The Phylogenetic Position of *Ambiortus*: Comparison with Other Mesozoic Birds from Asia[1]

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Abstract—Since the last description of the ornithurine bird *Ambiortus dementjevi* from Mongolia, a wealth of Early Cretaceous birds have been discovered in China. Here we provide a detailed comparison of the anatomy of *Ambiortus* relative to other known Early Cretaceous ornithuromorphs from the Chinese Jehol Group and Xiagou Formation. We include new information on *Ambiortus* from a previously undescribed slab preserving part of the sternum. *Ambiortus* is superficially similar to *Gansus yumenensis* from the Aptian Xiagou Formation but shares more morphological features with *Yixianornis grabaui* (Ornithuromorpha: Songlingornithidae) from the Jiufotang Formation of the Jehol Group. In general, the mosaic pattern of character distribution among early ornithuromorph taxa does not reveal obvious relationships between taxa. *Ambiortus* was placed in a large phylogenetic analysis of Mesozoic birds, which confirms morphological observations and places *Ambiortus* in a polytomy with *Yixianornis* and *Gansus*.

Keywords: Ornithuromorpha, *Ambiortus*, osteology, phylogeny, Early Cretaceous, Mongolia

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INTRODUCTION

Ambiortus dementjevi Kurochkin, 1982 was one of the first described Early Cretaceous ornithuromorph birds. It comes from the Khurilt Ulaan Bulag locality of the Andaikhudag Formation (Hauterverian—Barremian) in the Central Mongolian Altai (Kurochkin, 1982, 1985, 1999, 2000). Although dwarfed by the current Mesozoic bird collections in China, several other isolated Mesozoic bird taxa are also known from Mongolia, including *Apsaravis ukhaana* Norell et Clarke, 2001, *Hollanda luceria* Bell et al., 2010, *Nanantius valifanovi* Kurochkin, 1996, *Elsornis keni* Chiappe et al., 2006, and several specimens of *Gobipteryx minuta* Elzanowski, 1974 (Elzanowski, 1974; Kurochkin, 1996; Norell and Clarke, 2001; Chiappe et al., 2006; Bell et al., 2010); these taxa span the ornithothoracine clade, making Mongolia one of the richest places for Mesozoic birds in the world. Only enantiornithines (*Nanantius*, *Gurilynia nessovi* Kurochkin, 1999 and *Elsornis*) and ornithuromorphs (*Apsaravis, Hollanda, Ambiortus*) are known and, except for *Ambiortus*, these taxa are all from the Late Cretaceous; no primitive long-tailed birds or basal pygostylians (e.g. Sapeornithiformes, Confuciusornithiformes), which form major components of the rich Early Cretaceous Jehol avifauna, are known. The holotype and only known specimen of *Ambiortus dementjevi* is a well-preserved

and articulated partial skeleton, preserving several cervical and thoracic vertebrae, and parts of the left thoracic girdle and wing (specimen PIN, nos. 3790/271-273; Figs. 1—3). The specimen preserves morphologies that were at first indicative of a fairly derived ornithuromorph bird (e.g. curved scapula, bent acromion process, well-developed procoracoid process); the taxon was originally considered a paleognathous bird, however its position within Aves has shifted with the discovery of new taxa from the Jehol Biota. Most recently in a large cladistic analysis aimed towards Mesozoic birds as a whole, *Ambiortus* is resolved as a basal ornithuromorph (O'Connor et al., 2011a).

