (Witmer 1997). *Pengornis* also possesses an additional small rostrocaudally elongate oval foramen that pierces the nasal at the level of the rostral margin of the antorbital fenestra.

Mandible

There is a general lack of fusion between the dentary and postdentary bones, and the dentaries are typically not fused into a mandibular symphysis; the only specimen with fusion between mandibular bones is from the Late Cretaceous (e.g. *Gobipteryx* ZPAL-MgR-I/12; Elzanowski 1977). The degree of mandibular fenestration is unclear, but all known adult mandibles are imperforate.

Dentary. The dentary varies in morphology and dentition. This bone is most commonly unfused, toothed, and straight with an unforked ventrally sloping caudal articulation with the surangular (e.g. *Longipteryx*, *C. yandica*, *Alethoalaornis*, *Shenqiornis*). Caudally, the ventral margin of the dentary often expands ventrally at the level of the lacrimal while the dorsal margin remains straight (e.g. *Hebeiornis*, *Shenqiornis*, *Eocathayornis*). In the longipterygids *Longirostravis*, *Rapaxavis* and *Longipteryx*, the dentary is overall slightly concave ventrally (Hou

et al. 2004; Morschhauser *et al.* 2009; O'Connor *et al.* 2009). *Gobipteryx* reportedly differs from Early Cretaceous enantiornithines in that the mandibular bones are nearly completely fused (dentaries strongly ankylosed in IGM - 100/1011; Chiappe *et al.* 2001) and the caudal articulation of the dentary is forked, as in more advanced birds (Elzanowski 1977). These specimens however, reportedly have undergone some diagenetic recrystallization, which may have obscured sutures and other interosseous connections (Elzanowski 1977).

Dentary teeth range from absent (i.e. *Gobipteryx*) to rostrally restricted (e.g. Longipterygidae) to present throughout (e.g. *Pengornis*, *C. yandica*, *Shenqiornis*). The number of teeth ranges from low in the longipterygids to 6–7 in the typical enantiornithine (e.g. *Hebeiornis*, *Shenqiornis*), with an estimated 13 teeth marking the known upper limit (i.e. *Pengornis*; Zhou *et al.* 2008).

Surangular. Usually unfused to the dentary, this bone is typically shorter than the dentary, robust and straight (e.g. *Rapaxavis*, *Hebeiornis*, DNHM D2510/1). The articulation with the dentary is long and slopes rostradorsal—ventrocaudally so that the rostral third of the surangular tapers to a blunt tip rostradorsally (e.g. *Dapingfangornis*, *Longipteryx*, *Protopteryx*). No coronoid bone is known but *Gobipteryx* ZPAL-MgR-I/12 and *Rapaxavis* possess a rounded coronoid process on the dorsal margin of the surangular (Fig. 2A).

Angular. Often difficult to differentiate from possible hyoid bones (e.g. *Rapaxavis*, *Longirostravis*), the angular appears to be a thin, straight and rod-like element that forms the ventrolateral margin of the postdentary portion of the mandible (e.g. *Shanweiniao*, DNHM D2567/8). The angular is slightly curved so that it is convex ventrally in some taxa (e.g. *Hebeiornis*, *Longipteryx*). The rostral end is wider than the caudal end in lateral view (e.g. *Hebeiornis*, *Longipteryx*, DNHM D2567/8).

Splénial. This bone is usually not visible but in a few specimens it is unfused and disarticulated into view (e.g. *Hebeiornis*, *Dapingfangornis*). In *Hebeiornis* the bone is more than half the length of the dentary. The ventral margin of this bone is slightly concave ventrally. The dorsal margin defines the apex of an obtuse triangle; the rostral ramus is twice the length of the caudal ramus and tapers more sharply. In *Archaeopteryx* the rostral and caudal rami are closer to subequal in length, although the rostral ramus is still longer (Elzanowski 2002).

Prearticular and articular. Preserved in *Hebeiornis*, the prearticular is rostrally lancet-shaped (rostral ramus is tapered sharply) as in *Archaeopteryx* (Elzanowski 2002), differing from the rounded margin in enantiornithines (Zhang

et al. 2004). The articular is preserved in LP 4450 but no information can be discerned.

