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A reappraisal of *Boluochia zhengi* (Aves: Enantiornithes) and a discussion of intraclade diversity in the Jehol avifauna, China

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A careful reappraisal of the only known specimen of the poorly understood fossil enantiornithine bird *Boluochia zhengi* reveals numerous morphological similarities that suggest this taxon is closely related to the well-known *Longipteryx chaoyangensis*, and so is assignable to the most diverse recognized clade of Early Cretaceous enantiornithines, the Longipterygidae. This new study of the holotype of *B. zhengi* reveals new longipterygid synapomorphies and expands our knowledge of the temporal and geographical ranges and diversity of the clade. We suggest that the trophic specialization that characterizes longipterygids may have been a major factor contributing to the success of this clade.

Keywords: Enantiornithes; Ornithothoraces; Longipterygidae; *Boluochia*; *Longipteryx*; Jehol

Introduction

Since the first discoveries of enantiornithine birds in the Jehol Group of northeastern China in the early 1990s (Zhou *et al.* 1992), a steady flow of new forms have been discovered (Serenó & Rao 1992; Zhang *et al.* 2003; Zhou & Zhang 2006). This wealth of fossils has revealed more information about enantiornithine skeletal and integumentary morphology than those known from any other geological unit in the world, and specimens that substantially change our understanding of this diverse clade continue to be discovered (Zhou *et al.* 2008; Wang *et al.* 2010). The majority of these birds come from the younger two formations in the Jehol Group, the Yixian and Jiufotang formations, which preserve late Hauterivian—early Aptian lake deposits spanning approximately 5 million years (125–120 million years ago) (He *et al.* 2004; Yang *et al.* 2007; Zhu *et al.* 2007). The third and oldest member, the Dabeigou Formation, dated at 131 million years ago (He *et al.* 2006), has also produced a few birds such as the basal enantiornithine *Protopteryx fengningensis* (Zhang & Zhou 2000) and the basal confuciusornithid *Eoconfuciusornis zhengi* (Zhang *et al.* 2008); hence the Jehol records approximately 11 million years of this Early Cretaceous avifauna (Zhou 2006; Zhang *et al.* 2008).

Not only have fossil birds been unearthed from these sediments, but also a rich biota of fossil plants, insects and other invertebrates, fish, amphibians, pterosaurs, mammals and non-avian dinosaurs (Zhou *et al.* 2003). Recent discov-

eries of new avian taxa have, however, benefited from the surge of palaeontological activity in the Jehol region; the collecting process is much more methodical and meticulous. Because newly discovered fossils tend to be more complete and better prepared than earlier finds, they have the potential to reveal more anatomical information (Zhou *et al.* 2008). Although the discovery of new forms is not unexpected, the paucity of new specimens that can be referred to already known taxa is surprising; unlike more basal birds, such as *Confuciusornis sanctus* and, to a lesser degree, *Sapeornis chaoyangensis* and *Jeholornis prima*, most Jehol ornithothoracine birds are not known from multiple specimens (Zhou & Zhang 2003a, b; Chiappe *et al.* 2008). This may reflect the fact that many of the first ornithothoracine taxa discovered from this area were initially based on very incomplete holotype specimens (i.e. *Boluochia zhengi*, *Liaoningornis longidigitrus*, *Chaoyangia beishanensis*) (Hou & Zhang 1993; Zhou 1995; Hou 1997). With a very limited understanding of Early Cretaceous enantiornithine morphology and diversity, much initial identification, although generally accurate at the time, must now be reinterpreted in the light of new knowledge and additional comparative data. Here, using knowledge of the currently known avifauna to reappraise *B. zhengi*, we reveal new information and elucidate the phylogenetic relationships of this poorly known taxon.

Boluochia zhengi was one of the earliest enantiornithines to be named from the Jehol Group (Zhou 1995). Because the holotype and only known specimen is very incomplete, this

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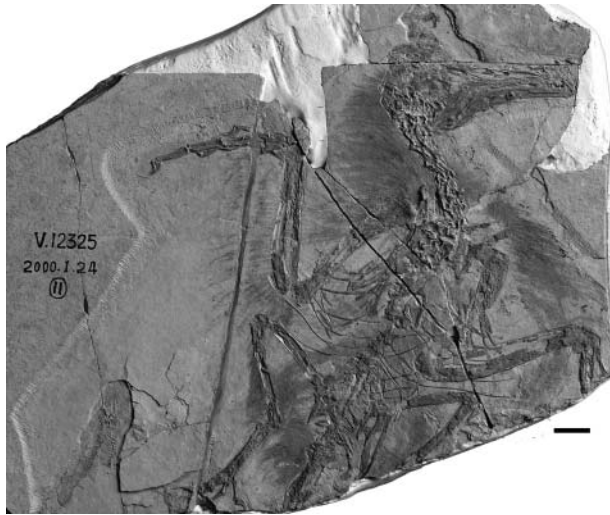


Figure 1. Photograph of the holotype of *Longipteryx chaoyangensis* (IVPP V12325). Scale bar represents 1 cm.

taxon has typically been excluded from phylogenetic analyses and other forms of comparative research (Chiappe *et al.* 2006; O'Connor *et al.* 2009; Zhou *et al.* 2009). Attention on *B. zhengi* has been focused instead on its purported rostral specializations (e.g. the presence of an edentulous, hooked premaxilla). The holotype is a single slab on which most bones are preserved as impressions; a mould that replicates the bones in positive relief was prepared for the purpose of this study. Our reassessment of this fragmentary specimen now suggests that this taxon is in fact closely related to the much more complete and well-known *Longipteryx chaoyangensis* Zhang *et al.* 2000 (Fig. 1) and is a member of the most speciose clade of Early Cretaceous enantiornithines, the Longipterygidae (Zhang *et al.* 2000; O'Connor *et al.* 2009). Here we re-describe the holotype specimen of *B. zhengi*, emphasizing comparison with contemporary longipterygids.

Institutional abbreviations

DNHM: Dalian Natural History Museum, Dalian, China;
IVPP: Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China.

Background information

Boluochia zhengi is currently known from a single, incomplete specimen (IVPP V9770) collected at the Xidagou locality of the Jiufotang Formation near Boluochi, Chaoyang, in Liaoning Province. IVPP V9770 preserves the voids of parts of the skull and sternum bones, the caudal half of the axial skeleton, and the pelvic girdle and hindlimbs. The voids of the bones in IVPP V9770 are largely overlap-

ping, which further obscures the morphology of this bird (Figs 2, 3).

