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A redescription of Chaoyangia beishanensis (Aves) and a comprehensive phylogeny of Mesozoic birds

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We review the enigmatic *Chaoyangia beishanensis*, one of the earliest birds described from the Jiufotang Formation, north-eastern China, and the first to be identified as an ornithurine (Aves: Ornithothoraces) and thus a member of the clade that includes living birds. A complete discussion of the validity of this taxon, which once included the holotype of *Songlingornis*, is provided, along with a revised diagnosis. The morphology of *Chaoyangia* is described, including extensive comparison with better known, recently discovered ornithurines as well as several other groups of Mesozoic birds (Confuciusornithiformes, Sapeornithiformes, Enantiornithes). Although preserved information is limited, the large number of fused sacral vertebrae and presence of a distal dorsal process on the ischium are among the features supporting early hypotheses that the only known specimen of *Chaoyangia* represents an ornithurine. Unique among ornithurines, *Chaoyangia* possesses two dorsal processes on the ischium, and thus remains a valid taxon. We include this taxon in a cladistic analysis to test morphological hypotheses regarding its systematic position. Although the results of the analysis are highly resolved and support the referral of *Chaoyangia* and *Zhongjianornis* to Ornithurae, support for the tree overall is very low. Recently discovered taxa have blurred the once clear morphological gap separating the two ornithothoracine clades (Ornithurae and Enantiornithes), and thus the increase in taxonomic diversity has caused a decrease in the stability of hypothetical relationships.

Keywords: *Chaoyangia*; Jehol; ornithurine; *Zhongjianornis*; Songlingornithidae

Introduction

Since the first discoveries in the early 1990s, new species, genera, subclades and lineages of archaic birds have continuously been uncovered from the Early Cretaceous lake deposits of the Jehol Group in north-eastern China (Chiappe 2007; Zhou & Wang 2010). This geological unit, which is composed of three formations (lower Dabeigou, middle Yixian and upper Jiufotang), has revealed more Early Cretaceous avian diversity than any other. Within the last three decades alone, the Early Cretaceous Jehol Biota of north-eastern China has produced an unprecedented amount of vertebrate diversity, revealing the feathers of dinosaurs and the largest known Mesozoic mammals, among other spectacular discoveries (Zhou *et al.* 2003). The Jehol biota has been key in revealing the early evolution of Aves, representing the second oldest and most diverse Mesozoic avifauna to date. The Jehol avifauna preserves a number of clades, spanning the entire phylogeny of Mesozoic birds, coexisting in a diverse forested coastal lake habitat. Known uniquely from this biota are Sapeornithiformes, Confuciusornithiformes, Jeholornithiformes (Li *et al.* 2010) (although other long-tailed birds are known in the Late Jurassic from the

Solnhofen Limestones of Germany and the Late Cretaceous from the Maehavaero Formation of Madagascar; Forster *et al.* 1996; Elzanowski 2002; O'Connor & Forster 2010), and the only transitional short-tailed non-pygostylian bird (*Zhongornis haoae*, too poorly known to be placed in a higher taxon; Gao *et al.* 2008). The Jehol avifauna also preserves the earliest record of ornithothoracine birds, including a huge diversity of the dominant Cretaceous enantiornithines and their sister clade, the more derived ornithurine birds (Zhou & Zhang 2006b). The origin and early evolution of the latter clade is of particular significance because this marks the appearance of the lineage leading to all living birds.

Prior to the numerous complete discoveries of basal ornithurines (= Ornithuromorpha) from the Jehol Group, the global record of ornithuromorph taxa was quite sparse, limited to isolated, fragmentary, partial skeletons (e.g. *Ambiortus dejemetvi*, *Gansus yumenensis*, *Patagopteryx deferransi*; Kurochkin 1982; Hou & Liu 1984; Alvarenga & Bonaparte 1992). Although these isolated materials preserved advanced morphologies that indicated their phylogenetic placement within Ornithuromorpha, they did little to help to piece together the biology of the early

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ancestors of modern birds. While specimens from other deposits continue to be largely incomplete (Bell *et al.* 2010), within the last decade the nearly complete discoveries from the Jehol (e.g. *Yanornis martini*, *Yixianornis grabaui*, *Archaeorhynchus spathula*, *Hongshanornis longicresta*, *Jianchangornis microdonta*) have revealed a wealth of morphological information, as well as data concerning the ecology, diet and integument of early members of the clade (Zhou & Zhang 2001, 2005, 2006a; Zhou *et al.* 2004; Zhou *et al.* 2009).

Early discoveries from the Jehol were typically incomplete and poorly prepared compared to more recent discoveries (e.g. *Liaoningornis longidigitrus*, *Boluochia zhengi*, *Cuspirostrisornis houi*; Zhou 1995; Hou 1997a, b; O'Connor *et al.* 2011a). These birds were described and assigned to a particular clade based on the knowledge of early birds available at the time, usually without applying cladistic analysis. However, since these discoveries, a wealth of new knowledge has been accumulated. With new fossils uncovered at such a high rate, very little revision has been conducted on early discoveries despite the potential for new information (O'Connor *et al.* 2011a). Here we review one of the first birds discovered from the Jehol Group, *Chaoyangia beishanensis* (Hou & Zhang, 1993), which later became the first bird from this sequence to be identified as an ornithurine (Hou *et al.* 1996). Despite the lack of clear support and justification, this classification is still widely used today (Zhou & Zhang 2006b; Zhou *et al.* 2008b). In order to better understand this enigmatic taxon, the morphology of the holotype specimen (IVPP V9934) is compared to that of the purportedly closely related taxa *Yixianornis*, *Yanornis* and *Confuciusornis*, as well as new controversial taxa with morphological similarities (e.g. *Zhongjianornis*). We also briefly redescribe *Songlingornis*, and the other specimen formerly assigned to *Chaoyangia*, IVPP V9937. All these taxa are treated together in a single analysis for the first time in order to test hypotheses regarding the phylogenetic position and interrelationships of these species.

Material and methods
Specimens were studied using a Leica S4E microscope. Anatomical nomenclature mainly follows Baumel & Witmer (1993) although 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 the English equivalents of the Latin terms.

Institutional abbreviations
CAGS: Chinese Academy of Geological Sciences, Beijing, China; **IVPP**: Institute of Vertebrate Paleontology and Paleoanthroplogy, Beijing, China; **PKUP**: Peking University Paleontological Collection, Beijing, China.

Background information

The holotype of *Chaoyangia beishanensis* (Hou & Zhang, 1993), IVPP V9934 (Figs 1–4), comes from the Boluochi locality of the Jiufotang Formation, Liaoning, north-eastern China. At the time, only the enantiornithines *Cathayornis* and *Sinornis* were known from the Jehol and available for comparison (Sereno & Rao 1992; Zhou *et al.* 1992). Specimen IVPP V9934 is a single partial skeleton preserved in a main slab with a small counter slab (that corresponds only to the proximal portion of the main slab), poorly preserving the impressions of the caudal half of the axial skeleton, the pelvis and proximal hind limbs (Figs 1–4). At the time of the initial description, the specimen was considered to be unique from known lineages, but not assigned to a new group (Hou & Zhang 1993). Later, as Early Cretaceous birds became better understood through additional discoveries, *Chaoyangia* was regarded as a fairly advanced bird and assigned to Ornithurae (Hou *et al.* 1996; Hou 1997b; Zhou & Hou 2002; Zhou *et al.* 2008b).

The taxonomic history of this species, however, is not as straightforward as it appears: although the original description of *Chaoyangia* was based on a single specimen (IVPP V9934), the justification for the assignment of this taxon to Ornithurae was based almost entirely on characters derived from referred specimens (IVPP V10913 and V9937; Figs 5, 6). These specimens do not preserve any overlapping elements with the holotype (IVPP V10913 is an incomplete pectoral girdle, while IVPP V9937 represents a partial foot), and their assignment was based on size, locality and the inference that all specimens belonged to an ornithurine bird (Hou *et al.* 1996). One of these specimens (IVPP V10913; Fig. 5) was later used to erect a new genus and species, *Songlingornis linghensis* Hou, 1997b, and publications after 1996 either split the two taxa (Hou *et al.* 1996; Hou 1997b; Clarke & Norell 2001; Clarke 2002) or lumped them together (Hou *et al.* 1996; Zhou & Hou 2002; Ji 2006). The original assignment of IVPP V10913 to *Chaoyangia* was never justified and currently where *Songlingornis* is considered a distinct taxon, hypotheses differentially place the two taxa in the same family and order, Chaoyangornithidae and Chaoyangornithiformes (Zhou & Zhang 2006b), or widely separate them into different clades using phylogenetic analysis (Clarke 2002). The second specimen assigned to *Chaoyangia beishanensis*, IVPP V9937 (Fig. 6), is an isolated partial foot that also does not preserve any overlapping elements with IVPP V9934. The morphology of this specimen has never been discussed or figured in detail.