Mandibular fenestrae

Completely perforated rostral and caudal mandibular fenestrae are only known in LP 4450, although since the specimen is a juvenile it is difficult to ascertain to what degree this is the result of incomplete ossification (Sanz *et al.* 1997). In this specimen, the fenestrae are elongate ovals (Fig. 3C). The rostral fenestra retains the ancestral condition in which the ventral margin is formed by the angular, as in non-avian dinosaurs (as opposed to the dentary of modern birds; Sanz *et al.* 1997). The caudal mandibular fenestra in LP 4450, which is largely enclosed by the surangular with a rostroventral contribution from the angular, is inferred to be homologous to the surangular foramen of non-avian theropods (Sanz *et al.* 1997; Weishampel *et al.* 2004). In *Gobipteryx* (ZPAL-MgR I/12), a small, depressed area on the rostral-most surangular is reported to correspond to the rostral mandibular fenestra while the caudal fenestra is reduced to a small foramen (Elzanowski 1977); the extent to which the alleged rostral fenestra perforates the mandible is unclear. GMV-2158 also possesses a single fully perforate caudal (surangular) fenestra (Chiappe *et al.* 2007); the mandibular fenestra of this juvenile is relatively smaller than that of LP 4450 and round. Given that the only two specimens with fully perforate mandibular fenestrae are juveniles (Chiappe *et al.* 2007; Sanz *et al.* 1997), the absence of mandibular fenestrae in specimens of adult enantiornithines could suggest their presence in these specimens reflects their ontogenetic stage. However, similar structures are absent in other juvenile specimens GMV-2159 and GMV 2156/NIGP-130723 (Chiappe *et al.* 2007).

Discussion

Enantiornithines display a unique mosaic of primitive and derived characters, reflecting their intermediate phylogenetic position between the basal-pygostylians and modern birds, and the scale of their Cretaceous evolutionary radiation (an alternative phylogenetic proposal for Enantiornithines—sharing a most common recent ancestor with *Archaeopteryx* [Martin 1983, 2004]—has been shown to be less parsimonious by phylogenetic analyses over the last two decades [e.g. Chiappe 1995a, 2002; Clarke and Norell 2002; O'Connor *et al.* 2009]). However, the pattern of character loss and/or plesiomorphic retention in certain areas of the skeleton is intriguing. Within the skull, the lack of derived characters relative to more basal birds such as *Archaeopteryx* is most notable. Instead, in many details the skull bears strong similarity to this basal taxon; enantiornithines retain teeth, a postorbital bone, a quadrate with a single headed otic process, bicondylar mandibular

process, and a broad orbital process, a complete osseous bar separating the orbit and antorbital fenestra, a small premaxilla, a squamosal unincorporated into the braincase, long paraoccipital processes, unfused skull bones, and the apparent absence of kinetic features. All these features are modified in modern birds. The absence of teeth and presence of a caudally forked dentary—features otherwise common to modern birds and present in the basal ornithuromorph *Apsaravis ukhaana* (Clarke & Norell 2002) and in the basal pygostylian *Confuciusornis sanctus* (Chiappe *et al.* 1999)—are only known in a single Late Cretaceous taxon (i.e. *Gobipteryx*), suggesting an overall trend towards more advanced morphologies in at least one lineage.

The absence of anatomically modern features in the skull of the Early Cretaceous enantiornithines is not unique to this one avian lineage, but plesiomorphic for basal birds. Sapeornithids and confuciusornithids, basal pygostylians also known from the Jehol Biota, share the presence of a postorbital, a squamosal unincorporated into the braincase, absence of element fusion, and an unforked dentary (forked in *Confuciusornis*); both these groups, however, have either reduced (e.g. *Sapeornis*) or lost (e.g. confuciusornithids) their dentition. Even the skulls of some sympatric Jehol basal ornithuromorphs (e.g. *Yanornis martini*, *Hongshanornis longicresta*; Zhou & Zhang 2001, 2005) are fairly primitive and highly unfused, having small premaxillae, teeth, and unforked dentaries, though no ornithuromorph is known to retain a postorbital bone and the skulls of ornithothoracine taxa are considerably less massive than those of basal taxa such as *Jeholornis*, *Sapeornis* and *Confuciusornis*. The absence of derived features in the skulls of early birds with advanced flight features, such as an alula, strut-like coracoid, and reduced manual digits, emphasizes that the refinement of powered flight dominated early avian evolution (Chiappe 1995b). Despite the conservative nature of enantiornithine skull morphology relative to more basal taxa and the absence of detailed morphologies preserved among a large number of specimens, variation within the group can be discussed at the level of skull shape and fenestration. Enantiornithine dentition and trophic specialization are also diverse relative to other sympatric avian clades and are discussed below.

Fusion

The extent of fusion between the bones of the skull varies widely between known enantiornithines; however, the degree to which this is an ontogenetic artefact is largely unknown. Given the absence of good growth series within the clade, it cannot be determined if the absence of fusion between two elements is due to incomplete growth, or represents a true feature of the species. This is further complicated by our poor understanding of enantiornithine developmental strategy and ontogeny (Chinsamy & Elzanowski 2001; Cambra-Moo *et al.* 2006). The complete fusion of

the basicranium (parietal and frontal fusion incomplete) in *Neuquenornis* may either represent the derived state, or the incomplete fusion observed in the basicrania of the holotype specimens of *Shenqiornis* and *Hebeiornis* may not be a true morphological state but the result of incomplete growth at the time of death, despite the adult appearance of the specimens based on their size, ossification of periosteal surfaces, and skull proportions.