When *Ambiortus* was first described (Kurochkin, 1982), the Mesozoic record of fossil birds was extremely sparse (Kurochkin, 1999). *Gansus yumenensis* Hou et Liu, 1984 was the first Mesozoic bird described from China (Hou and Liu, 1984). The holotype specimen was collected from the Early Cretaceous Aptian Xiagou Formation in Gansu Province, northwestern China (Hou and Liu, 1984); known from only a single foot, this taxon was never compared with *Ambiortus* because of the lack of overlapping material. Even a decade later, only a small handful of Early Cretaceous birds were known: primarily *Confuciusornis* Hou et al., 1995 and a handful of fragmentary enantiornithines (Hou, 1997). Two ornithurines, *Chaoyangia beishanensis* Hou et Zhang 1993 and *Liaoningornis longidigitrus* Hou, 1996, had also been described (Hou et al., 1996), but the former lacked

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overlapping material with *Ambiortus* and the unusual morphology of the latter has recently proven to be enantiornithine (O'Connor, 2012). In the last major study to address *Ambiortus*, the taxon was compared to the Inner Mongolian bird *Otogornis genghisi* Dong, 1993 from the Lower Cretaceous Yijinghouluo Formation (Kurochkin, 1999). This taxon, known from a partial thoracic girdle and pair of wings, was originally identified as an enantiornithine (Dong, 1993), although when fully described was unassigned to a specific clade (Hou, 1994). The comparative study, however, concluded that both taxa were paleognathous birds (Kurochkin, 1999). Although when comparative material was limited *Ambiortus* and *Otogornis* may have born some superficial similarity (Kurochkin, 1999), a relationship between these two taxa and their placement within Paleognathae is no longer supported; this is primarily due to lack of evidence and a greater understanding of Early Cretaceous ornithuromorph morphology. For example, Kurochkin (2000) noted that the presence of a U-shaped furcula and convex scapular cotyla on the coracoid indicated that *Ambiortus* was a neornithine, features now known to be present in most basal ornithuromorphs. In light of more recent finds and a greater understanding of Enantiornithes, *Otogornis* is considered a member of this large clade (Zhou et al., 2008), although the taxon has been difficult to place in a phylogenetic context and its taxonomic position within Enantiornithes is unstable (O'Connor, 2009). The short and robust shape of the humerus, absence of a procoracoid process on the coracoid and straight scapula, all support the enantiornithine affinity of this taxon (Zhou and Hou, 2002; O'Connor, 2009). Morphologies that suggested this taxon may be more advanced and in fact a paleognath bird (Kurochkin, 1999) are uncorroborated by the specimen; furthermore, the clearest characters that define Paleognathae are from the skull, which is preserved in neither *Ambiortus* nor *Otogornis*.

Record of the early radiation of Ornithuromorpha, the clade that includes modern birds (Neomithes), has grown rapidly during the last decade (Chiappe, 2007; O'Connor et al., 2010; Brocklehurst et al., 2012). Where previously the global record was dominated by largely fragmentary specimens (e.g. *Vorona berivotrensis* Forster et al., 1996, *Vegavis iaai* Clarke et al., 2005) and even in China known taxa were based on incomplete and poorly preserved specimens (e.g. *Chaoyangia*, *Gansus*, *Songlingornis linghensis* Hou, 1997), recent discoveries from the Early Cretaceous Jehol Group and Xiagou Formation are largely complete and well-preserved (e.g. *Yanornis martini* Zhou et Zhang, 2001, *Yixianornis grabaui* Zhou et Zhang, 2001, *Longicrusavis houi* O'Connor et al., 2010, *Jianchangornis microdonta* Zhou et al., 2009, *Schizooura lii* Zhou et al., 2012, *Archaeorhynchus spathula* Zhou et Zhang, 2006, *Hongshanornis longicresta* Zhou et Zhang, 2005, new specimens of *Gansus*), revealing a wealth of data (You et al., 2006; Zhou et al., 2009; O'Connor et al., 2011a; Zhou et al., 2012). Because

scientific understanding of Mesozoic birds has changed rapidly over the past three decades, reexamination of incomplete materials in light of recent information has the potential to reveal important new information (O'Connor et al., 2011b; O'Connor and Zhou, 2013). The holotype of *Ambiortus dementjevi* is one of the most complete Cretaceous ornithuromorph specimens known from outside of China, yet it has not been re-examined in light of the current taxonomic and morphological diversity. Here we redescribe *Ambiortus*, including previously unpublished data, and compare it to recently described taxa, revealing new information regarding the phylogenetic placement of this taxon and the distribution of ornithuromorph lineages in Asia as a whole.