The original diagnosis of *Chaoyangia* was based entirely on the holotype (Hou & Zhang 1993); this was later revised but the updated diagnosis incorporated a large number of features derived from the referred specimens IVPP V10913 and V9937 (e.g. the presence of teeth, paired fenestrae on the sternum, reduced ungual on pedal digit I; Zhou &
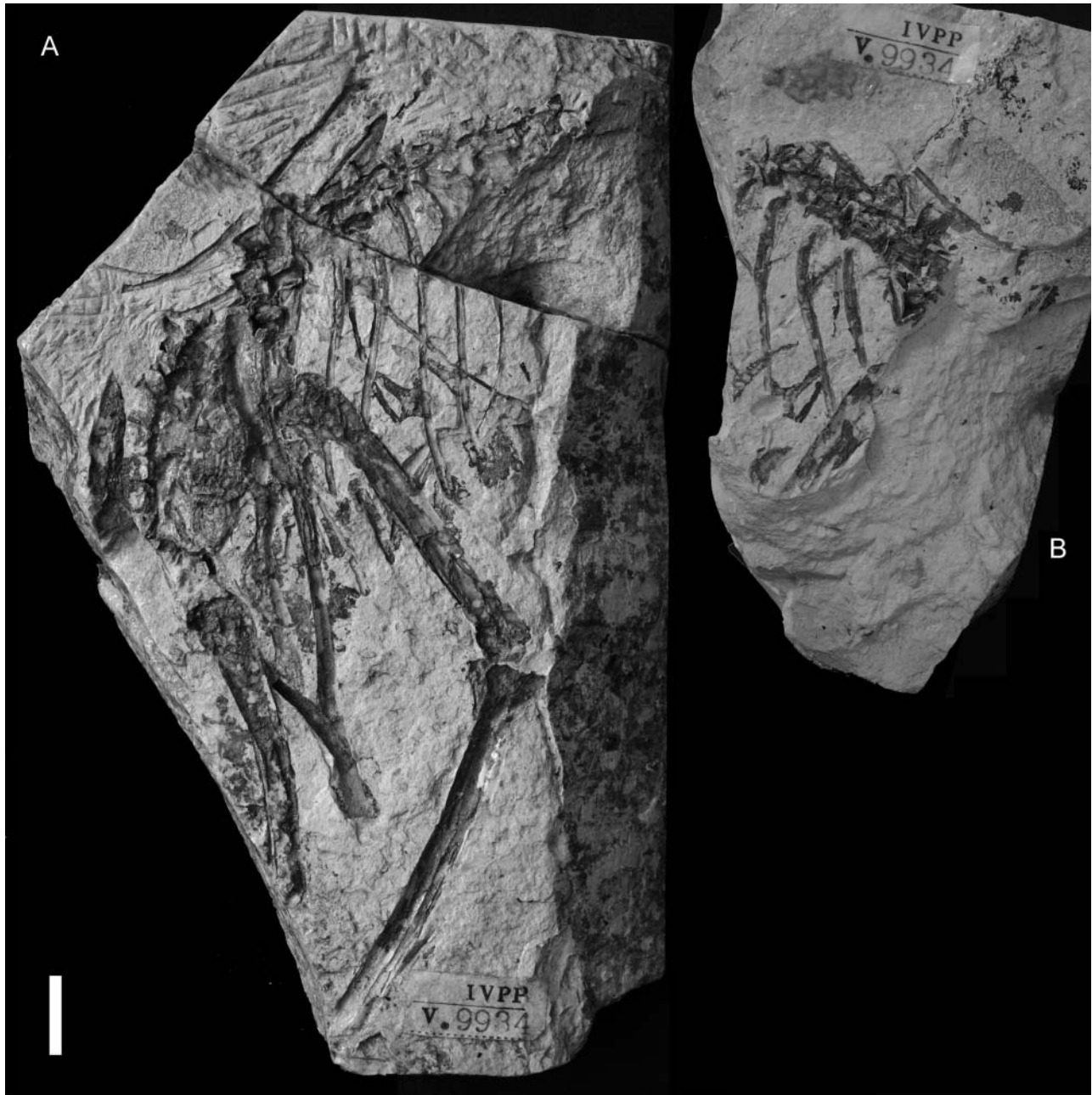
Figure 1. Photographs of the holotype specimen of *Chaoyangia beishanensis* (IVPP V9934). **A,** slab; **B,** counterslab. Scale bar = 1 cm.

Hou 2002). Although morphological characters that unite *Chaoyangia* with ornithurines rely heavily on the assigned material (IVPP V10913 and V9937), derived characters visible in the holotype (IVPP V9934) include the presence of uncinate processes, a large number of fused sacral vertebrae, and a proximocranially projecting cnemial crest (Zhou & Hou 2002). Currently, uncinate processes are known to occur in a wide range of taxa, including some non-avian theropods (e.g. dromaeosaurids, such as *Deinonychus* and *Microraptor*, oviraptorosaurs, such as *Citipati*; Codd

et al. 2008), basal birds (e.g. *Confuciusornis*, *Zhongjianornis*), as well as more advanced birds within Ornithuromorpha (Tickle *et al.* 2007). The latter two characters that place *Chaoyangia* in Ornithuromorpha are still consistent with this clade; however, the holotype specimen is poorly preserved (bones are absent, preserved as impressions) and very incomplete and these morphologies are difficult to confirm from published data.

A recently discovered nearly complete basal pygostylian, *Zhongjianornis zhengi* (Zhou *et al*. 2010), is strikingly
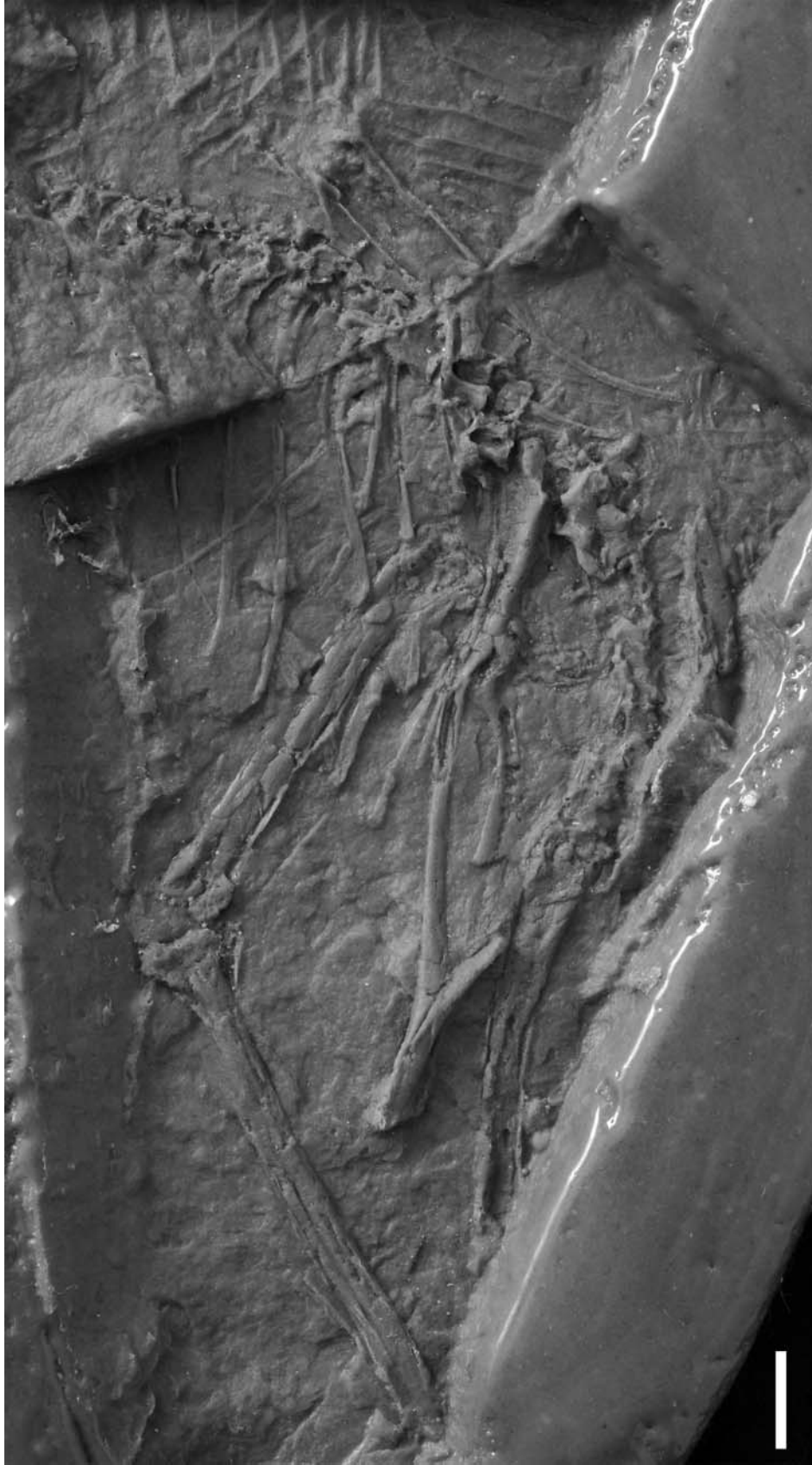
Figure 2. Photograph of the cast of the main slab of IVPP V9934. Scale bar = 1 cm.