Despite this, there is no doubt that the few Late Cretaceous skull specimens available show greater degrees of premaxillary, basicranial and mandibular fusion compared to Early Cretaceous specimens, given that the only definitively known fused premaxillae, basicranium and mandible are all known from the Late Cretaceous.

Fenestration

The main cranial fenestrae in enantiornithines are very similar to those of *Archaeopteryx*, with large external nares and orbits as in modern birds, rather than the small external nares (relative to the antorbital fenestra) of most non-avian theropods (Currie & Chen, 2001; Norell & Makovicky 2004; Gölich & Chiappe 2006). The antorbital fossa of *Archaeopteryx*, *Dalianraptor* and closely related non-avian theropods typically possesses two small foramina (promaxillary and maxillary fenestrae) in addition to the larger antorbital fenestra (Elzanowski 2002; Norell & Makovicky 2004; Gao & Liu 2005). This condition is unknown among enantiornithines, although a single additional foramen within the antorbital fossa is known to occur in *Pengornis* (Fig. 2H). Basal pygostylians *Sapeornis* and *Confuciusornis* also possessed an accessory maxillary foramen, but this feature is unknown in birds more advanced than enantiornithines. In *Confuciusornis*, the round shape of the foramen and its position suggest it may be the maxillary fenestra of non-avian theropods, although this homology is uncertain (Witmer 1997; Chiappe *et al.* 1999). Preservation in *Sapeornis* is unclear and it cannot be determined if one or two accessory foramina are present, nor can their possible homology be determined. The rostradorsal position of the accessory foramen in *Pengornis* suggests that, unlike *Confuciusornis*, this feature may not be homologous to the accessory maxillary fenestrae in the antorbital fossa of *Archaeopteryx* and non-avian theropods. Although only identifiable in a single exceptionally well preserved specimen, the ‘accessory foramen’ present in *Pengornis* indicates that, like in modern birds (Witmer 1997; Witmer & Ridgely 2008), enantiornithines had evolved additional pneumatic features. Given the poor preservation of the maxilla in most specimens and the thinness of the recessed bone that lines the antorbital fossa, this feature may have a wider distribution within the clade.

Modern birds, having lost their postorbital bone, no longer possess fully isolated supra- and infratemporal fenestrae. Basal birds like *Confuciusornis* that possess a

diapsid skull are considered to have secondarily derived the primitive condition (Chiappe *et al.* 1999), an inference supported by the presence of a reduced postorbital in *Archaeopteryx* that does not contact the jugal as in non-avian maniraptoran dinosaurs (Elzanowski 2002). While the postorbital is a bone rarely preserved, in enantiornithines it also appears to be typically reduced (e.g. *Pengornis*, LP 4450). One specimen (DNHM D2950/1, the holotype of *Shenqiornis*) preserves a large T-shaped bone interpreted as the postorbital based on its morphology; however, the caudal half of the skull, including the presumed postorbital, is disarticulated and our interpretation is not unequivocal (Figs. 1D, 2G). The large size of the presumed postorbital of *Shenqiornis* suggests not only that a supratemporal fenestra may have been present in this enantiornithine taxon (also inferred for *Pengornis* and LP 4450), but that this bone may also have completely enclosed an infratemporal fenestra. However, the jugal morphology in this specimen suggests that if a fully delimited infratemporal fenestra was present, the bone interpreted as a postorbital would have contacted the medial or lateral surface of the jugal bar, a different configuration from the long articulation of the postorbital and postorbital process of the jugal in non-avian theropods and confuciusornithids. This supports the hypothesis that the condition in *Shenqiornis* is also secondarily derived. Alternatively, the presence of a postorbital with an elongate jugal ramus in Sapeornithidae, Confuciusornithidae and one enantiornithine (i.e. *Shenqiornis*), as well as in non-avian theropods (Ostrom 1969; Clarke *et al.* 2002; Xu *et al.* 2002), may suggest that a large postorbital is the plesiomorphic avian condition with the postorbital in *Archaeopteryx* being reduced during the evolution of this lineage. As the phylogenetic position of the known pre-pygostylian taxa (e.g. *Jeholornis*, *Rahonavis*, *Zhongornis*) becomes better understood, we may be able to differentiate between these two hypotheses.