Terminology in this paper primarily follows Baumel and Witmer (1993); Latin is retained for muscles (Baumel et al., 1993), while English equivalents are used for osteological features.

Institutional abbreviations: CAGS, Chinese Academy of Geological Sciences, Beijing, China; FRDC, Fossil Research and Development Center, Third Geology and Mineral Resources Exploration Academy, Gansu Provincial Bureau of Geo—Exploration and Mineral Development, Lanzhou, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; PIN, Borissiak Paleontological Institute of Russian Academy of Sciences, Moscow, Russia.

SYSTEMATIC PALEONTOLOGY

AVES

ORNITHUROMORPHA

Genus *Ambiortus* Kurochkin, 1982

Diagnosis. An ornithuromorph bird the size of extant teal *Anas crecca*, with the unique combination of the following features: a wide procoracoid process perpendicular to the shaft; scapular blade long and thin; scapular acromion hooked; lateral trabecula of the sternum mediolaterally wide, with a concave medial margin and convex lateral margin so that the distal end of the process appears to curve medially; ventral edge of the proximal end of the humerus strongly developed and with a distinct tubercle on its cranial surface; transverse groove is short, fossa-like, and runs dorsoventrally; pneumotricipital fossa of the humerus not developed; deltopectoral crest projected dorsally; bicipital crest distally abruptly ending (revised from Kurochkin, 2000).

Generic composition. Type species only.

Comparisons. From the superficially similar neornithine birds of the family Lithornithidae *Ambiortus* differs in the presence of the following features: well-developed procoracoid process of the coracoid; flat (apparently non-excavated) sulcus m. supracoracoidei of the coracoid; mediolaterally wide and bowed lateral sternal trabeculae; dorsally projected deltopec-
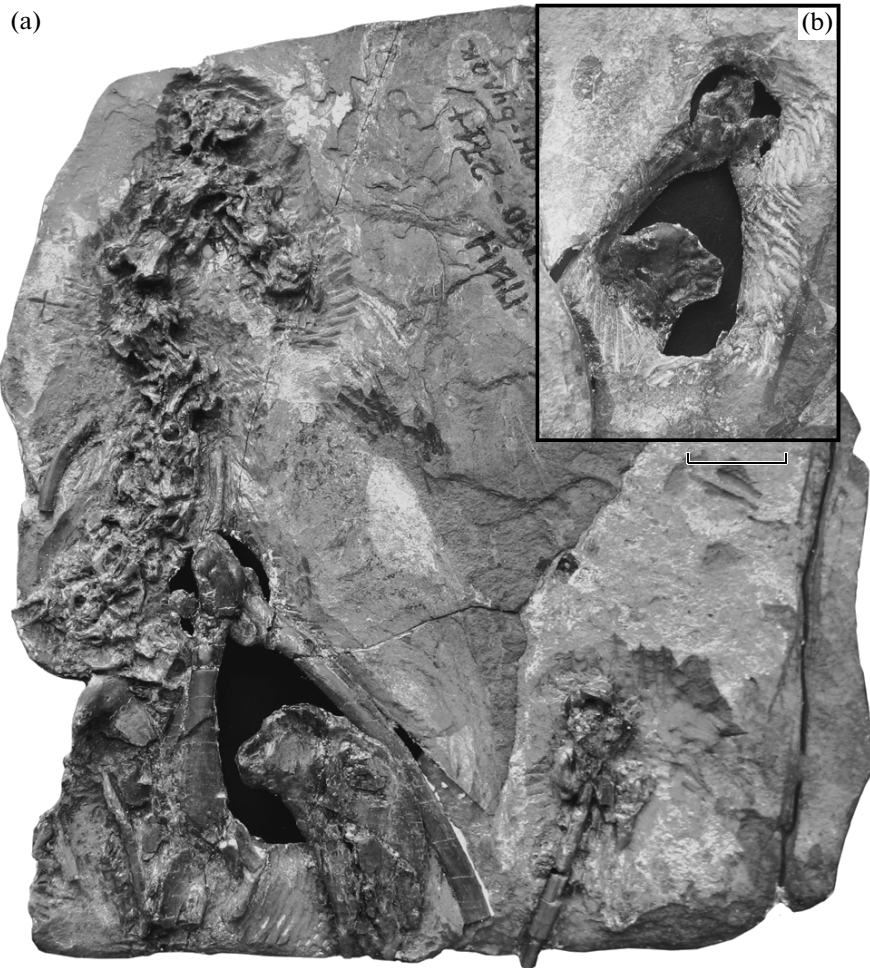
Fig. 1. *Ambiortus dementjevi*, holotype PIN, no. 3790/271; photographs in dorsal (a) and ventral (b) views. Scale bar, 1 cm.