Figure 3. Camera lucida drawing of the main slab of the holotype specimen of *Chaoyangia beishanensis* (IVPP V9934). White indicates well-preserved bone and light grey represents poorly preserved bone. Anatomical abbreviations: cc, cnemial crest; dp, dorsal process; fc, fibular crest; fem, femur; fib, fibula; ili, ilium; isc, ischium; ob, obturator process; pub, pubis; rib, ribs; syn, synsacrum; tbt, tibiotarsus; thv, thoracic vertebrae; tmt, tarsometatarsus; up, uncinate process. Scale bar = 1 cm.
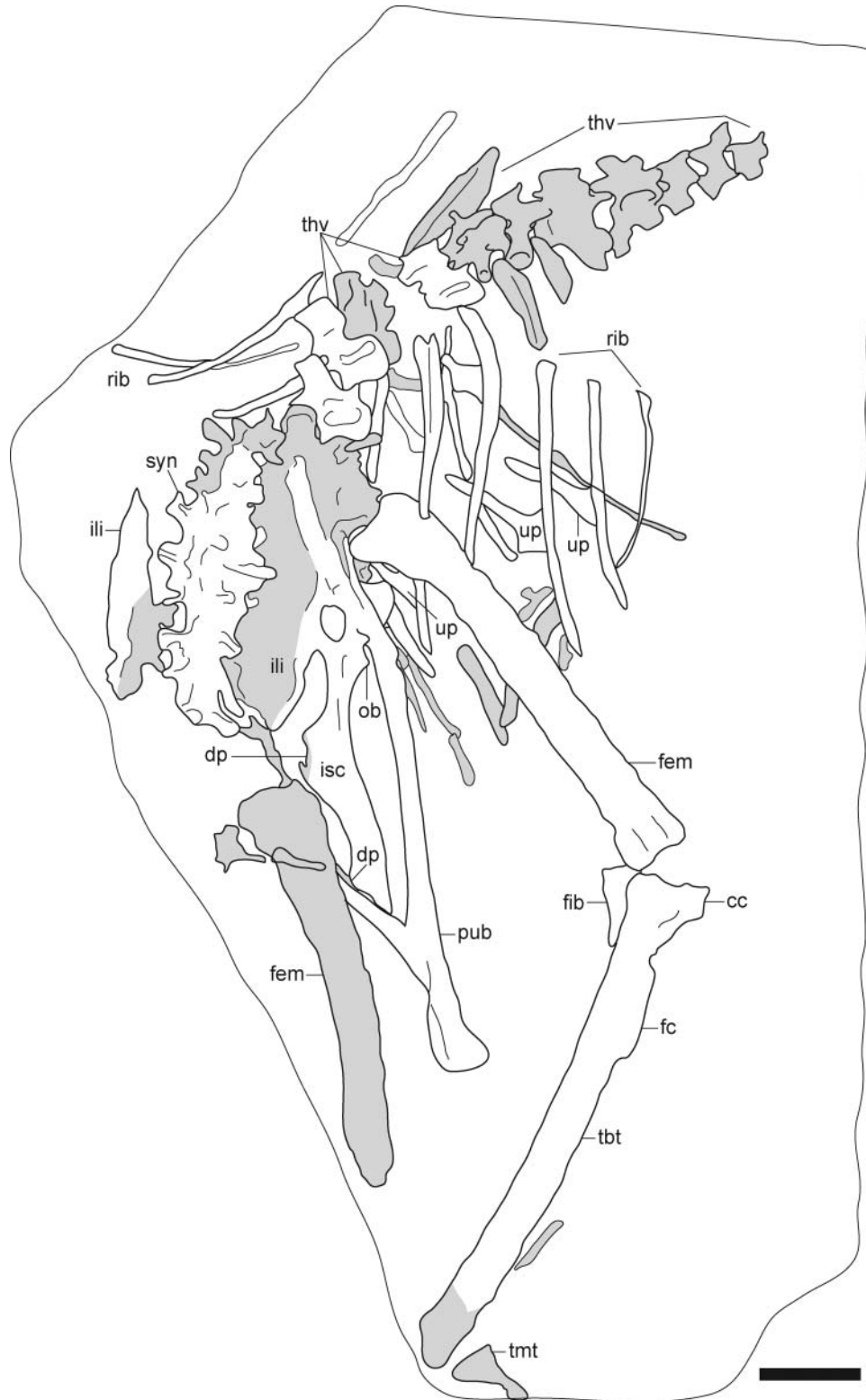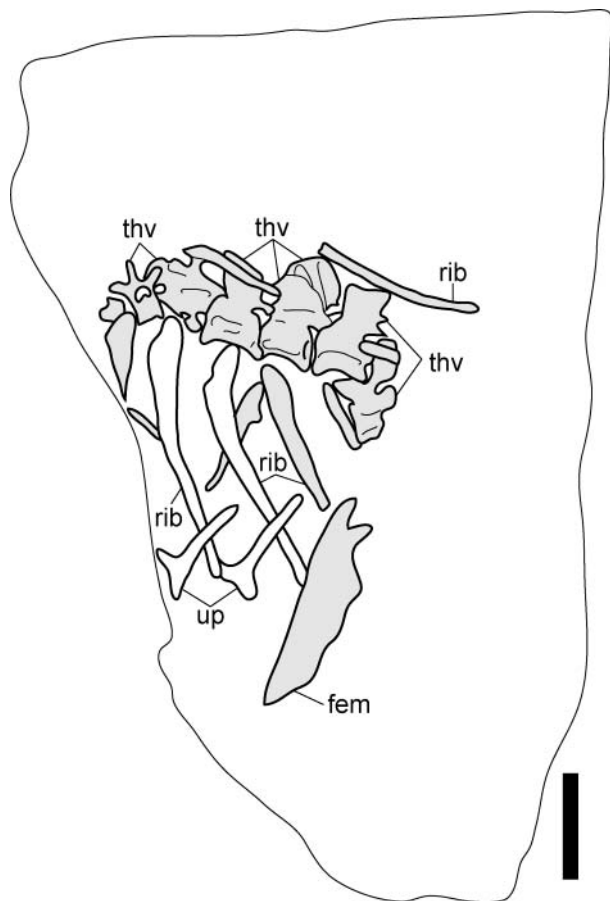
Figure 4. Camera lucida drawing of the counterslab of the holotype specimen of *Chaoyangia beishanensis* (IVPP V9934). Light grey represents poorly preserved bone. For anatomical abbreviations see Fig. 3 caption. Scale bar = 1 cm.

similar in appearance to *Chaoyangia* where preservation allows comparison (Fig. 7). This taxon also shows some morphological similarities with *Confuciusornis* (as does *Chaoyangia*, noted by Clarke 2002), such as the edentulous robust beak, and the quadrangular shape of the deltopectoral crest of the humerus. Although *Z. zhengi* does not clearly preserve the tail, cladistic analysis resolves *Zhongjianornis* as a basal pygostylian, more derived than *Jeholornis* and *Sapeornis* but basal to *Confuciusornis* and Ornithothoraces (including *Songlingornis*; Zhou *et al.* 2010).

The relationships between *Chaoyangia* and other taxa have never been fully explored through cladistic analysis; most studies do not include the fragmentary *Chaoyangia* and rarely include *Songlingornis*. Of the few phylogenetic analyses to include this taxon, one early study confirmed the hypothetical placement of *Chaoyangia* as a basal ornithurine but included morphological data derived from the referred specimens as well as the holotype (Zhou 1999). In her comprehensive analysis of the phylogenetic position of *Ichthyornis*, Clarke (2002) briefly addressed the issues surrounding *Chaoyangia*. Using data only from the

holotype specimen, this analysis resolved *Chaoyangia* as a basal pygostylian in a polytomy with some enantiornithines and *Confuciusornis* (Clarke 2002). It was further suggested that based on available morphological data, *Chaoyangia* may be junior synonym of *Confuciusornis* (Clarke 2002).

The holotype of *Songlingornis linghensis* (IVPP V10913), because it is more complete and slightly better preserved than the holotype of *Chaoyangia* (IVPP V9934), has appeared in several recent cladistic analyses (Clarke *et al.* 2006; Zhou *et al.* 2008a, 2009, 2010). These analyses have all placed *Songlingornis* in a clade together with the nearly complete and well-known ornithurines *Yixianornis grabaui* and *Yanornis martini* (Zhou & Zhang 2001; Clarke *et al.* 2006); this clade, called Songlingornithidae (Hou 1997b), is one of the few recognized Early Cretaceous ornithurine subclades. Although true for nearly all known Mesozoic bird relationships, this clade is only weakly supported; the original analysis optimized the clade based on four unambiguous characters, none of which are actually unique to this group of taxa (i.e. presence of a procoracoid process, absence of a medial groove on the coracoid, and edentulous tip of premaxilla, which define a majority of ornithuromorphs, and the presence of caudal sternal fenestrae, also seen in *Gansus*; Clarke *et al.* 2006). Unambiguous support in more recent analyses is based entirely on the similar morphology of the sternum (with a pair of caudal fenestra and only a single pair of free caudal trabeculae). Although the relationship may not hold as taxonomic diversity increases (e.g. the presence of caudal sternal fenestrae in other basal ornithurines), the nearly complete holotype specimens of *Yixianornis grabaui* and *Yanornis martini* allow for direct morphological comparison with *Chaoyangia*, not possible with the holotype of *Songlingornis linghensis*, to test the current phylogenetic position of *Chaoyangia* within Ornithurae. The lack of agreement in the phylogenetic position of *Chaoyangia* reflects the fragmentary nature of the only known specimen, a problem that is exacerbated by the mosaic distribution of morphologies among Mesozoic Aves (Chiappe 2007).