Skull geometry

The great diversity of skull morphologies of modern birds has been subdivided into two general geometric types: extended and flexed (Marinelli 1928; Van der Klaauw 1948). While skull geometry is associated with the position of the brain, rotated in flexed skulls, it can be determined osteologically from the position of the foramen magnum. In extended crania the skull units (i.e. rostrum, orbit, braincase) are aligned in lateral view and the foramen magnum is directed caudally; in flexed skulls, the units are decoupled, not limited to the same plane in lateral view, and the foramen magnum is ventrally located (Marugán-Lobón & Buscalioni 2006). The avian skull is incredibly diverse in form and proportion; however, a number of morphologies are limited to the flexed type of skull, leading to the hypotheses that this specific design is derived within Aves and that the evolutionary decoupling of the skull units within the group facilitated the evolution of a wider

range of morphologies (Marugán-Lobón & Buscalioni 2006). The rotation of the brain characteristic of many modern lineages probably occurred after the ornithothoracine split, within the lineage moving towards modern birds. Currently there is no evidence that enantiornithines or any other basal bird developed a flexed cranial geometry; all three preserved enantiornithine basicrania—belonging to taxa of substantially different size, morphology and geological age (i.e. *Hebeiornis*, *Neuquenornis*, *Shenqiornis*)—possess caudally directed foramina magna (Fig. 5). Taxa in which the skull is well preserved in lateral view all show the skull units aligned in a single plane (e.g. *Longipteryx*, *Shenqiornis*, *Protopteryx*, *Pengornis*; Figs 1–3), suggesting that during the evolution of Enantiornithes the brain remained un-rotated. This conclusion is equivocal, based on the limited information available, but even without the rotation of the brain, the range of morphological variation observed in modern birds was not impossible for enantiornithines to achieve. However, if enantiornithines did not develop flexed type skulls, the development of morphologies comparable to those of modern flexed type skulls would probably have involved developmental pathways different from those in living birds.

Several enantiornithines were measured and added to the archosaur skull geometry morphospace of Marugán-Lobón & Buscalioni (2003) in order to determine how the clade compares to neornithines (modern birds) and other archosaurs (Fig. 6). The range of enantiornithine cranial morphospace is based on a sample size of only five taxa (several of which are longipterygids, thus the sample size is biased towards longer rostra). Given the preservation

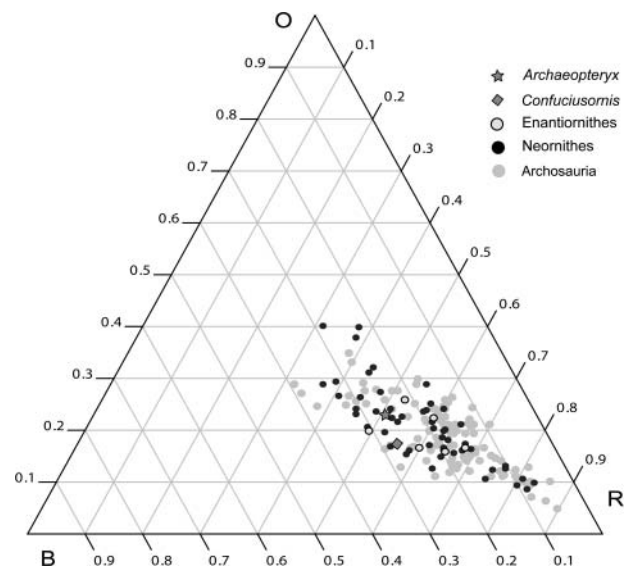


Figure 6. Ternary diagram showing the relative proportions of skull units among Enantiornithes, relative to Neornithes. Abbreviations: B, braincase; O, orbit; R, rostrum.

of fossil specimens (disarticulated, compressed, damaged and/or incomplete), it is impossible to measure as accurately as with modern specimens. Thus the measurements used (Fig. 6) are considered best estimates, even in the most exceptionally preserved specimens such as the holotype of *Pengornis*. Consequently, it is premature to make detailed inferences about variation and proportions and these results will have to be explored further when a larger number of well-preserved specimens are available. Nevertheless, all five enantiornithines fall approximately within the known range of avian mesorostrine morphospace—the only slight outlier is the poorly preserved *Protopteryx* (IVPP V11665). *Archaeopteryx* (measurements taken from the juvenile Eichstatt specimen) and *Confuciusornis* (GMV 2132) were plotted in order to determine whether basal bird skull geometry is conservative; the two taxa plot distinct from each other and enantiornithines. *Archaeopteryx* and *Confuciusornis* differ in that the latter has a smaller orbit, but both taxa fall within the range of extant mesorostrine birds (this difference is exaggerated due to the juvenile status of the Eichstatt *Archaeopteryx*, resulting in a proportionately larger orbit in this specimen). Enantiornithines form a cluster in the centre of the archosaur spectrum, and vary in proportions of all skull units, not just the rostrum. The braincase and orbit show the most variation; however, these dimensions are much more difficult to measure than the rostral length and this variation is considered an artefact of poor preservation.

The rostrum is the most variable skull unit within Theropoda, and the same holds true for avian as well as non-avian taxa (Marugán-Lobón & Buscalioni 2003). Such a wide range of rostral morphological variation has been explained by greater functional constraints on the orbit and the postorbit (to house and protect the eye and brain) as opposed to those acting on the rostrum, which has a greater freedom to respond to selective pressures and to evolve a wide range of morphologies associated with specialized trophic function (Marugán-Lobón & Buscalioni 2003). Following the terminology for rostral proportions set forth by Busbey (1995) and maintained by Marugán-Lobón & Buscalioni (2003), the archosaur skull is broken into three categories according to rostral proportions: brevirostrine (rostrum 30–50% of total skull length), mesorostrine (50–70%) and longirostrine (70–90%).