The original study of *B. zhengi* was further hindered by the limited information available regarding the anatomy of enantiornithines during the mid-1990s. Despite this, *B. zhengi* was the first enantiornithine from the Jehol Group to be recognized as such (Zhou 1995); the specimen was referred to this clade on the basis of a reduced metatarsal IV, a proximally located dorsal process of the ischium, a narrow intercondylar incisure of the tibiotarsus, and slender outer (lateral) sternal trabeculae (Zhou 1995). IVPP V9770 was further distinguished from other enantiornithine taxa known at the time on the basis of its hooked beak, the concave surface between the premaxillary corpus and the nasal processes (processus frontalis), a small lateral expansion of the outer trabeculae of the sternum, and because metatarsals II–IV are approximately equal in their distal extent (Zhou 1995). This original diagnosis was subsequently updated in light of more recent discoveries of other enantiornithines; the most current iteration (Zhou & Zhang 2006) differentiates *B. zhengi* from all other enantiornithines by the absence of premaxillary teeth, the presence of a rostrally hooked premaxilla, a narrow intercondylar incisure on the tibiotarsus, tibiotarsal condyles that are approximately equal, a medial tibiotarsal condyle with a flat cranial margin in distal view, metatarsals II–IV that are subequal in length and extend distally to approximately the same level, and a trochlea for metatarsal II that is wider than those of metatarsals III and IV (Zhou & Zhang 2006). Because most of the skull in this specimen is missing, whether or not *B. zhengi* possesses the rostral elongation that characterizes other known longipterygids cannot be determined. Furthermore, because of its poor preservation, interpretations of some other areas of the specimen are equivocal. Nevertheless, as discussed below, *B. zhengi* is still considered a valid taxon, although several of its ‘diagnostic’ features are reinterpreted here.

In contrast to *B. zhengi*, *L. chaoyangensis* is known from several, nearly complete, single-slab specimens (including a subadult), all of which are preserved as recrystallized bone that has been crushed (Zhang *et al.* 2000) (Fig. 1). The published specimens and referred materials all come from localities around Chaoyang, Liaoning, approximately 50 km from the Boluochi locality where *B. zhengi* was found (Zhang *et al.* 2000; Zhou & Hou, 2002; Gao, C-H. personal communication 2010). At the time of its description, the rostrum of *L. chaoyangensis* was considered elongate relative to other known enantiornithines, and unique in that it possesses large, recurved teeth only in its premaxilla and rostral portion of the dentary. This rostral elongation and unique dental pattern suggests that *L. chaoyangensis* was specialized for a piscivorous feeding niche (Zhang *et al.* 2000); this taxon was the first recognized enantiornithine to possess a major morphological innovation

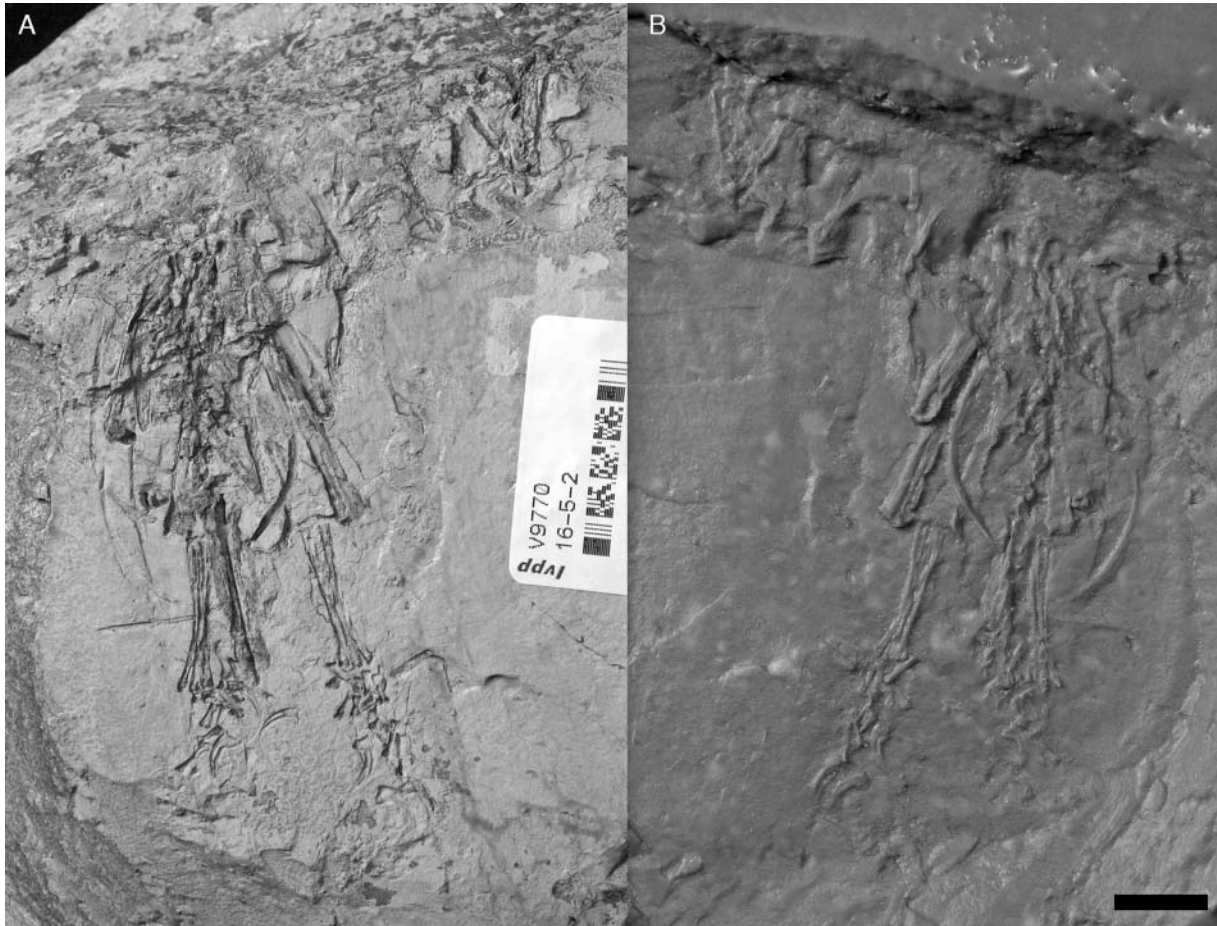


Figure 2. Photographs of the holotype of *Boluochia zhengi* (IVPP V9770). **A**, slab; **B**, mould. Scale bar represents 1 cm.

associated with a particular trophic specialization, with its rostral elongation paralleling adaptations seen within crown group Aves.