Systematic palaeontology

Class **Aves** Linnaeus, 1758
Ornithothoraces Chiappe & Calvo, 1994
Ornithuromorpha Chiappe, 2002
Ornithurae Haeckel, 1866 *sensu* Gauthier & de Quieroz, 2001
Genus ***Chaoyangia*** Hou & Zhang, 1993
Chaoyangia beishanensis Hou & Zhang, 1993
(Figs 1–4)

Revised diagnosis. A small basal ornithurine bird with the unique combination of the following characters: synsacrum composed of more than eight vertebrae; uncinate processes

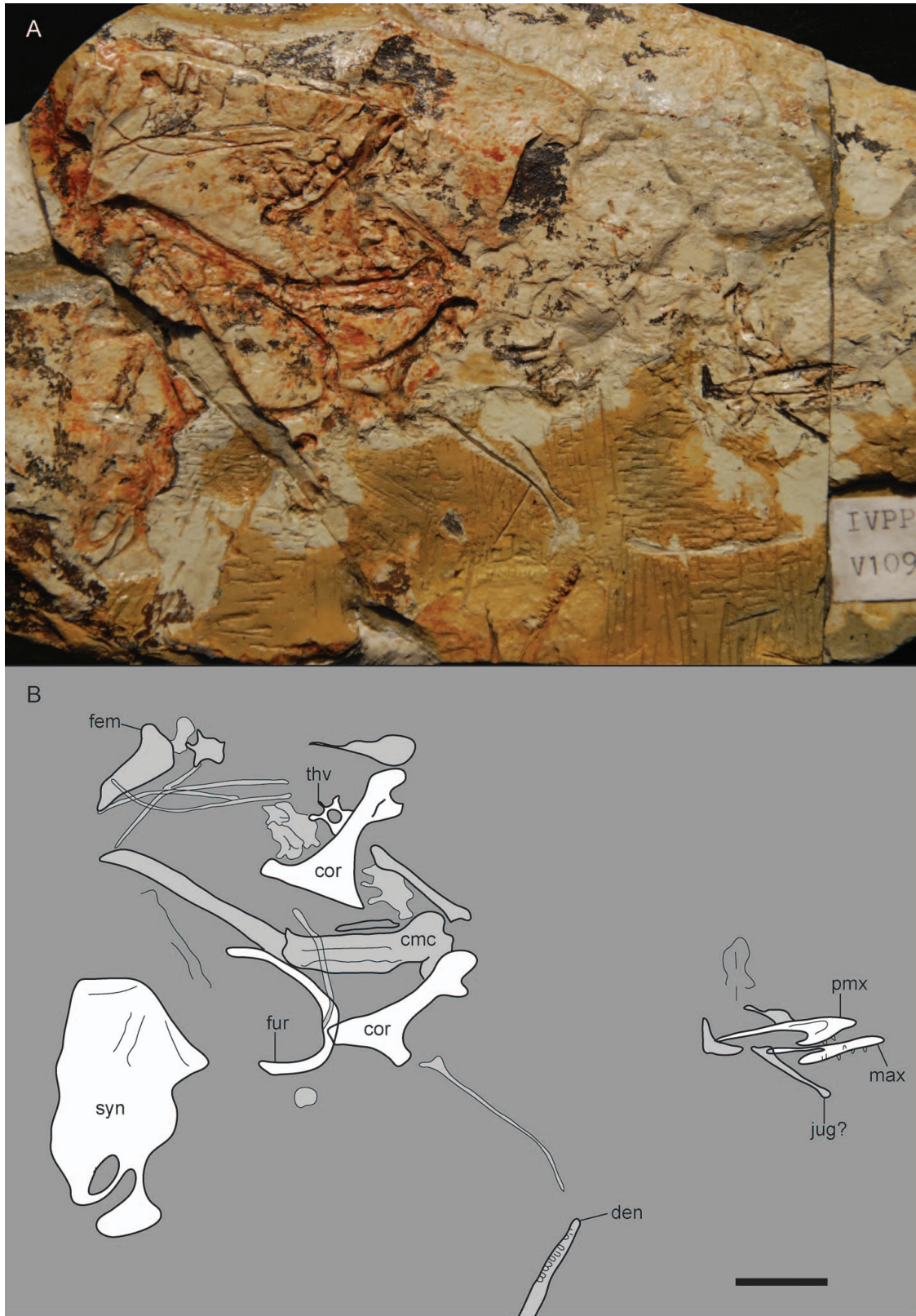**Figure 5.** Holotype of *Songlingornis linghensis* IVPP V10913, formerly assigned to *Chaoyangia beishanensis*. **A,** photograph; **B,** interpretative drawing. Light grey represents poorly preserved bone. Anatomical abbreviations (not listed in Fig. 3 caption): cmc, carpometacarpus; cor, coracoid; den, dentary; fur, furcula; jug?, possible jugal; max, maxilla; pmx, premaxilla. Scale bar = 1 cm.
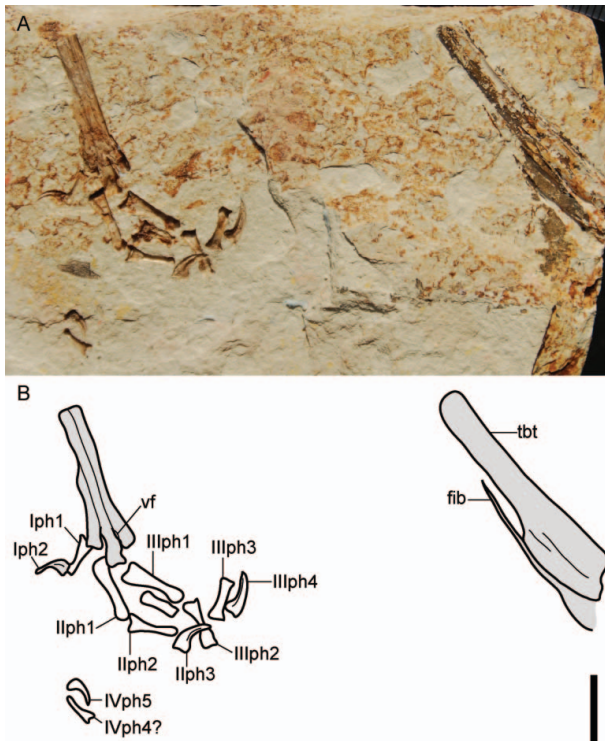
Figure 6. Specimen IVPP V9937, formerly assigned to *Chaoyangia beishanensis*. **A,** photograph; **B,** interpretative drawing. Poorly preserved bones indicated by light grey. Anatomical abbreviations (not listed in Fig. 3 caption): Iph1, pedal digit I first phalanx; Iph2, pedal digit I second phalanx; IIph1, pedal digit II first phalanx; IIph2, pedal digit II second phalanx; IIph3, pedal digit II third phalanx; IIph4, pedal digit II fourth phalanx; IVph4?, pedal digit IV fourth phalanx?; IVph5, pedal digit IV fifth phalanx; vf, vascular foramen. Scale bar = 1 cm.

on ribs long (crossing 1.5 ribs) and slender; uncinate processes expanded basally, forming a 55° angle with the rib; ischium with two, gradually expanding, dorsal processes; ischia distally contacting; pubic symphysis extending one-third length of the pubis; femoral neck, poorly defined; proximocranially projecting cnemial crest on proximal tibiotarsus (modified from Zhou & Hou, 2002).

Material. IVPP V9934, single slab with partial counterslab, preserving the impressions of bones.

Stratigraphical distribution. Jiufotang Formation of the Jehol Group, Lower Cretaceous, 125–120 Ma (Swisher *et al*. 2002; He *et al*. 2004; Zhu *et al*. 2007).

Geographical distribution. Xidagou, Boluochi, Chaoyang, western Liaoning Province, north-eastern China.

Description and remarks. Description is based solely on the holotype specimen (IVPP V9934); morphology was taken from the slab and counterpart as well as a cast of the main slab.

   Axial skeleton. Only thoracic vertebrae and ribs and the synsacrum are preserved (Figs 1–4); an estimated 11–13

Figure 7. Holotype of *Zhongjianornis zhengi*, IVPP V15900. Boxed area approximates region that can be compared to the holotype of *Chaoyangia*, IVPP V9934.

thoracic vertebrae are present. Several of the thoracic vertebrae are preserved partially in articulation (preserved best in the counter slab; Fig. 1B) and in lateral view (Fig. 1). The vertebrae are spool-shaped, excavated laterally by broad deep fossae, and bearing tall dorsal spines. The parapophyses appear to be cranially located, visible in the second to last preserved thoracic.

   The synsacrum is preserved as an impression of the ventrolateral surface. Based on the number of transverse processes, it appears nine vertebrae form this element; however, the proximal and distal ends of the synsacrum are unclear, and up to 11 vertebrae may have been incorporated. This large number of fused sacral vertebrae, even higher than originally estimated, is consistent with the derived placement inferred for *Chaoyangia*. Primitive long-tailed birds typically possess five (*Archaeopteryx*; Elzanowski 2002) or six sacrals (e.g. *Rahonavis*, *Jeholornis*; Forster *et al*. 1996; Zhou & Zhang 2003b), while the basal pygostylians *Sapeornis* and *Confuciusornis* both possess seven sacral vertebrae (Chiappe *et al.* 1999; Zhou & Zhang 2003a); the enantiornithine synsacrum is composed of seven (e.g. *Rapaxavis*, *Pengornis*, *Protopteryx*) to eight sacrals (e.g. *Cathayornis*, *Longipteryx*, *Vescornis*;

O'Connor 2009). Members of Ornithuromorpha typically possess a larger synsacrum formed by nine or more vertebrae; *Yixianornis* and *Yanornis* possess nine fully fused sacral vertebrae (Zhou & Zhang 2001), while the more derived *Gansus* and the ornithurine clade of foot-propelled divers, the Hesperornithiformes, possessed 10 fused sacral vertebrae (You *et al.* 2006). However, the more recently discovered basal ornithuromorph, *Archaeorhynchus*, possesses only eight fused sacrals (Zhou & Zhang 2006a), suggesting that basal ornithuromorphs, like enantiornithines, had fewer fused sacral vertebrae. The basal bird *Zhongjianornis* reportedly preserves no more than eight sacral vertebrae (Zhou *et al.* 2010); however, preservation is unclear, transverse processes are not preserved, and the distal third is covered by the ilium (IVPP V15900).

The synsacrum is not preserved fused to the pelvis (IVPP V9934). Because the synsacrum is preserved at an angle, it is difficult to make unequivocal statements about the relative lengths of the transverse processes (which appear to be slightly longer among the central vertebrae) or mediolateral width of the bone (which appears widest in the centre). However, the transverse processes are all clearly directed laterally except for the caudalmost one or two vertebrae (Fig. 3). The synsacrum appears slightly dorsoventrally bowed so that the dorsal surface would be convex, a feature observed in other ornithurines (Clarke 2004). The proximal synsacrum appears dorsoventrally thicker than its distal end. The midline of the ventral surface appears to have possessed a faint groove, only preserved on the distal half, which may have been more extensive.