Archaeopteryx, *Confuciusornis* and the enantiornithines fall in the mesorostrine range (Fig. 6), suggesting that this condition is basal within Aves, as in all Archosauria (Marugán-Lobón & Buscalioni 2003). Though few skulls are preserved well enough to be measured accurately, observations and measurements indicate that enantiornithines typically possess skulls that are approximately 50% rostrum. The longipterygid clade represents an enantiornithine incursion into new morphospace, with rostral proportions approaching and exceeding 60% skull length.

Currently, there are no enantiornithine or other Mesozoic avians unequivocally known to have possessed a brevirostrine or true longirostrine skull, suggesting that brevirostrality and longirostrality are derived conditions within Aves.

Dental variation

A majority of enantiornithine taxa, for which cranial material is known, possess teeth (Figs 1, 2, 7), except the Late Cretaceous *Gobipteryx minuta* (Fig. 2L, M; Elzanowski 1974). Taxa vary considerably in the morphology of their teeth, their size, distribution, number, and where they are located. With the exception of LP 4450 (Sanz *et al.* 1997), all specimens used in this discussion are from the Early Cretaceous Jehol Group. Even within this single geological unit, a diversity of dental morphologies can be recognized. Teeth are typically similar to those of *Archaeopteryx* (Elzanowski 2002): simple, conical, slightly constricted at the base, recurved, and without serrations (e.g. *Hebeiornis*, *C. yandica*, *Eocathayornis*, LP 4450). The degree of caudal curvature is relatively low, with the tip of the tooth located just caudal to the midpoint of the alveolus (e.g. *C. yandica*, *Pengornis*, GMV 2158, *Shenqiornis*). In taxa in which teeth are more strongly recurved, the tip reaches the caudal margin of the tooth socket (i.e. *Eoenantiornis*; Fig. 7A, B), and in extreme taxa, projects beyond it (i.e. *Longipteryx*; Fig. 7I–L).

Teeth range in size from very small, reduced peg-like teeth (e.g. *Longirostravis*, Fig. 7G, H) to the large, robust teeth of *Shenqiornis* and *Longipteryx* (Fig. 7I–L). Tooth size relative to body size also varies considerably; the teeth of *Longirostravis* (c. 0.45–0.5 mm; Fig. 7G, H) are nearly the same size as those of *Pengornis* (c. 0.55–0.65 mm; Fig. 7E, F), despite the fact that the latter specimen is several times the size of the former. The teeth of *Shenqiornis* are among the largest and most robust currently recognized within enantiornithines; fat with circular cross sections (Fig. 7C, D), they taper rapidly into a slightly caudally deflected tip. The teeth of *Shenqiornis* represent one extreme within the clade; another extreme is exemplified by the numerous low crowned teeth of *Pengornis* (Fig. 7E, F). It has been suggested that the teeth of this specimen bear wear facets and evidence for primitive-style tooth replacement, with teeth replaced throughout the organism's life span (Zhou *et al.* 2008). This detail is difficult to verify and could equally represent heterodonty or differential preservation. Currently, despite the large number of known toothed taxa, there are no known enantiornithines that clearly preserve a resorption pit or newly erupting replacement teeth, therefore evidence for dental replacement remains elusive.

Trophic specialization

The diversity of recognized dental patterns, such as in the longipterygids, which possess rostrally-restricted dentition, suggests that a great deal of trophic specialization evolved