Following this discovery, another enantiornithine from the Jehol Group was reported with a similar elongated rostrum and rostrally restricted dentition, but this time from the stratigraphically lower Yixian Formation (Hou *et al.* 2004). The similarity in rostral morphology suggested that the new taxon, *Longirostravis hani* Hou *et al.*, 2004, may be related to the previously discovered *L. chaoyangensis* (Chiappe *et al.*, 2006); however, major morphological differences in the sternum and manus suggest that *Longirostravis hani* is more derived despite its older geological age (Chiappe *et al.* 2006; O'Connor *et al.* 2009). Nevertheless, these taxa were resolved together in a clade of rostrally specialized enantiornithines, Longipterygidae (Zhang *et al.* 2000; Chiappe *et al.* 2006; O'Connor *et al.* 2009). The presence of the more derived longipterygid in the older formation of the Jehol suggested that this clade has further diversity yet to be found. This hypothesis was confirmed with the subsequent discoveries of *Shanweinia cooperorum*

O'Connor *et al.*, 2009 and *Rapaxavis pani* Morschhauser *et al.*, 2009, although morphology aligns these new taxa more closely with *Longirostravis hani* than *L. chaoyangensis*. Currently, primitive longipterygids (forms comparable to *L. chaoyangensis*) are unknown from the Yixian Formation.

Longipterygidae is not only supported by observed morphological similarities among taxa, but also receives unambiguous support in phylogenetic studies (Chiappe *et al.* 2006; O'Connor *et al.* 2009). The clade has been resolved in several cladistic analyses, including one that incorporated all four longipterygids recognized at the time (O'Connor *et al.* 2009). As a result, Longipterygidae is the most diverse subclade currently recognized within the Jehol avifauna and one of the only enantiornithine clades that consistently receives phylogenetic support. The fact that this clade is so diverse may reflect the ease with which synapomorphies (i.e. elongate rostra and rostrally restricted teeth) can be recognized; it may also suggest that the elongation of the rostrum in this lineage facilitated greater diversification.



Figure 3. Interpretative drawing of the holotype specimen of *Boluochia zhengi* (IVPP V9770). Scale bar represents 1 cm. Anatomical abbreviations: c2?, possible claw of second digit; den?, possible dentary fragment; fe, femur; il, ilium; isc, ischium; mt1, metatarsal I; mt4, metatarsal IV; ot, outer trabeculae; pmx, premaxilla; pub, pubis; pyg, pygostyle; stn, sternum; tbt, tibiotalus; th, tooth; tmt, tarsometatarsus; xp, xiphoid process.

Morphological reassessment and comparison

The holotype of *B. zhengi* was studied from the original slab as well as from a mould (Fig. 2). Despite preservational

limitations, the morphology that can be observed suggests a close relationship between this taxon and *L. chaoyangensis*. From the preserved material, the two taxa cannot be differentiated except in size, with *B. zhengi* being smaller, falling outside the known size range of *L. chaoyangensis* (Table 1),

Table 1. Selected measurements of known longipterygids. An asterisk denotes estimated measurements; parentheses indicate incomplete elements. All measurements are taken from the holotype specimens, with the exception of the subadult *Longipteryx chaoyangensis*, IVPP V12552.

	<i>Boluochia zhengi</i>	<i>Longipteryx chaoyangensis</i>	<i>Longipteryx chaoyangensis</i> subadult	<i>Shanweinia cooperorum</i>	<i>Rapaxavis pani</i>	<i>Longirostravis hani</i>
Sternum, L	(18.9)	(19)	25.7	(11.7)	16.2	16.3
Ilium, post-acetabulum	7.5*	10.5	8*	—	4.8*	6.1*
Ischium	17	19.7	17.7	—	14	10*
Pubis	25.15	28.2	22.4	18.2*	19.3	19.8
Pygostyle	21.5	24*	24.5	12.4	14.5	13
Tibiotarsus	(24.3)	30.1	29*	22.7	24.5*	25.1
Tarsometatarsus	17.4L – 17.7R	20	19.2	11.8	13.4	13.7

and a difference in the morphology of the tarsometatarsus. As a result of this difference in size, extensive comparisons are made here with a juvenile specimen of *L. chaoyangensis* and the several smaller known longipterygids (*Longirostravis hani*, *R. pani* and *S. cooperorum*).

Skull

The skull of the holotype of *B. zhengi* is largely incomplete, preserving only part of the premaxilla and fragments of the nasal and dentary (Figs 4A, B). The only element that can be clearly identified is the premaxilla. Preservation in this region is extremely poor, which resulted in the identification of a hooked bill and other morphologies not actually present. The premaxilla is missing the caudal half of the nasal process and the maxillary process is damaged (Figs 4A, B). As in *L. chaoyangensis* (Figs 4C, D) and other longipterygids, the dorsal and ventral margins of the premaxillary corpus are nearly parallel, forming a long imperforate region before diverging into nasal and maxillary processes (Fig. 4). In enantiornithines that do not possess an elongated rostrum, the premaxillary corpus is short, and the dorsal and ventral margins are not parallel (e.g. *Cathayornis yandica*, *Eoenantiornis buhleri*, *Pengornis houi*) (O'Connor & Chiappe forthcoming). This strongly suggests that the rostrum was elongate in *B. zhengi*.

In *B. zhengi*, the region immediately rostral to the nasal process was described as slightly concave dorsally (Zhou 1995) (Figs 4A, qB). Although this cannot be determined in the holotypes of *L. chaoyangensis* (IVPP V12325) or *S. cooperorum* because of the preservation, a juvenile referred specimen of *L. chaoyangensis* (IVPP V12552) with a well-preserved rostrum has the same slight concavity (Fig. 4C). On closer inspection this morphology is also present in *Longirostravis hani* and *R. pani*, although less defined in the delicate rostrum of the former and exaggerated by crushing in the latter (Hou *et al.* 2004; Morschhauser *et al.* 2009). In *B. zhengi*, the margins of the premaxilla appear abraded in this region; this morphology is therefore rein-

terpreted as present but slightly exaggerated. The rostral-most tip of the premaxilla in *B. zhengi* appears slightly sharper than that of *L. chaoyangensis*, which we consider an artefact of poor preservation; the distinct hook previously considered characteristic of this taxon, and unique among known enantiornithines, is absent in this taxon (*contra* Zhou 1995).