Ribs. Six pairs of ribs are preserved in articulation with the thoracic vertebrae. Two more ribs (from the other side) are disarticulated and preserved parallel to the thoracic series. Additional rib fragments are scattered over the hip region. The ribs are slightly sigmoidal, (proximal half slightly cranially convex and caudal half very slightly cranially concave) considered an autapomorphy of the species (Zhou *et al.* 2008b). In most taxa where preservation permits comparison (preserved in lateral view) the ribs are broadly concave cranially (e.g. ornithuromorph *Yanornis* IVPP V13358, enantiornithine *Longipteryx* IVPP V12325). *Zhongjianornis*, however, does show a similar morphology where the middle portion of rib is straight (IVPP V15900), which contributes to their sigmoid shape as in *Chaoyangia* (Figs 1, 3). The distal ends of the ribs are covered in IVPP V15900 and it cannot be determined if distally the ribs became concave dorsally as in *Chaoyangia*. The ribs in a newly described specimen of *Cathayornis* (Zhang *et al.* 2010) are also slightly sigmoidal, suggesting that additional specimens are required before it can be determined if this is a diagenetic effect.

Three uncinate processes are clearly preserved in the main slab in articulation with the thoracic ribs (Figs 1–4); some disarticulated fragments may also represent uncinate processes. The smaller slab preserves the counterparts to two of these processes (Fig. 1B). The contact between the rib and the uncinate process is identifiable, indicating these processes were not fully fused. The uncinate processes are directed dorsally, defining approximately a 55° angle with the ribs. The base of the process is broad, expanding proximally and distally along the rib. The uncinate processes are relatively short, crossing only a single rib (from their origin), tapering distally, with the distal margin located just over halfway to the next rib (Fig. 8). Ossified uncinate processes are known throughout Aves, as well as in some related non-avian dinosaurs (Clark *et al.* 1999; Norell & Mackovicky 1999; Zhou *et al.* 2000; Codd *et al.* 2008). These processes are absent (or unossified) in the most basal known bird, *Archaeopteryx* (Mayr *et al.* 2005), and other long-tailed birds (e.g. *Jeholornis*; IVPP V13353). Ossified processes are present in the basal bird *Confuciusornis* but are not preserved in any specimen of *Sapeornis* (Chiappe *et al.* 1999; Zhou & Zhang 2003a). In *Confuciusornis*, these processes are unfused, simple without an expanded base, and less than two rib lengths (Chiappe *et al.* 1999). Although reported in two enantiornithines (*Eoenantiornis buhleri* (IVPP V11537) and *Longipteryx chaoyangensis* (IVPP V12325); Zhang *et al.* 2000; Zhou *et al.* 2005), the short, straight, free strap-like fragments identified as uncinate processes in these specimens are not morphologically consistent within a single specimen and no uncinate processes have been reported in any of the referred specimens of *Longipteryx* (IVPP V12552), suggesting that these bones may have been misidentified. Uncinate processes are most common among ornithurines (*Yixianornis*, *Hongshanornis*, *Archaeorhynchus*; Zhou & Zhang 2005, 2006a; Clarke *et al.* 2006), although they are absent (or unossified) in some taxa (i.e. *Gansus*; You *et al.* 2006). This absence is considered real, not preservational, given the large number of excellently preserved specimens of this taxon (You *et al.* 2006). The uncinate processes in *Chaoyangia* most resemble those present in the ornithurine *Yixianornis* (Clarke *et al.* 2006). In this taxon, the processes are slightly expanded at the base, and long, extending across two ribs; it cannot be determined if they were fused to the ribs (Clarke *et al.* 2006). In *Archaeorhynchus* the uncinate processes are shorter, approximately one rib length and L-shaped, rather than expanding at the base in both directions (IVPP V14287), while in *Hongshanornis* they are similar in morphology but longer, crossing two ribs, and forming a 70° angle with the rib (IVPP V14533).

Pelvic girdle. The pelvis is nearly complete (Figs 1–3); both ilia are preserved although they do not reveal many morphological details. The right one is poorly preserved and the left is slightly disarticulated. It appears the ilia were not fused to the synsacrum, although the ilium, pubis and ischium were partially fused at the level of the acetabulum. The impression of the preacetabular wing of the right ilium is deeply concave craniolaterally, however preservation
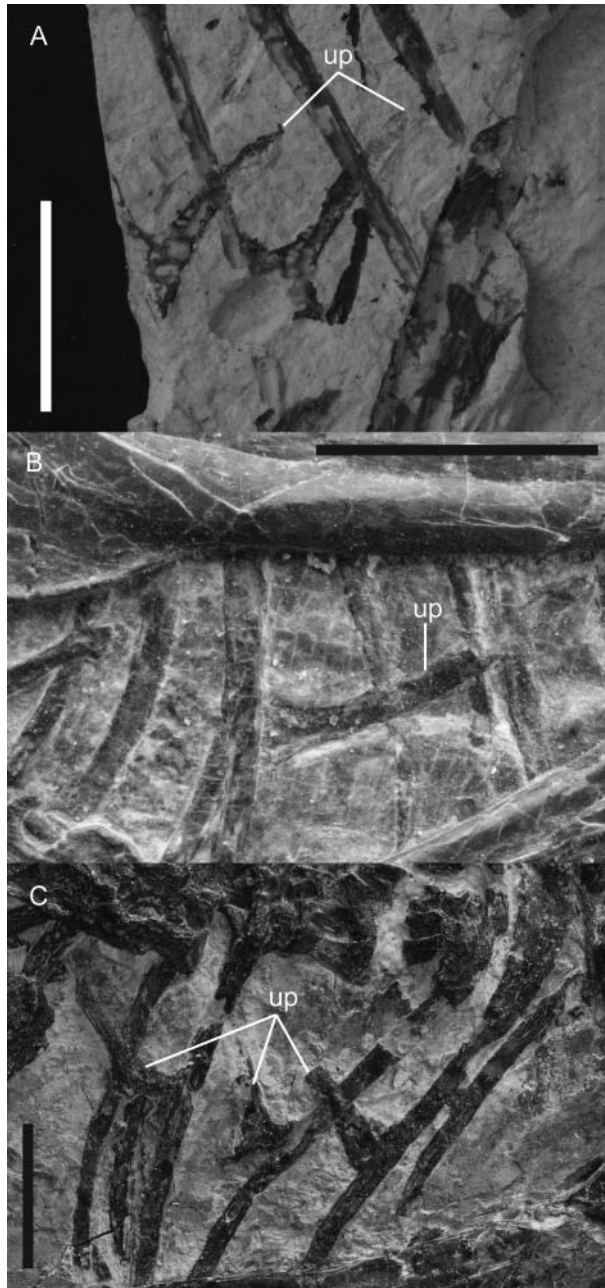
Figure 8. Comparative anatomy of Mesozoic bird uncinate processes: **A,** *Chaoyangia*; **B,** *Yixianornis*; **C,** *Zhongjianornis*. Anatomical abbreviation: up, uncinate process. All scale bars represent one centimetre.

makes it difficult to tell if this is the result of another bone overlying this part of the ilium; *Zhongjianornis* IVPP V15900 preserves a similar deep dorsolateral concavity on the preacetabular wing of the right ilium. In the cast of IVPP V9334, the preacetabular ilium is preserved primarily in dorsal view (dorsolateral view); in this view, the preacetabular ilium appears thickest proximally and laterally excavated by a shallow fossa. What is preserved

of the left ilium appears narrow and tapered cranially in both the slab and cast (Figs 1, 2), suggesting the rostral margins of the ilia were sharp and tapered rostrally as in *Zhongjianornis* (Zhou *et al.* 2010). The morphology of the postacetabular wing of the right ilium is unclear due to overlapping bone impressions (Fig. 1A).

The ischium is the most interesting element preserved in this specimen; it bears two dorsal processes and possibly a very small obturator process (Fig. 2). Just distal to the pubic peduncle of the ischium is a small ventrally directed process, which may be the reduced obturator process; it does not contact the pubis. The first dorsal process is located at approximately the midpoint of the ischium; it is not a distinct process like that of enantiornithines and *Confuciusornis*, which is also more proximally located in both groups (Chiappe *et al.* 1999; O'Connor *et al.* 2009), but a gradual dorsal swelling that defines an obtuse triangular process, very similar to that present in some ornithurine taxa (e.g. *Yixianornis* (IVPP V12631), *Gansus* (CAGS-IG-04-CM-002); absent in *Archaeorhynchus* (IVPP V14287) and *Hongshanornis* (IVPP V14533)). The apex of the process is not preserved and the exact morphology is unclear; however, the base of the proximal process accounts for almost one-third the length of the ischium. The second process is similar but smaller and located at the distal end of the ischium; the corpus swells dorsally, forming the second process, and then tapers to a triangular point (Figs 1–3). The ischium in other ornithurines (e.g. *Gansus* (CAGS-IG-04-CM-002), *Hongshanornis* (IVPP V14533), *Yixianornis* (IVPP V12631) and *Yanornis* (IVPP V13358)) tapers sharply to the distal end with no additional distally located swelling; however, a second distal process is also present on the ischium in *Confuciusornis* (IVPP V 11374, V13168), although it is located slightly more proximal than that preserved in *Chaoyangia*. The ischium in *Zhongjianornis* is similar to that of ornithurines, with a distally located proximal process (Zhou *et al.* 2010); however, damage and poor preservation prevents an accurate assessment of the distal morphology. The ischium in this taxon, however, is strongly concave ventrally, a morphology absent in *Chaoyangia*. Distally, it appears the two ischia contact each other; a portion of the left ischium is visible in contact with the right one (Fig. 3).