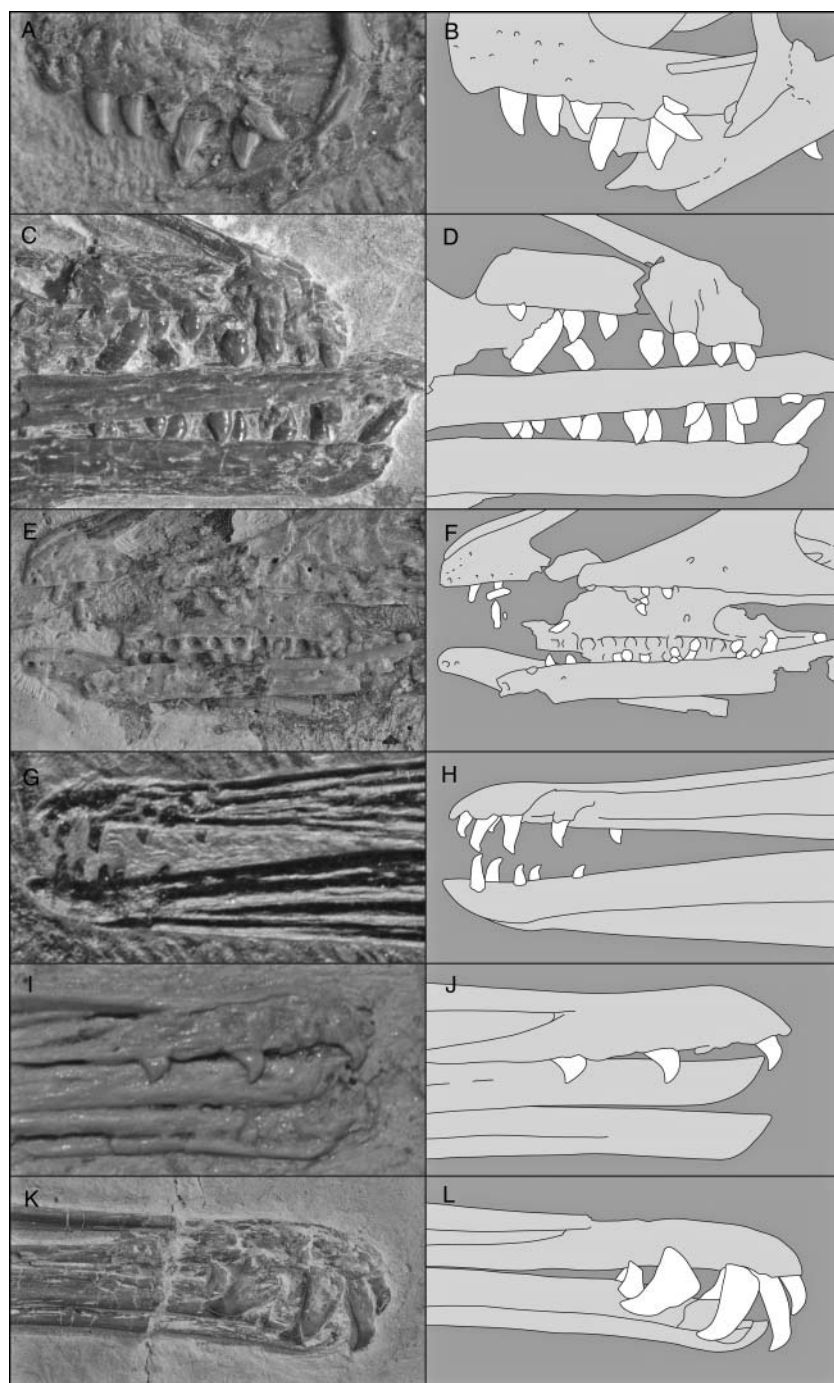


Figure 7. Enantiornithine teeth, photographs and interpretative drawings: **A, B**, *Eoenantiornis buhlerei*, IVPP 11537; **C, D**, *Shenqiornis mengi*, DNHM D2951; **E, F**, *Pengornis houi*, IVPP 15336; **G, H**, *Longirostravis hani*, IVPP V11309; **I, J**, *Longipteryx chaoyangensis*, IVPP V12552; **K, L**, *Longipteryx* sp., DNHM D2889.

within Enantiornithes. Stomach contents are known from two specimens, the holotypes of *Eoalualvis* and *Enantiophoenix* (Sanz *et al.* 1996; Dalla Vecchia & Chiappe 2002; Cau & Arduini 2008). *Eoalualvis* preserves the remains of arthropods associated with the visceral region, while

Enantiophoenix is associated with bits of amber scattered among the skeletal elements, and is interpreted as a sap-eater (Dalla Vecchia & Chiappe 2002). Neither preserves any skull material, thus morphologies of the rostrum and teeth associated with such diets cannot be determined. No

enantiornithine is known to preserve gastroliths, which have been found in a number of sympatric ornithuromorphs (pers. obs.; Zhou *et al.* 2004; Zhou & Zhang 2006b).

Without stomach contents, dietary inferences for fossil taxa are weak; however, the following interpretations are based on tooth morphology and observations of related taxa. The teeth of *Archaeopteryx* are interpreted as too weak for crushing hard foods, and the taxon is interpreted as a general insectivore, limited to small arthropods with softer cuticles (Elzanowski 2002). The tooth morphology in a number of enantiornithines is largely consistent with *Archaeopteryx*, but a number of taxa depart from this morphology, thus indicating specialization for a unique niche. *Longipteryx*, *Pengornis* and *Shenqiornis* represent the most extreme deviations from the typical tooth morphology within the clade (Fig. 7). The teeth of *Shenqiornis* are relatively the largest and most robust known within Enantiornithes (Fig. 7C, D); this taxon is interpreted as having a duraphageous diet, utilizing food items unavailable to other birds of a similar size. Longipterygids all possess rostrally restricted dentition, and most taxa bear very small, reduced teeth (Fig. 7G, H); *Longirostravis* has been suggested to be a mud-prober, using its delicate rostrum to retrieve worms and other soft-bodied organisms from the littoral substrate (Hou *et al.* 2004). The teeth of *Longipteryx* are large, recurved, and slightly laterally compressed, features associated with increased predatory capability (Fig. 7I–L). The rostral restriction of the teeth and their morphology indicates that *Longipteryx* may have been piscivorous. The numerous small teeth of *Pengornis* are blunt, brachydont, and may bear wear facets (Fig. 7E, F; Zhou *et al.* 2008); low-crowned teeth, however, are inconsistent with a diet of abrasive food items. The morphology of the teeth of *Pengornis* is more consistent with a diet of soft-shelled arthropods, which were abundant in the Jehol lake system (Chang *et al.* 2003).