As described by Zhou (1995), the maxillary process of the premaxilla in *B. zhengi* is long and tapers sharply whereas the nasal process is robust and rod-like; both of these features are also present in *L. chaoyangensis* (Zhang *et al.* 2000) (Fig. 4). These morphologies are also shared by other longipterygids, although the morphology of the premaxillary processes are less clear in *S. cooperorum* and *Longirostravis hani* (Hou *et al.* 2004; O'Connor *et al.* 2009). In contrast with earlier claims that *B. zhengi* may have an edentulous premaxilla, we interpret the recurved and tapering structures protruding from the ventral margin of the premaxilla as teeth. Only one tooth clearly preserves its morphology but we estimate that four teeth were present (Figs 4A, B). The large size and curvature of the teeth in *B. zhengi* are consistent with those of *L. chaoyangensis*, whereas the teeth in *S. cooperorum* and *Longirostravis hani* are proportionally much smaller and more 'peg-like' (Hou *et al.* 2004; O'Connor *et al.* 2009). In *B. zhengi*, the teeth appear to be more caudally inclined than in *L. chaoyangensis*, however, given the nature of the preservation of IVPP V9770, we cannot tell if this is an actual morphology or an artefact of preservation (Fig. 4). Just ventral to the distal end of the preserved nasal process of the premaxilla, two small bone fragments are present, interpreted as the sharply tapering rostral ends of the nasal premaxillary processes (Figs 4A, B). Other known longipterygids possess schizorhinal nostrils in which the nasals lack a descending maxillary process (O'Connor & Chiappe forthcoming) (Figs 4C, D); this morphology cannot be confirmed in *B. zhengi* but may also have been present. Ventral to the proximal end of the preserved premaxilla, a fairly large, straight bone fragment is preserved, interpreted as the rostral end

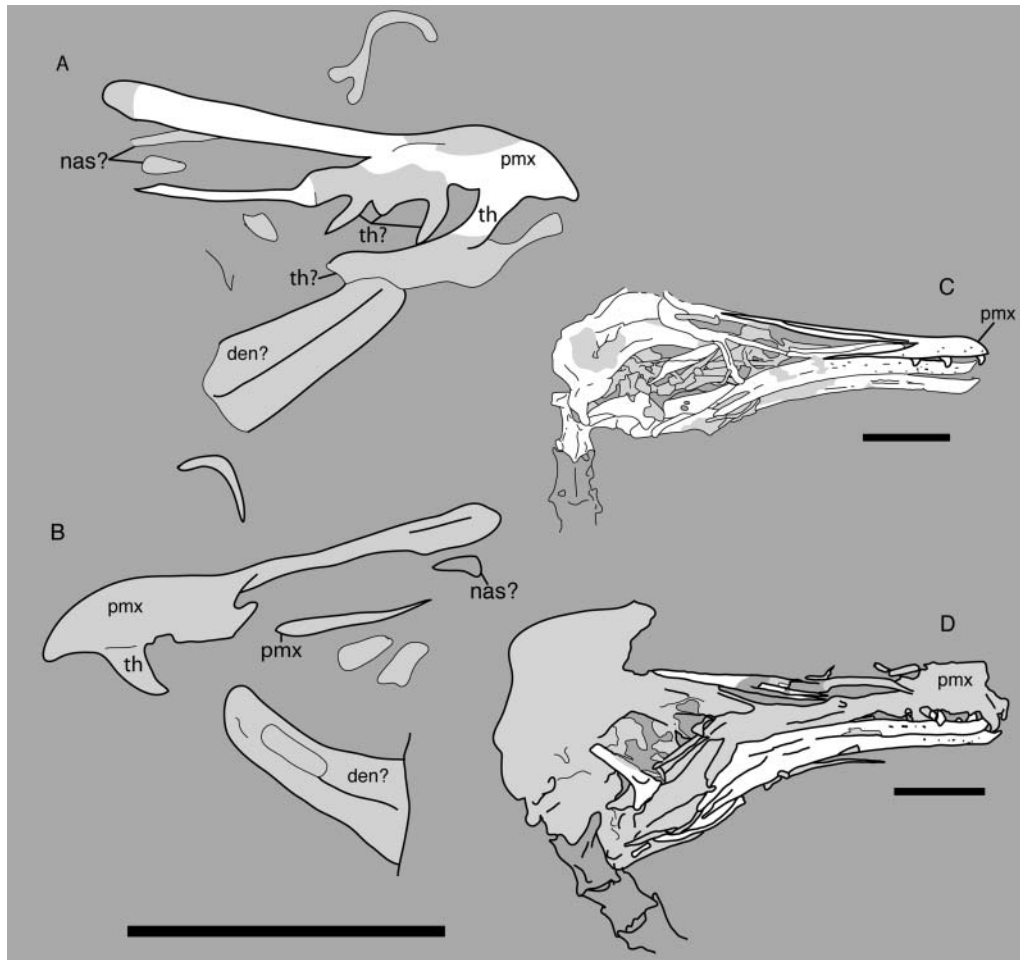


Figure 4. Camera lucida drawings of skulls. **A, B**, *Boluochia zhengi*, IVPP V9770; **A**, from slab; **B**, from cast. **C**, *Longipteryx chaoyangensis*, IVPP V12552; **D**, *Longipteryx chaoyangensis*, IVPP V12325 (holotype). Scale bars all 1 cm; same scale for A and B. Anatomical abbreviations: den?, possible dentary fragment; nas?, possible nasal fragments; pmx, premaxilla; th, tooth; th?, possible tooth.

of the dentary (Figs 4A, B). A single dentary tooth was reported to be present, but this cannot be confirmed (*contra* Zhou 1995); the rostral-most end of the dentary preserves a dorsal projection that may represent a single tooth but this region is poorly preserved and difficult to interpret (Figs 4A, B).

Axial skeleton

The vertebral column of *B. zhengi* is nearly entirely preserved, starting with the synsacrum, although overlap and poor preservation of bones provides virtually no anatomical information (Figs 2, 3). The pygostyle is the only vertebral element for which information can be obtained (Fig. 3); although preservation is unclear, its shape appears typical of other enantiornithines (e.g. *C. yandica*, *Halimornis thompsoni*, *L. chaoyangensis*, *Sinornis santensis*) (Zhou *et al.* 1992; Chiappe *et al.* 2002; Sereno *et al.* 2002). The presence of a dorsal fork cannot be determined, although ventrolaterally projecting lateral processes

and a distal constriction are clearly present (Chiappe & Walker 2002). What is distinct about the pygostyles in both *B. zhengi* and *L. chaoyangensis* (Figs 1, 3), relative to other enantiornithines, is their unusual size and robustness. The pygostyle is shorter than the tarsometatarsus in *Longirostris hani*, approximately equal in length in *S. cooperorum* and 10% longer in *R. pani* (we use the tarsometatarsus for comparison because of preservational limitations in the *Boluochia* holotype, acknowledging that the proportions of the tarsometatarsus vary slightly between taxa; see Table 1 for comparative measurements of longipterygids). In *B. zhengi* and *L. chaoyangensis*, in contrast, the pygostyle is 20% longer than the tarsometatarsus and very robust when compared with other enantiornithines in which the pygostyle is typically shorter and narrower than the tarsometatarsus (e.g. *Dapingfangornis sentisorhinus*, *Vescornis hebeiensis*, *E. buhleri*,) (Chiappe & Walker 2002; Zhang *et al.* 2004; Zhou *et al.* 2005; Li *et al.* 2006) (Figs 1, 3).