The pubis forms the ventral two-thirds of the acetabulum; the pubic pedicel of the ilium is more than twice as wide as the narrow pedicel for the ischium (Fig. 3). The pubis is nearly parallel to the ischium, but both bones are directed caudoventrally demarcating an acute angle with the post-acetabular ilium (as opposed to parallel in advanced ornithurines). The articulation, although in place and preserving the acetabulum, appears to be slightly crushed (Fig. 2); still we estimate the pubis and ischium were retroverted at an acute angle of less than 45°. Just rostroventral to the acetabulum, the pubis appears to form a robust pectineal process. The pubis is more than

two-thirds the length of the ischium. The shaft has an oval cross-section; proximally the orientation of the long axis is unclear but distally the shaft appears to become more robust and the long axis of the oval cross-section is angled dorsolaterally–ventromedially. The distal third of the pubes contact each other, although they remain incompletely fused. The contact is expanded dorsoventrally, not forming a distinct boot in which the expansion occurs primarily dorsally, perpendicular to the shaft as in some enantiornithines (e.g. *Longipteryx* (IVPP V12325)). Portions of the pubic shaft are pitted, on the right just proximal to the symphysis and on the left on the proximal portion of the symphysis (visible in the cast). The pubes of *Chaoyangia* are more robust than in some ornithuromorphs (especially relative to *Yixianornis* (IVPP V12631) and *Hongshanornis* (IVPP V14533)), but fairly comparable to those preserved in *Zhongjianornis* (IVPP V15900).

Pelvic limb. The hind limb is very incomplete; both femora are preserved (the left is incomplete), but only the right tibiotarsus (missing its distal end) and a fragment of the right tarsometatarsus are present (Figs 1–3). The proximal end of a distal condyle of the tibiotarsus is preserved, allowing for an estimate of the total length of this bone. The femur is fairly long: it is more than two-thirds the estimated length of the tibiotarsus and nearly as long as the pubis. The femur is straight and robust in *Chaoyangia*, comparable to the morphology of *Zhongjianornis* (the femur is bowed in most enantiornithines; O'Connor 2009); in both specimens, the proximal head is fairly large, and separated by a very shallow neck, which also characterizes other basal ornithurines (e.g. *Yanornis*, IVPP V12558, V10996). A well-defined posterior trochanter (Chiappe & Walker 2002), as present in enantiornithines and some non-avian theropods, is absent. Impressions of the condyles of the right femur are preserved in the main slab; no indication of a fibular trochlea is apparent. The condyles are proximodistally elongate narrow ovals, and are widely separated. The medial condyle appears approximately 50% wider than the lateral condyle, which is more poorly preserved (visible in cast). The reduction in width of this outer condyle may suggest the presence of an incipient fibular trochlea.

The right tibiotarsus appears to be in caudal view (impression of cranial surface); the proximal end bears a small cnemial crest that projects proximocranially and laterally. The feature appears to be a true morphology of the specimen, although a diagenetic origin cannot be completely ruled out given the poor overall preservation of the specimen. This crest is limited to the proximal 15% of the shaft length. In the cast, a second ridge appears visible, ending just distal to where the first crest ends (Fig. 2). This second possible crest cuts laterally, and for most of its length appears to be running underneath (lateral to) the larger crest. This may represent a second cnemial crest or a break in the large proximally projecting cnemial crest. Although small low cranial crests are

present in some enantiornithines (Chiappe & Walker 2002), a proximally projecting cnemial crest is only known within Ornithuromorpha (e.g. *Gansus*, *Hongshanornis*, *Yixianornis*; O'Connor *et al.* 2011b). Basal pygostylians *Sapeornis* and *Confuciusornis* are not known to possess cnemial crests (Chiappe *et al.* 1999; Zhou & Zhang 2003a) and the hind limb of *Zhongjianornis* is exposed in caudal view, thus preventing identification (IVPP V15900). The lateral margin bears a short fibular crest; it begins just distal to the proximal crests and extends for less than one third of the preserved tibiotarsus. A small triangular bone preserved just medial to the proximal end of the tibiotarsus is interpreted as the fibula. It is incomplete and preserves no real morphological information.

A fragment of the proximal right tarsometatarsus is preserved at the edge of the slab, most clearly visible in the cast (Fig. 2). The fragment, interpreted as the impression of the cranial surface, only preserves part of the tarsal cap and the proximal-most bit of metatarsal IV, but these elements appear well fused, characteristic of ornithurine birds; intermetatarsal fusion is poor or absent in enantiornithines (O'Connor *et al.* 2011b).

<div align="center">

Genus *Songlingornis* Hou, 1997b
Songlingornis linghensis Hou, 1997b
(Fig. 5)

</div>

Revised diagnosis. A small ornithurine bird with the unique combination of the following characters: dentary straight and toothed; sternum elongate with a pair of caudally located proximodistally elongate fenestrae that taper distally; sternum lateral margin, single large lateral (zyphoid) process; sternum with single free pair of robust lateral trabeculae with large asymmetrical distal expansion; and furcula U-shaped, with a flat and broad base (modified from (Zhou *et al.* 2008b).

Material. IVPP V10913, single slab preserving the impressions of several skull bones, the nearly complete pectoral girdle, and partial wing and hind limb elements.

Stratigraphical distribution. Jiufotang Formation of the Jehol Group, late Early Cretaceous, 125-120 Ma (Swisher *et al.* 2002; He *et al.* 2004; Zhu *et al.* 2007).

Geographical distribution. Xidagou, Boluochi, Chaoyang, western Liaoning Province, north-eastern China.

Morphology and remarks. Specimen IVPP V10913, formerly a referred specimen of *Chaoyangia* and now the holotype of *Songlingornis linghensis*, is a partial, disarticulated skeleton, preserving only the impressions of bones (Fig. 5). The rostral half of the skull is preserved slightly disarticulated. The premaxilla preserves two teeth but the rostral tip is edentulous as in *Yixianornis* and *Yanornis* (Zhou & Martin 2011). The poorly preserved toothed maxilla has a long and delicate nasal process

and a short jugal process, approximately half the length of the premaxillary process. The dentary is straight and toothed – there are approximately six to eight teeth, widely spaced proximally, and more densely spaced caudal in the jaw. The teeth are slightly recurved apically and constricted at the base of the crown. Voids of several thoracic vertebrae suggest that the vertebral foramen was proportionately wide. Several thoracic ribs are also preserved; although their morphology is unclear, they do not appear to be sigmoidal, as in *Chaoyangia* (IVPP V9934).

The furcula is delicate and nearly U-shaped, similar to that in *Yixianornis* (Clarke *et al*. 2006); as in this taxon, the sternal margin at the interclavicular symphysis (apophysis) is straight so that the distal margin is not curved throughout. The coracoid has a proximally located triangular procoracoid process, with a straight cranial margin, tapering into the shaft distally. A procoracoid process is only known among ornithurines, although one enantiornithine possesses a similar feature (*Protopteryx*; Zhang *et al*. 2000). Both the medial and lateral margins are concave; the sternal margin is straight and laterally expanded to form a rectangular lateral process that does not project cranially, a morphology common among basal ornithurines (e.g. *Longicrusavis*, PKUP V1069). The sternum is similar to that in *Yixianornis* and *Yanornis* (Clarke *et al.* 2006); the rostral margin forms a tall apex, bounded by triangular craniolateral processes (Fig. 5). The dorsal margin of the coracoidal sulcus is contiguous with this process. A rectangular lateral (zyphoid) process projects laterally for approximately the middle quarter of the lateral margin; *Yixianornis* possesses two lateral processes, the proximal one much smaller than the other (IVPP V12631). The lateral trabecula is directed caudolaterally and distally bears a large asymmetric expansion that is wider medially (Fig. 5). The caudal margin is rounded; it encloses a pair of large, fenestra, caudolaterally bounded by a thin strap of bone. The long axis of the fenestra is craniocaudally oriented, slightly angled proximolateral–mediodistally as in *Yanornis* (IVPP V13358), and the distal margin is tapered so that the fenestra is lachrymiform. The fenestrae preserved in both *Yanornis* (IVPP V13358) and *Yixianornis* (IVPP V12631) are proportionately wider, and the distal margin is less tapered.

A carpometacarpus is also preserved, however not much information can be discerned.

Ornithuromorpha indet. Hou *et al.*, 1996
(Fig. 6)

Material. IVPP V9937, single slab preserving the impression of a partial hind limb.

Stratigraphical distribution. Jiufotang Formation of the Jehol Group, late Early Cretaceous, 125–120 Ma (Swisher *et al*. 2002; He *et al*. 2004; Zhu *et al*. 2007).

Geographical distribution. Xidagou, Boluochi, Chaoyang, western Liaoning Province, north-eastern China.

Morphology and remarks. The isolated partial foot IVPP V9937 (Fig. 6) assigned to *Chaoyangia* is either lumped with this taxon or ignored; it has never been described, and like *Chaoyangia*, its assignment to the derived clade of birds was loosely based on limited information (Hou *et al*. 1996). The specimen is a single slab preserving the voids of an incomplete left tibiotarsus and foot as an impression of its caudal surface (Fig. 6). The tibiotarsus is very poorly preserved, missing both the proximal and distal ends; the fibular crest is the only feature that can be identified. It is short and appears rounded, although the latter is most likely an artefact of preservation. The fibula is preserved next to the crest and is fat proximally and tapers to a sharp point. It extends for more than half of the preserved tibiotarsus (Fig. 6). The lateral margin bears a small tubercle located nearly at the bone's midpoint, presumably the attachment site of the *m. iliofibularis*. The tubercle appears laterally directed; however, given the preservation (impression), cranial projection would largely not be visible and caudal projection is difficult to determine.