Cranial kinesis

The absence of a complete jugal-postorbital bar in some enantiornithine taxa indicates that cranial kinesis was at least possible. Without jugal and postorbital contact, the jugal is free to rotate forward and elevate the skull as in modern birds (Zusi 1984; Bühler 1987; Bock 2002). Osteologically, kinesis can be determined by identifying thinned regions of bone, representing bending zones, or true mobile hinges such as a frontal-nasal hinge, where the movement occurs. All modern birds possess some form of cranial kinesis and are able to move their upper jaw with respect to the lower jaw to some degree (Zusi 1984). Among modern taxa there are many forms of kinesis (amphikinesis, prokinesis and rhynchokinesis) which reflect where the bending occurs within the rostrum (Zusi 1984). These different types of kinesis are associated with different specialized trophic functions; for example, rhynchokinesis (rostrally located bending zone) is common among (although not limited to)

the longirostrine shore birds (e.g. Scolopacidae, sandpipers and their relatives) and aids the removal of food items from the substrate as well as the capture of planktonic prey (Zusi 1984; Estrella & Masero 2007).

It has been observed within Neornithes that all schizorhinal skulls are rhynchokinetic, though not all rhynchokinetic skulls are schizorhinal (Zusi 1984). *Longirostravis*, a purported mud-prober (Hou *et al.* 2004), has schizorhinal nostrils, as does the closely related *Rapaxavis*; together with the absence of a preserved postorbital in these specimens, it is possible that the skulls of these taxa may have been capable of rhynchokinesis (Fig. 2A, B). If so, given that rhynchokinesis is generally considered to be derived among modern birds, such a condition must have evolved independently from that in neornithines. Unfortunately, the incomplete and 2D preservation of these taxa and most other enantiornithine specimens makes it impossible to determine if bending zones were present. No cranial hinges have been reported or observed in any enantiornithine. The nature of the postorbital-jugal contact in taxa such as *Shenqiornis* is currently unknown but future discoveries may prove that some enantiornithines may have had limited (if any) kinetic potential in the skull, as in the confuciusornithids (Chiappe *et al.* 1999).

Evolutionary trends

The Late Cretaceous record of enantiornithine skull material is extremely limited compared to that of the Early Cretaceous; as a result, any inferences made regarding trends in enantiornithine evolution through time are inherently weak. Despite this, the obvious trends should be noted. An increase in the degree of fusion between skull bones is apparent, evidenced by the highly fused premaxillae of *Gobipteryx*, although greater information on the ontogeny of enantiornithines may affect this hypothesis. The complete loss of teeth within Enantiornithes is only known in a Late Cretaceous taxon (i.e. *Gobipteryx*), but occurred much earlier in other lineages of Mesozoic birds (e.g. Confuciusornithidae, Ornithuromorpha; Hou *et al.* 1995; Zhou & Zhang 2006a). The foramen magnum of the Late Cretaceous *Neuquenornis* is proportionately much larger than the occipital condyle relative to Early Cretaceous enantiornithines (Fig. 5), a derived feature of modern birds that also independently arose in Late Cretaceous non-avian theropods such as alvarezsaurids (Chiappe *et al.* 2002). The premaxilla is enlarged in *Gobipteryx* relative to Early Cretaceous taxa, and the maxilla is reduced, both morphologies characteristic of modern birds (Fig. 2L, M; Zusi 1993). An enlarged premaxilla is also present in the highly modified skull of confuciusornithids (Chiappe *et al.* 1999), although absent in basal ornithuromorphs indicating convergence between these three clades. The increased fusion, loss of teeth, greater ratio of foramen magnum to occipital condyle, and greater premaxilla/maxilla ratio can all be considered derived features, consistent with morphologies