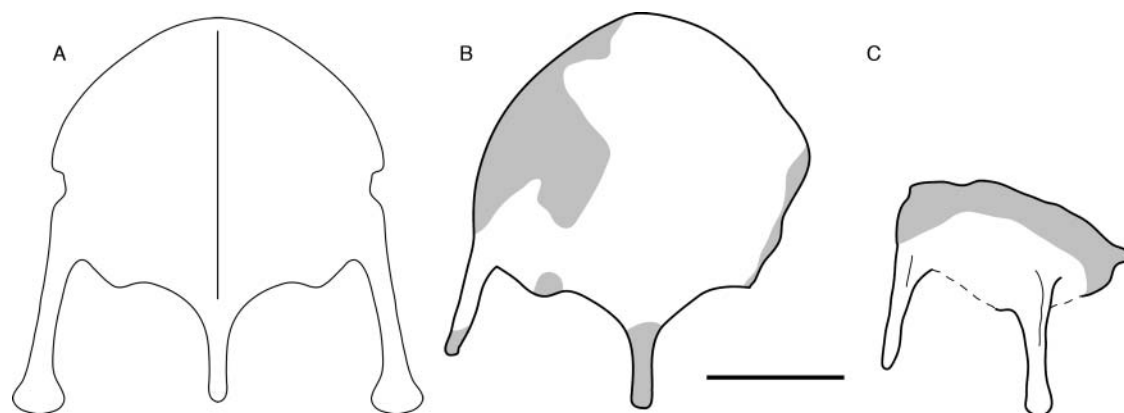


Figure 5. Longipterygid sterna. **A**, reconstruction of the sternum of *Longipteryx chaoyangensis* based on IVPP V12325; **B**, preserved sternum of juvenile *Longipteryx chaoyangensis*, IVPP V12552; **C**, preserved sternum of *Boluochia zhengi*. Scale bar represents 1 cm.

Sternum

Only the distal half of the sternum is preserved in *B. zhengi*, and what is present is extremely poorly preserved (Figs 3, 5). The xiphoid process (xiphial region) and strap-like outer trabeculae are consistent with morphologies seen in *L. chaoyangensis* in that the trabeculae are slightly splayed laterally and the caudal end of the xiphoid process is simple and blunt (Fig. 5A). Distal expansions of the outer trabeculae, present in *L. chaoyangensis* and other taxa (e.g. *C. yandica*, *Concornis lacustris*) (Sanz & Buscalioni 1992), are either not preserved in the holotype of *B. zhengi* or were absent in this species (Fig. 5C). They are also not preserved in the juvenile *L. chaoyangensis* (IVPP V12552; Fig. 5B), which suggests that this feature develops during the course of ontogeny; this, however, remains purely speculative in the absence of a more complete growth series. Unlike the morphology preserved in *B. zhengi*, in *Longirostravis hani* the medial margins of the outer trabeculae are strongly concave and the xiphoid process is expanded slightly and has a flat caudal margin. The outer trabeculae of *R. pani* and *S. cooperorum*, although less clearly preserved in the latter, are oriented caudally as opposed to caudolaterally (as in *B. zhengi* and *L. chaoyangensis*) (Morschhauser *et al.* 2009; O'Connor *et al.* in press).

Pelvis

The pelvic girdle is preserved in near articulation at the level of the acetabulum in the holotype specimens of both *B. zhengi* and *L. chaoyangensis* (Figs 2, 3). However, comparisons are limited by the large overlap between elements in the former. Only the postacetabular wing of the ilium is clearly preserved in both specimens; this wing is triangular and tapers distally. Although proportions cannot be compared between the two holotypes, in both *B. zhengi* and *L. chaoyangensis* the ischium is long and strap-like and has a proximally located dorsal process, as is typical of other enantiornithines (Chiappe & Walker 2002). The

distal ends of the ischia in *B. zhengi* approach and appear to contact each other (Figs 2, 3), a morphology that cannot be confirmed in *L. chaoyangensis* (Fig. 1), but that is also present in the longipterygid *R. pani* (O'Connor *et al.* in press). In both *B. zhengi* and *L. chaoyangensis*, the pubis is gently curved caudodorsally so that its ventral margin is convex (Figs 1, 3). In *B. zhengi* and most other enantiornithines the entire pubic shaft is gently curved; the proximal portion of the pubis in *L. chaoyangensis*, however, is relatively straight (Fig. 1). The poor preservation of the pubis in IVPP V9770 prevents the use of this character to further differentiate *B. zhengi* and *L. chaoyangensis*. The pubis of *R. pani* was described as kinked mid-shaft rather than curved (Morschhauser *et al.* 2009); however, we reinterpret this morphology as being broadly concave dorsally throughout (O'Connor *et al.* in press). The distal end of the pubis in *B. zhengi* has a boot-like expansion that appears fairly large, tapered distally, and oriented nearly perpendicular to the long axis of the pubis, as is typical of other Early Cretaceous enantiornithines (Serenó & Rao 1992; Zhang *et al.* 2000; Morschhauser *et al.* 2009).

Hindlimbs

In the holotype of *B. zhengi*, both hindlimbs are preserved in their entirety; however, the only element preserved clearly on both sides is the tarsometatarsus. The voids of the proximal bones of the legs are heavily damaged and obscured by overlap with other elements (Fig. 2). The femora provide no anatomical information and the deep longitudinal groove mentioned by Zhou (1995) is reinterpreted here as a preservational artefact. The proximal end of neither tibiotarsus reveals any anatomical information; distally the tibiotarsi are also poorly preserved but no longer overlap with other elements (Fig. 3). The size and proportions of the distal condyles have been described previously (Zhou 1995) but the specimen is reinterpreted here as preserved in caudal view so these morphologies are in fact equivocal (Figs 3, 6).