Only the distal half (approximately) of the tarsometatarsus is preserved; the metatarsals appear highly fused compared to primitive birds (e.g. Sapeornithiformes, Enantiornithes; O'Connor *et al*. 2011b), although fusion was not complete and the margins of individual metatarsals can easily be discerned. Weak intermetatarsal fusion characterizes derived enantiornithines and basal ornithurines (O'Connor 2009). The third metatarsal is the longest, followed by the fourth and then the second. The metatarsals end in the same plane, proximally and distally; proximally, the impression is shallowest centrally, suggesting that the caudal surface may have been slightly excavated in this region. The dorsal excavation caused by the caudal displacement of metatarsal III common in most ornithuromorphs (e.g. *Yanornis* (IVPP V12558), *Hongshanornis* (IVPP V14533)) cannot be determined. The first metatarsal is located high on the caudomedial surface of the tarsometatarsus. A distal vascular foramen is located between metatarsals III and IV as in other ornithurines (e.g. *Yixianornis*, *Gansus*; Clarke *et al*. 2006; You *et al*. 2006), and a second foramen may also have passed between metatarsals II and III.

The hallux is very short; the proximal digit is slightly longer than the small claw it bears (Fig. 6). The second digit is formed by three phalanges; the first is twice the length of that in the first digit. The second phalanx is two-thirds of its size, followed by a small claw, approximately 50% larger than that of the hallux. The third digit is very robust; the first phalanx is larger than all other pedal phalanges in all dimensions. The following two phalanges reduce in size distally and articulate with the largest claw in the foot. The fourth digit appears incomplete; three small,

short phalanges (approximately the size of the first hallucal phalanx) and a small claw are all that is preserved. The claw associated with the ungual of this digit is the smallest and most delicate ungual of the foot. All digits bear deep extensor pits and all claws are relatively small and unrecurved as in other Jehol ornithurines (e.g. *Yixianornis* (IVPP V12631), *Yanornis* (IVPP V13358), *Hongshanornis* (IVPP V14533)).

The relative lengths of the metatarsals, their arrangement (III long, I high), pedal proportions (longest phalanx proximal in digit), robust size of digit III, and the small size of the claws are all consistent with a cursorial ecological habitat (Hopson 2001; Zhang 2006). Interpretations of this taxon as cursorial also support the inferred phylogenetic position, with Jehol enantiornithines showing arboreal adaptations such as large, recurved pedal claws while ornithurines are more highly adapted for the ground.

Phylogenetic analysis

Methods
Chaoyangia IVPP V9934 was scored using the O'Connor *et al*. (2011b) character list; *Zhongjianornis*, two confuciusornithids (*Jinzhouornis zhangjiyingia* and *Confuciusornis dui*), the enantiornithine *Boluochia zhengi*, and the recently discovered ornithurines *Jianchangornis microdonta* and *Schizooura lii* were also added to the matrix (see Online Supplementary Material). *Dalianornis cuhe*, a taxon whose avian status is controversial, was removed. This analysis thus included 60 taxa scored across 245 characters, making it the largest sampling of Mesozoic birds within a single analysis to date. The dataset was analysed using TNT (Goloboff *et al.* 2008). Thirty-one characters were treated as ordered; all characters were weighted equally. We conducted a heuristic search retaining the single shortest tree from every 1000 trees followed by an additional round of tree bisection and reconnection (TBR) branch swapping. A Nelson strict consensus tree was generated from the resulting trees (Fig. 9). In order to determine how the most fragmentary taxa affect the resolution of the resultant tree, strict reduced consensus trees (Wilkinson 1999) were generated using TNT (Goloboff *et al.* 2008) individually removing *Vorona*, *Zhongjianornis*, and *Chaoyangia*. In order to test the strength of alternative hypotheses, constraint trees were built using TNT; the analysis was run using the same parameters as in the first analysis and the difference in tree lengths were compared.

Results
The heuristic search, retaining the single shortest tree from every 1000 trees, returned 17 trees of 836 steps. An additional round of TBR revealed 162 trees, 835 steps long. The strict consensus of these trees resolves both *Chaoyangia* and *Zhongjianornis* as basal ornithurines (Fig. 9).

As in most other analyses, *Archaeopteryx* is resolved as the most basal bird; all other long-tailed birds form an unresolved polytomy with the clade that includes all more derived birds. Sapeornithiformes form the basal pygostylian clade and *Zhongornis* is resolved as the confuciusornithiform outgroup (or basalmost confuciusornithid). The *Zhongornis* + Confuciusornithiformes clade forms the ornithothoracine outgroup. Enantiornithes is well resolved, forming a series of ingroups; however, these relationships are only weakly supported. Notably, *Boluochia* and *Longipteryx* form a relationship, supporting interpretations that these taxa are closely related (O'Connor *et al.* 2011a), although a monophyletic Longipterygidae is no longer supported (O'Connor *et al.* 2009), and *Liaoningornis* is resolved as an enantiornithine (O'Connor 2012), rather than an ornithuromorph (Zhou & Zhang 2006a). *Otogornis*, a fragmentary, rarely analysed taxon, is resolved as a basal enantiornithine, contra the suggestion this taxon may be closely related to *Ambiortus* (Kurochkin 1999).

Ornithurae (or Ornithuromorpha) is well resolved, except for a polytomy of taxa with mainly basal characters, which unfortunately includes the taxa in question here. *Archaeorhynchus* is resolved as the basalmost ornithurine; *Patagopteryx*, *Jianchangornis*, *Schizooura*, *Vorona*, *Zhongjianornis* and *Chaoyangia* form a polytomy outside all more derived taxa (Songlingornithidae, Hongshanornithidae and derived ornithuromorphs). The basal positions of these taxa have been supported in previous cladistic analyses (Clarke *et al.* 2006; Zhou *et al.* 2009, 2012; O'Connor 2012).

The basal ornithurines, including *Chaoyangia*, show the least resolution; *Chaoyangia* and *Vorona* are known from fairly incomplete specimens, while the nearly complete holotype of *Zhongjianornis* is poorly preserved. TNT (Goloboff *et al.* 2008) was used to create strict reduced consensus trees (Wilkinson 1999), removing each of these taxa individually in order to try to increase resolution in this polytomy. Removal of either *Vorona* or *Zhongjianornis* does not affect the polytomy. However, excluding *Chaoyangia* does increase resolution in this region of the tree. Alternative hypotheses suggest *Chaoyangia* may be related to confuciusornithiforms (Clarke 2002). However, in this analysis constraint trees indicate the tree would have to be four steps longer to accommodate this relationship. To force a similar relationship for *Zhongjianornis*, which was originally described as a basal pygostylian, tree length would be at least 14 steps longer.

Discussion

Phylogenetic problems
A comprehensive morphological review of *Chaoyangia beishanensis*, one of the first birds from the Jehol Group, supports initial hypotheses that this taxon is an ornithurine
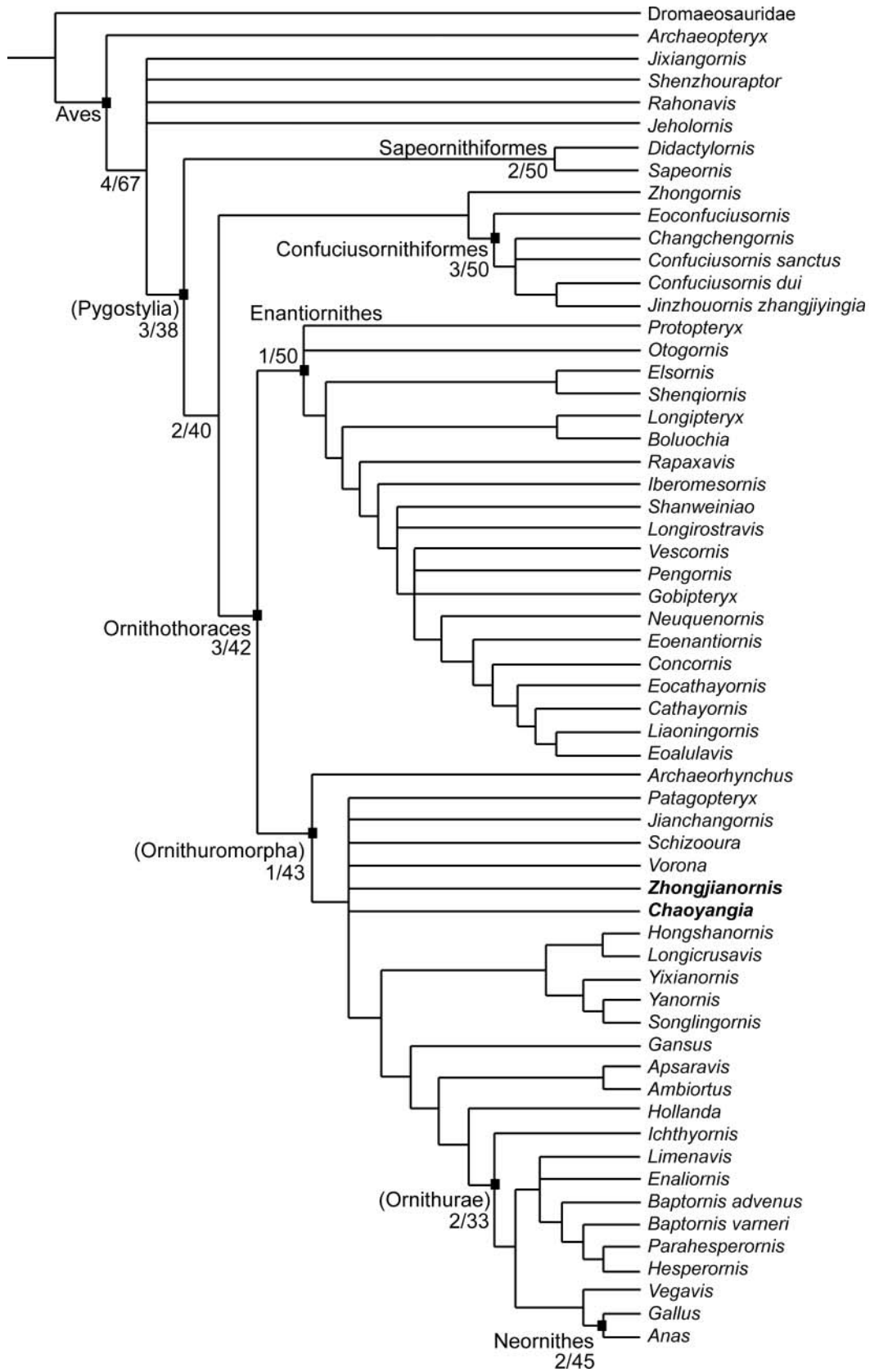
bird (Hou *et al.* 1996). Although the only valid known specimen of *Chaoyangia* is extremely fragmentary and reveals limited anatomical information, when placed in a cladistic analysis the resulting hypothesis concurs with morphological observations. The results also support morphological inferences that this taxon may be closely related to the more complete *Zhongjianornis*, which is here also resolved as a basal ornithurine.