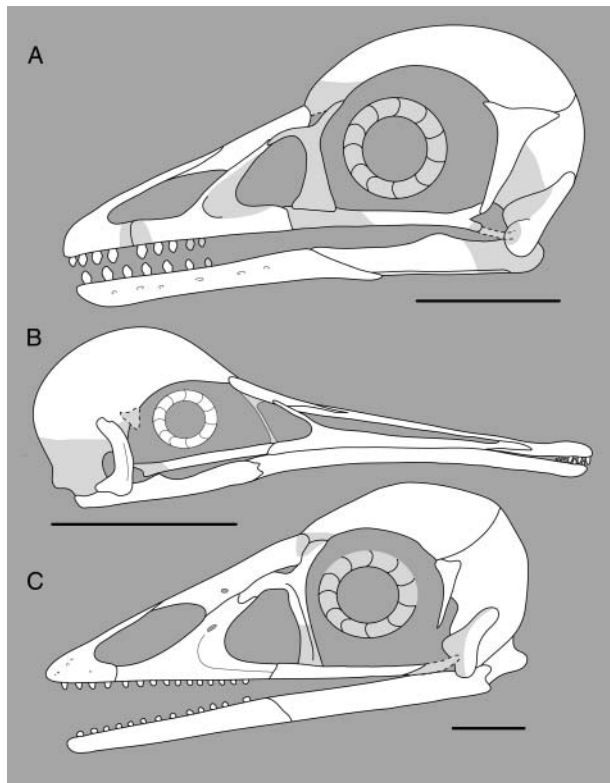


Figure 8. Reconstructions of the skulls of enantiornithines: **A**, *Shengjiornis mengi*; **B**, *Rapaxavis pani*; **C**, *Pengornis houi*. All scale bars = 1 cm.

present in modern birds. Thus despite the extremely fragmentary information available for Late Cretaceous taxa, a weak, general trend from more basal to derived features is observed during enantiornithine evolution—a trend that given the phylogenetic position of Enantiornithes is interpreted as having developed in parallel to Ornithuromorpha. This trend is also observed in the postcrania, with an increase in size and degree of fusion in compound bones such as the tarsometatarsus in the Late Cretaceous (Chiappe & Walker 2002). The well-sampled Jehol avifauna, however, indicates that by the Early Cretaceous, enantiornithines were already incredibly diverse in form and function.

Conclusions

The enantiornithine skull can be described as plesiomorphically unfused, retaining a small premaxilla, a postorbital bone, a squamosal not incorporated to the braincase, teeth, and a primitive quadrate with a single headed otic process and broad orbital process. The premaxilla, maxilla and nasal show considerable morphological variation, which results in a diversity of skull shapes, most notably the elongate skull of Longipterygidae; schizorhinal nostrils are

also known to have evolved within this particular clade. Despite the current diversity of published skull material and numerous undescribed specimens, some areas of the enantiornithine skull remain unclear. The lacrimal, jugal and postorbital bones are poorly preserved in most specimens and the articulation between and degree of morphological variation within them cannot be determined from currently available specimens. The palatal complex and basicranium are preserved in only one or two specimens, thus variation between groups in the morphology of these regions is also incompletely known. Based on this morphological review, however, we offer updated reconstructions of the enantiornithine skull (Fig. 8).

Fossils from the Late Cretaceous are rare, but comparison with older specimens indicates a general trend towards more advanced morphologies (e.g. enlarged premaxilla, absence of teeth, increased fusion between elements) in stratigraphically younger taxa. Currently there is no evidence that this clade evolved the flexed type skull with ventrally oriented foramen magnum associated with unique skull shapes in many modern birds, or truly brevirostrine or longirostrine proportions. In parallel with groups of more advanced birds and some non-avian theropods, the enantiornithine skull developed pneumatic features absent in primitive birds, as evidenced by *Pengornis*.

The available skull material reveals abundant evidence of trophic specialization; a diversity of dental morphologies and patterns are recognized. The elongated rostrum of longipterygids is interpreted as trophic specialization for aquatic environments, and intraclade diversity suggests adaptation to a wide range of ecological niches. No specimen preserves a skull that can be clearly identified as possessing cranial kinesis; however, the reduced postorbital in most specimens, where preserved, suggests that this feature may have been present as it is in all modern birds.

In reviewing the enantiornithine skull, it is clear that the high level of evolutionary experimentation characterizing the transition from non-avian theropods to modern birds (Chiappe & Dyke 2007) also involved many skull morphologies. For example, nearly every basal bird between *Archaeopteryx* and Ornithothoraces has reduced dentition to some degree, yet only one Late Cretaceous enantiornithine is known to have possessed a beak. Instead a number of enantiornithines show teeth larger and more robust than those of *Archaeopteryx*. Likewise, enantiornithines show a number of skull morphologies more primitive than those present in more basal birds, such as the absence of a caudally forked dentary (a condition present in the more basal Confuciusornithidae). Overall, the enantiornithine skull is characterized by a large amount of morphological diversity but very few major apomorphies, with the skull remaining morphologically more comparable to non-avian theropods than to modern birds. This contrasts with the enantiornithine post-cranial skeleton, which shows numerous advancements over more primitive birds, e.g. a

rostrocaudally elongate sternum and narrow furcula. This suggests that during the early evolution of Aves, while morphological experimentation did extend to the skull, this region lagged behind the post-cranial skeleton in terms of apomorphic change, with even basal ornithuromorphs retaining a skull that remains fairly conservative and similar to *Archaeopteryx* in morphology.

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