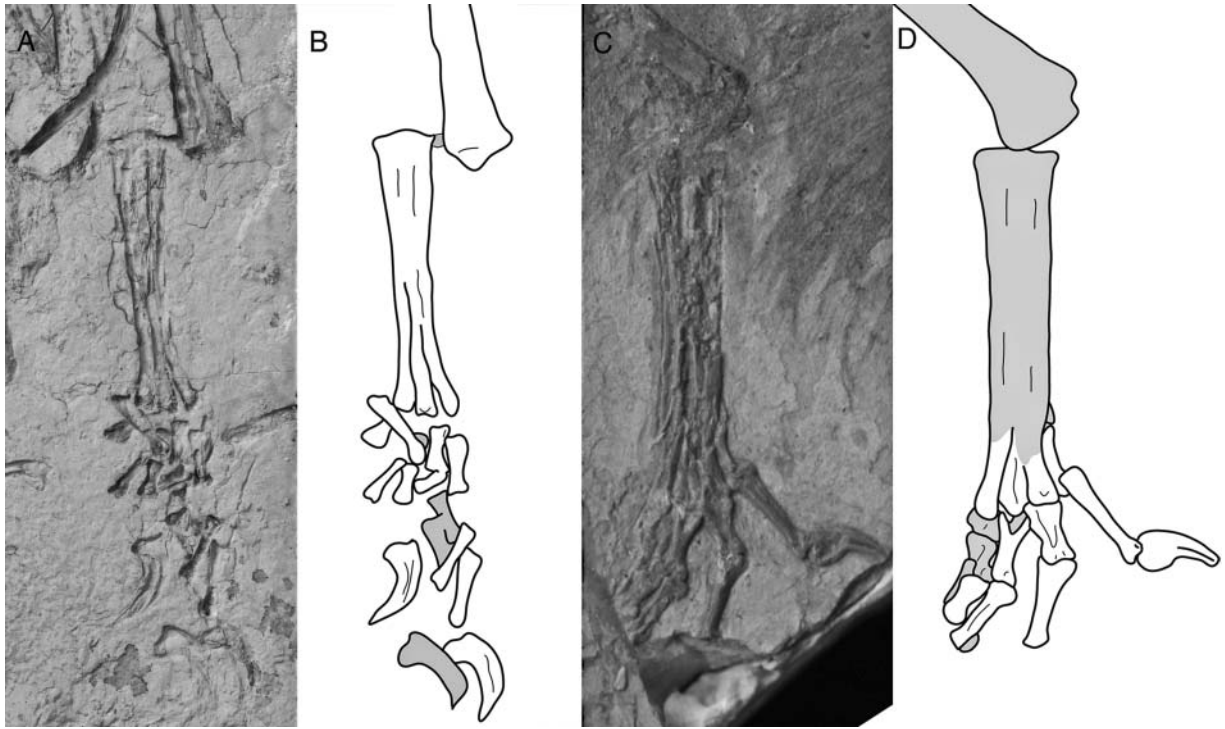


Figure 6. Photographs and interpretive drawings of left ankles and feet: **A, B**, *Boluochia zhengi*, IVPP V9770; **C, D**, *Longipteryx chaoyangensis*, IVPP V12325.

In caudal view, the medial condyle appears to be larger than the lateral condyle on the right tibiotarsus (Fig. 7) and subequal on the left (Fig. 6). The morphology is unclear in both the slab and the mould because of the incomplete removal of bone from the voids, however, it appears that fusion was not complete in IVPP V9770. The proximal tarsals can be distinguished from the tibia on the right tibiotarsus in caudal view, where the tarsals cap the tibia forming the caudodistal and distal margins of the tibiotarsus (Fig. 7).

Both tarsometatarsi are completely preserved in IVPP V9770 (Figs 2, 3, 6); although it appears that there was some degree of proximal fusion between the distal tarsals and metatarsals, preservation makes interpretation difficult. The distal tarsals form a single element that caps the proximal ends of the metatarsals; the metatarsals are poorly co-ossified if at all, and can still be distinguished (Figs 6, 7). A similar morphology is preserved in *R. pani*, in which the distal tarsals appear fully fused into a single cap, but fusion is absent between the tarsal cap and the metatarsals and between the metatarsals themselves (O'Connor *et al.* in press). As such, these two specimens provide direct evidence for the presence of a tarsal cap in Enantiornithes (*contra* Martin 1987). The apparently incomplete fusion of the tibiotarsus and tarsometatarsus may suggest that IVPP V9770 is not fully mature, although with no significant bone fragments preserved a histological analysis can never be conducted to confirm this hypothesis.

The morphology of the tarsometatarsus in both *B. zhengi* and *L. chaoyangensis* is unique compared with the typical enantiornithine condition, in which metatarsal III is the longest, followed by IV and II (e.g. *Avisaurus*, *Concornis lacustris*, *Pengornis houii*, *Sinornis santensis*) (Chiappe & Walker 2002; Zhou *et al.* 2008). In *B. zhengi* and *L. chaoyangensis*, in contrast, metatarsal IV slightly exceeds

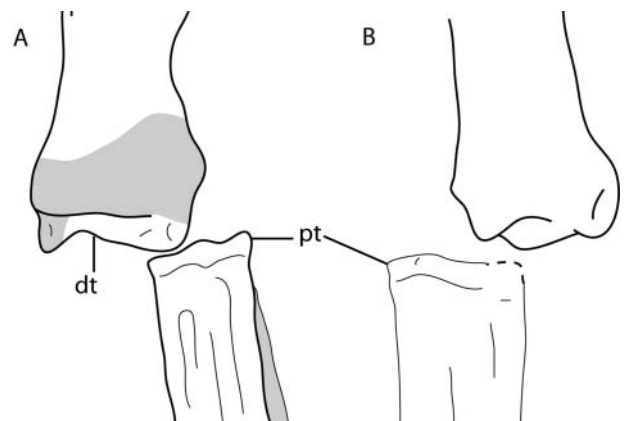


Figure 7. Interpretive drawing of the right ankle of *Boluochia zhengi* (IVPP V9770), illustrating the incomplete fusion of the tarsals and the presence of a tarsal cap. **A**, from slab; **B**, from mould. Anatomical abbreviations: dt, distal tarsals; pt, proximal tarsals.

III in length, followed by metatarsal II, which is the shortest (Fig. 6). This configuration is currently known among Early Cretaceous birds only in these two taxa. *Longirostravis hani*, *R. pani* and *S. cooperorum* possess similar morphologies but are more comparable to other enantiornithines; in these specimens, metatarsal III is longer than IV, which exceeds II in distal projection. In all longipterygids, the trochlea of metatarsals II and IV extends beyond the proximal surface of the metatarsal III trochlea such that they articulate at nearly the same level, as opposed to taxa in which metatarsals II and IV end at the proximal end of the metatarsal III trochlea, so that there is a significant difference in length between metatarsals II and IV, and III (e.g. *Avisaurus*, *P. houi*, *Soroavisaurus australis*) (Chiappe & Walker 2002; Zhou *et al.* 2008). In modern birds, in which the metatarsals distally terminate at the same level, this configuration is usually indicative of a perching ecology (Zhang 2006). Together with the specialized rostral morphology of these specimens, this suggests that *B. zhengi* and *L. chaoyangensis* may have been piscivores well-suited for arboreal lifestyles, similar to modern kingfishers. Although specialized arboreal pedal proportions have been observed in some other Early Cretaceous enantiornithines (Hopson 2001), the pedal proportions of the longipterygid *R. pani* are farther along this spectrum than other known enantiornithines because of the proportionally longer distal phalanges (Morschhauser *et al.* 2009). However, the presence of specialized pedal proportions cannot be inferred directly from the holotypes of either *B. zhengi* or *L. chaoyangensis* because of disarticulation and lack of preservation (Figs 1, 2).