The phylogenetic hypothesis resulting from the current cladistic analysis is very weakly supported (CI: 0.389; RI: 0.670); however, given the fragmentary nature of the taxa we seek to understand (e.g. *Chaoyangia*) and the lack of resolution typical of recent cladistic analyses targeted at Mesozoic birds (O'Connor *et al.* 2011b), any resolution at all is encouraging. Adding two steps to the consensus tree (L = 837) causes Enantiornithes and Ornithuromorpha to collapse. In trees of equal length, poorly preserved and primitive taxa, particularly *Zhongjianornis* and *Chaoyangia*, begin to move between the two major ornithothoracine clades, sometimes resolved as basal enantiornithines. Despite the inability of the cladistic analysis to support strongly this hypothesis, *Chaoyangia* preserves distinct features, such as an elongate synsacrum and a well developed cnemial crest that are only known within the ornithurine clade, and thus the results of this study concur with initial studies (Hou *et al.* 1996), contra more recent hypotheses (Clarke 2002).

On the other hand, *Zhongjianornis*, although nearly complete and superficially similar to *Chaoyangia*, does not definitively preserve any clear ornithurine synapomorphies, largely due to poor preservation. No cnemial crest can be observed on the tibiotarsus, which is in caudal view, the number of fused sacral vertebrae is unknown, details of the furcula are unclear (although it appears robust, similar to *Schizooura*, IVPP V16861), and no sternum or cora-

coid can be observed. However, while the taxon might shift between the two ornithothoracine clades in trees only two steps longer than the most parsimonious tree, the chances this taxon will be resolved again as a basal pygostylian (Zhou *et al.* 2010) are low; this analysis required an additional 14 steps in order to resolve *Zhongjianornis* as a basal pygostylian, suggesting that this relationship is not likely. Given the limited morphological information available from this largely complete specimen, the phylogenetic position of this taxon may continue to fluctuate until more data are available, and until then the taxon should not be considered unequivocally to be a member of any particular clade, although research here suggests this taxon is likely not a basal pygostylian.

Although each node within the consensus tree is supported by numerous synapomorphies, these are coded ambiguously in some taxa due to bad preservation, while others are homoplastic, and Bremer support values for the consensus tree are extremely low (Fig. 9). Preservational differences between key collections of fossil birds make it nearly impossible to identify synapomorphies that can be scored in all taxa for a given clade. Meanwhile, many of the existing synapomorphies have collapsed in light of the discovery of new morphological diversity. For example, one recently described basal ornithurine, *Schizooura lii*, although clearly ornithurine, possesses a Y-shaped enantiornithine-like furcula, the coracoid lacks a lateral process, and the cranial surface of the humerus is flat (Zhou *et al.* 2012), all features that were until recently, within Ornithothoraces, restricted to the enantiornithines. Despite these primitive features, previously unknown among Early Cretaceous members of this derived clade, the taxon preserves a typically ornithurine craniocaudally elongate and largely imperforate sternum with an extensive keel, features absent in another basal

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Figure 9. Cladogram of the strict consensus tree (length, 835 steps) showing the hypothetical phylogenetic relationships of these Mesozoic birds. Note that *Chaoyangia* and *Zhongjianornis* are resolved as basal ornithurines. Only unambiguous synapomorphies are considered here; all synapomorphies are strict, unless stated otherwise. Sapeornithiformes is supported by two synapomorphies: 130, fenestrated deltopectoral crest (homoplastic); 154, semilunate carpal fused to the major and minor metacarpal (coding uncertain in some taxa). Confuciusornithiformes is supported by three synapomorphies: 173, ungual phalanx of major digit smaller than of the alular and minor digits; 174, proximal phalanx of minor digit much shorter than the following phalanges; 232, J-shaped metatarsal I with articular surface planes perpendicular (coding uncertain in some taxa). Ornithothoraces is supported by 11 ambiguous synapomorphies: 26, pneumatic quadrate; 46, caudal mandibular fenestra absent; 56, 11–12 thoracic vertebrae; 61, thoracic vertebrae laterally excavated; 84, scapula articulating below the shoulder end on coracoid; 92, supracoracoidal nerve foramen displaced medially; 105, interclavicular angle less than 70°; 114, rostral margin of sternum broad and rounded; 150, semilunate ridge on dorsal condyle of ulna; 215, condyles of the tibiotarsus equal in cranial projection; 244, alula present. Enantiornithes is supported by 11 synapomorphies (coding uncertain in some taxa): 34 dentary teeth present (reversal); 78, pygostyle distally constricted; 106, furcula dorsolaterally excavated; 107, elongate hypocleidium present; 123, humerus proximal margin centrally concave, rising dorsally and ventrally; 126, ventral tubercle separated from humeral head by a deep capital incision; 139, humerus distal margin angled to long axis of shaft (homoplastic); 142, humerus distal condyles weakly defined; 167, minor metacarpal projects distally more than major metacarpal; 203, femoral posterior trocanter hypertrophied (reversal); 221, distal tarsals free (reversal). Ornithuromorpha is supported by four synapomorphies (coding uncertain in some taxa): 96, curved scapular shaft (homoplastic); 160, shelf-like articular surface on alular metacarpal for alular digit; 168, alular digit short (homoplastic); 212, cnemial crests on tibiotarsus (homoplastic). Consistency index: 0.389; retention index: 0.670. Values listed at nodes indicate absolute and relative Bremer support.

ornithurine, *Archaeorhynchus*, whose sternal morphology is reminiscent of enantiornithines (Zhou & Zhang 2006a). This mosaic distribution of morphologies among taxa and the dwindling number of clear morphological differences between Enantiornithes and Ornithurae as basal taxa are uncovered has diminished the number of synapomorphies in support of each node, resulting in weak support for most traditional clades (e.g. Enantiornithes, Ornithuromorpha, Ornithothoraces) and a collapse in others (e.g. Pygostylia, Longipterygidae). The only way to rectify this problem is to identify new synapomorphies for each clade and increase the amount of morphological data incorporated into the character matrix, no easy task given the varying preservational limitations set by the known diversity and the rapid rate of discovery in China. Currently, all synapomorphies in support of Ornithothoraces, Enantiornithes, and Ornithuromorpha are ambiguous because of the large number of taxa and substantial amount of preservational variability between specimens.

Despite the fact that increasing the number of included taxa causes a decrease in support at certain nodes, it is also only because of this large taxonomic diversity that *Zhongjianornis* and *Chaoyangia* were recognized as ornithurine birds. When an analysis includes a small number of complete taxa which only reflect more derived ornithurines (e.g. *Hongshanornis*, *Yixianornis*, *Apsaravis*, *Gansus*, *Ichthyornis*), the analysis will be unable recognize a relationship with very primitive members and their disparate morphologies. The current analysis included a very large number of basal ornithurine taxa (ornithuromorphs), including recent discoveries such as *Archaeorhynchus* and *Schizooura* that preserve 'enantiornithine-like' morphologies. Although the results of this analysis exemplify the increasing resolution among hypothetical Mesozoic bird relationships that results from the increase in taxa and morphological data, the increase in recently discovered taxa with previously unknown morphological combinations of primitive and derived characters have also reduced the strength of the resulting hypothetical relationships.

Tooth loss

All modern birds possess a beak and no teeth, and thus the loss of teeth among Mesozoic birds is an important step in the evolution of the modern avian rostrum. Teeth have been lost within Dinosauria on multiple occasions (e.g. ornithomimosaurs, oviraptorosaurs), and several times within Aves alone (Makovicky *et al.* 2004). Tooth loss is common among basal birds, with Sapeornithiformes and Jeholornithiformes both having reduced their dentition, while Confuciusornithiformes have lost their teeth entirely (O'Connor *et al.* 2011b); *Zhongjianornis*, which is interpreted as a basal pygostylian, exemplifies this pattern. Among basal ornithurines, several edentulous taxa are also recognized: *Archaeorhynchus*, potentially the hongshanornithids, and *Zhongjianornis* (Zhou & Zhang 2005, 2006a;

O'Connor *et al.* 2010). With basal taxa resolved in a polytomy, it is impossible to determine the pattern of loss within this clade; however, we can infer that teeth were lost on multiple occasions: the edentulous *Archaeorhynchus* is resolved as the basalmost taxon while derived ornithurines *Ichthyornis* and *Hesperornis* retain teeth. Tooth loss among enantiornithines, however, is not as common, with only one Late Cretaceous taxon known to be edentulous and a clade of Early Cretaceous taxa that have lost their maxillary teeth (Elzanowski 1976; O'Connor *et al.* 2011a). This may reflect dietary differences between the two ornithothoracine clades that may relate to the eventual extinction of the larger and more successful Mesozoic clade, Enantiornithes.

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Supplementary material

Supplementary material can be viewed online doi:10.1080/14772019.2012.690455. [doi should be article tag to title page on the website]

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