Boluochia zhengi differs from *L. chaoyangensis* and all other known enantiornithines in that the distal end of metatarsal IV is deflected laterally such that metatarsals III and IV are separated for the distal one-fifth of their lengths (Fig. 6). This is not considered a diagenetic artefact because of the similar appearance of both the right and left tarsometatarsi in the holotype. In *L. chaoyangensis* the metatarsals, though unfused, contact each other along their entire lengths, even in the juvenile specimen (IVPP V12252), which suggests that this is not an ontogenetic feature in the *B. zhengi* holotype. Furthermore, the tarsometatarsus is an element that ossifies early during the ontogeny of precocial birds including enantiornithines (Starck & Ricklefs 1998; Starck & Chinsamy 2002). Although its precise ontogenetic stage is unknown, given that IVPP V9770 is not a hatchling, we consider the morphology of the tarsometatarsus unlikely to change further with age.

The first metatarsal is known to show considerable variation within Enantiornithes, ranging from straight in some taxa (*R. pani*) (O'Connor *et al.* in press), to strongly J-shaped in others (avisaurids) (Chiappe & Walker 2002). The first metatarsals are preserved in the holotype specimens of both *L. chaoyangensis* and *B. zhengi* and display

identical morphologies. The first metatarsal is preserved disarticulated on the right foot of *B. zhengi* (Fig. 3) and in articulation with the medial surface of the left metatarsal II in *L. chaoyangensis* (Fig. 1). The bone is straight proximally, distally expanding caudomedially so that it is shaped like an inverted P. In other longipterygids this element is poorly preserved, with the exception of the holotype of *R. pani* in which it appears to be straight (*contra* Morschhauser *et al.* 2009).

The preserved unguis in IVPP V9770 are fairly large and heterogeneous. One claw is clearly more robust than the others, although disarticulation of the toes makes it difficult to determine which digit it belongs to (Fig. 3). Only the hallux claw is preserved in the holotype of *L. chaoyangensis*, but the feet are completely preserved in the juvenile specimen IVPP V12252. In this specimen it is clear that the same unguis heterogeneity also characterizes *L. chaoyangensis*, and that the robust claw belongs to the second digit.

Discussion

Boluochia zhengi shares a number of morphologies with *L. chaoyangensis*—premaxilla with elongate and imperforate rostral portion, large recurved teeth, robust nasal processes, large and robust pygostyle, laterally splayed outer trabecula of the sternum, metatarsal I 'p'-shaped, and metatarsals II–IV subequal in length—that suggest the two taxa are closely related. Despite these features, the holotype of *B. zhengi* can be differentiated from *L. chaoyangensis* by the lateral deflection of the distal end of metatarsal IV (Fig. 6). For this reason, we consider *B. zhengi* to be a distinct taxon but because it shares several of the synapomorphies that unite longipterygids, we feel justified in assigning *B. zhengi* to this diverse clade. The following new synapomorphies of Longipterygidae are recognized: premaxilla with elongate imperforate rostral end; dorsal surface of premaxilla with a slight concavity rostral to the nasal processes; pygostyle subequal to, or larger than, the tarsometatarsus; trochlea for metatarsals II and IV extending beyond the proximal surface of the trochlea for metatarsal III.

Because *B. zhengi* was published 5 years before *L. chaoyangensis*, the 'first discovered longipterygid' paradoxically does not preserve the characteristic 'longirostrine' skull morphology. Although the premaxillary morphology preserved in *B. zhengi* does leave clues as to the presence of an elongate rostrum, this could not have been determined until the subsequent discovery of more complete longipterygids, which rendered synapomorphies of the clade apparent. In addition, although *B. zhengi* was named earlier, higher level taxonomic names (Boluochiformes, Boluochidae) were erected after Longipterygidae and Longipterygiformes so the latter names have priority

over all other clade names that have been proposed (Zhou & Zhang 2006).

Systematic palaeontology

Enantiornithes Walker, 1981

Longipterygidae Zhang *et al.*, 2000

Stratigraphical distribution. Yixian and Jiufotang formations of the Jehol Group, Lower Cretaceous, 125–120 million years ago (Swisher *et al.* 2002; He *et al.* 2004; Zhu *et al.* 2007).

Geographical distribution. Chaoyang, Lingyuan and Yixian, western Liaoning Province, northeastern China.

Revised diagnosis. Small to medium-sized enantiornithine birds with the rostral portion of the skull equal to, or exceeding, 60% of the total skull length; premaxilla with elongate imperforate rostral end with parallel dorsal and ventral margins; dorsal surface of premaxilla with slight concavity just rostral to the nasal processes; dentition restricted to the premaxilla and rostral-most portion of the dentary; coracoid with nearly straight lateral margin; pygostyle approaches or exceeds tarsometatarsus in length; trochleae of metatarsals II and IV extend beyond proximal surface of metatarsal III trochlea (modified from O'Connor *et al.* 2009).

Boluochia zhengi Zhou, 1995

Revised diagnosis. A small enantiornithine bird characterized by the unique combined presence of the following morphologies: premaxilla rostral to external nares imperforate with parallel dorsal and ventral margins; dorsal surface of premaxilla with slight concavity just rostral to the nasal processes; premaxilla with large, recurved teeth; large and robust pygostyle 20% longer than tarsometatarsus; metatarsals II–III subequal in length and ending distally at approximately the same level; metatarsal IV longer than II and III and laterally deflected along the distal one-fifth of the tarsometatarsus (modified from Zhou & Zhang, 2006).

Mesozoic avian taxonomy

We have provided evidence that *B. zhengi* is closely related to *L. chaoyangensis*, but maintain the taxa as distinct genera not only for taxonomic simplicity but because the two taxa can be distinguished by osteological differences. Among living birds, species within a genus are typically distinguished by behaviour, DNA and other differences that do not typically fossilize, and even in living taxa were not apparent until the advent of more advanced observational techniques (Amadon 1963; Isler *et al.* 1999; Zimmer & Whittaker 2000). Within avian fossil taxonomy, species-level distinctions will always have a degree of ambiguity (O'Connor & Dyke 2010).

We do not present a phylogenetic analysis with which to support our morphological observations because of the incompleteness of the *B. zhengi* holotype. Enantiornithine inter-relationships are notoriously difficult to unravel (Chiappe *et al.* 2006; Chiappe & Walker 2002) because of the incompleteness of many of the named taxa (nearly half of all taxa are known from a single bone or less) (O'Connor 2009), and the extreme morphological similarity that characterizes the clade. A recent cladistic analysis sampled every known valid enantiornithine, including *B. zhengi* and *L. chaoyangensis*, but resulted in an almost complete lack of resolution, supporting neither a longipterygid clade nor a relationship between *B. zhengi* and *L. chaoyangensis* (O'Connor 2009). Conservative phylogenetic analyses have typically not included *B. zhengi* because the only known specimen is so fragmentary. Therefore, pending new, more complete discoveries of *B. zhengi*, the phylogenetic position of this taxon relative to *L. chaoyangensis* is inferred based on preserved morphology alone.

Currently there are a large number of names that refer to included species of 'Longipterygidae' at various taxonomic levels (i.e. Boluochidae, Boluochiformes, Longirostravisidae, Longirostravisiformes). We have discussed why Longipterygidae and Longipterygiformes take priority; however, because we use Linnaean terminology we feel a discussion of the implications of their usage is also necessary. Here we follow O'Connor *et al.* (2009) and use the name Longipterygidae to refer to the clade formed by the most common ancestor of *Longirostravis hani* and *L. chaoyangensis* and all its descendants. Although no Linnaean taxonomic categorical level was explicitly applied to this term by O'Connor *et al.* (2009), the ending denotes a familial relationship between included taxa. The amount of morphological disparity encapsulated by extant families differs throughout Aves. Although we use this name, we recognize that the fairly large variation among longipterygid taxa (e.g. hand reduced vs unreduced, major morphological differences in the sternal trabeculae, caudal rectrices present or absent) could be argued as indicative of a family-level or even order-level relationship.

Although Longipterygidae is one of few enantiornithine clades resolved in multiple cladistic analyses (which only include the most complete taxa), support (although unambiguous) is often weak (limited to one or two characters) and published analyses differ in the taxa included and their relative placement (Chiappe *et al.* 2006; Cau & Arduini 2008; O'Connor *et al.* 2009); new fossils continue to add to the diversity and change the resultant phylogenetic hypotheses. For example, a recent phylogenetic study suggested that smaller longipterygids, especially *R. pani* and *Longirostravis hani*, form a more exclusive relationship (or clade) (O'Connor *et al.* 2009), a conclusion later not supported in a larger, more inclusive analysis (O'Connor 2009). Given the plasticity between the results of current cladistic analyses,

we find it most parsimonious to await either the discovery of more complete specimens of *B. zhengi* or a well-supported phylogenetic hypothesis before outlining a more definite taxonomic hierarchy. We hope this helps to avoid confusion and the further proliferation of superfluous taxonomic names. Pending a normalization of Mesozoic avian phylogeny, groups of related taxa should simply be referred to as clades.

Early Cretaceous subclade diversity

With the addition of *B. zhengi*, the diversity of Longipterygidae is increased to five taxa, and is the most diverse known clade within Enantiornithes (although there are numerous species assigned to *Cathayornis*, the taxonomy is unsupported; for further discussion on this issue see O'Connor & Dyke 2010). There is markedly greater diversity than that observed in sympatric subclades of ornithothoracine Jehol birds, supporting inferences that enantiornithines were the dominant avian clade during the Cretaceous (Chiappe & Walker 2002; Chiappe 2007). Within the enantiornithine sister clade, Ornithuromorpha, the largest subclade includes three taxa: *Songlingornis linghensis*, *Yanornis martini* and *Yixianornis grabaui* (Clarke *et al.* 2006). The greater diversity of the enantiornithine subclade may simply reflect the ecological dominance of the enantiornithines at that time; alternatively the diversity of this subclade may be high for two reasons. The first and simplest reason is that the synapomorphies of this clade are easily identifiable and a large-scale detailed inspection of all known specimens is not needed to identify clade synapomorphies (with the exception of some fragmentary specimens, as demonstrated here). The higher diversity may also be reflected in the nature of the diagnostic features of the clade: the elongate rostra and unique dental patterns represent trophic specializations that depart from the morphologies of other known enantiornithines (O'Connor & Chiappe forthcoming). This suggests that members of the clade were able to retrieve food items from sources unavailable to other enantiornithines. The diversity of the clade was probably further facilitated by niche partitioning among closely related species within the group; longipterygid taxa preserve a wide range of dental and pedal morphologies that suggest different primary food items and habitats, respectively (O'Connor & Chiappe forthcoming). Longipterygidae also occupies a fairly large range of body sizes (Table 1), another form of resource partitioning. By using otherwise unused resources, longipterygid enantiornithines may have facilitated the speciation of their clade.

Longipterygids are known from the Yixian Formation through the Jiufotang Formation, which spans approximately 5 million years (O'Connor *et al.* 2009). The success and diversity of this clade suggests that trophic specialization was a major factor in the success of early birds, and perhaps, in this clade, second to flight ability, given that numerous adaptations related to the refinement of

flight have been recognized within Longipterygidae, including both skeletal and integumentary specializations. The Jiufotang Formation longipterygid *R. pani* preserves the most reduced manus known within Enantiornithes with a manual formula of 1-2-2-x-x (Morschhauser *et al.* 2009). This taxon also preserves a pair of bizarre bones (paracoracoidal ossifications, O'Connor *et al.* in press) whose location, dorsal to the coracoid–sternum articulation, suggests that they may be related to flight. These features are also known in *Concornis lacustris* (Sanz & Buscalioni 1992), although the absence of preserved skull material in this Spanish enantiornithine prevents the identification of the most obvious characters that could potentially align this taxon with other longipterygids. Although it is not known how these ossifications affected flight, the reduction of the manus certainly increased aerodynamic capabilities in *R. pani* by streamlining the wing and decreasing weight.

Another longipterygid, *S. cooperorum*, preserves the only evidence of an aerodynamic feathered tail within Enantiornithes (O'Connor *et al.* 2009). The morphology of this taxon represents a distinct departure from the typical enantiornithine that either does not have elongate rectrices (Zhou *et al.* 2005) or possesses no more than two or four very elongate display feathers (Zhang & Zhou 2000; Zheng *et al.* 2007). The holotype of *S. cooperorum* preserves more than four rectrices of unknown length (distal ends not preserved) overlapping to form a single surface, a morphology that would have represented a considerable aerodynamic advantage over other known enantiornithine feathered tails (O'Connor *et al.* 2009). The phylogenetic position of *S. cooperorum* suggests that this morphology is derived within the lineage that includes this taxon but excludes more primitive longipterygids (O'Connor *et al.* 2009). Where feathers are preserved, a fan-shaped tail appears absent in all known specimens of *L. chaoyangensis*; the holotype (IVPP V12325) preserves a halo of short feathers without any elongate tail rectrices around the pygostyle. The absence of elongate tail feathers in the basal longipterygid *L. chaoyangensis* is considered a true feature rather than an artefact of preservation, given that several specimens are known. Tail morphologies are unknown for *Longirostravis hani*, *R. pani* and *B. zhengi*. The evolution of advanced aerodynamic features would surely have facilitated the survival of this clade of small birds, especially in a wooded habitat, as inferred for the Jehol (Zhou 2006).

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