toral crest of the humerus; distal end of bicipital crest of the humerus abrupt; and articular surface of the humeral head facing proximally and caudally, but not cranially (humeral head not fully globe-shaped).

Ambiortus differs from all other Cretaceous birds by the apomorphic condition of the caudal portion of the sternum (see above) and from all Cretaceous birds except *Apsaravis* in the morphology of its proximal scapula. The acromion of *Ambiortus* is well-developed; the caudal portion is robust while its apex is sharply tapered in mediolateral view. The longitudinal axes of the caudal and cranial halves of this process have different orientations (craniodorsal and cranial, respectively) so that the dorsal margin of the acromion is not straight but bent. *Apsaravis* shows a somewhat similar morphology of the proximal scapula but the bend in the acromion demarcates an acute angle in *Apsaravis* while this angle is obtuse in *Ambiortus*, and the process is untapered cranially in *Apsaravis*.

Ambiortus differs from all Cretaceous ornithuromorph except *Gansus, Yixianornis* and *Yanornis* by the presence of a wide procoracoid process perpendicular to the shaft. *Ambiortus* further differs from *Yanornis* by having a much less robust furcula, and from *Gansus* by lacking a delicate omal projection on the lateral process of the coracoid and by the abrupt distal margin of the bicipital crest of the humerus. *Ambiortus* further differs from *Yixianornis* by the presence of a slight groove on the distal half of the lateral surface of the scapula and the curved sternal margin of the furcula.

Ambiortus dementjevi Kurochkin, 1982

Ambiortus dementjevi: Kurochkin, 1982, p. 453, Figs. 1, 2; 1985, p. 272, Fig. 1; 1999, p. 272, Figs. 1–5; 2000, p. 549. Figs. 27.7, 27.8.

H o l o t y p e. PIN, nos. 3790/271, 273, partial skeleton preserved in three slabs.

D e s c r i p t i o n (comparative). *Axial skeleton*. As described by Kurochkin (1982, 1985, 1999), only cervical and thoracic vertebrae are preserved in *Ambiortus*; the entire series is in articulation but poorly preserved (Figs. 1, 2). Approximately seven cervical vertebrae are present; the most cranial cervical vertebrae are missing and the total number of cervicals is

unknown. A slight disarticulation between the fourth and fifth preserved cervical vertebrae suggests the articular surfaces were amphicoelous, as originally reported by Kurochkin (1985). However, Kurochkin (1999) reported on a cervical that was prepared free of the matrix that was fully heteroceolous. Heterocoely limited to the cranial cervical vertebrae (caudal cervicals amphicoelous) is present in a number of ornithothoracine taxa (e.g. *Yixianornis, Gansus, Pengornis houi* Zhou et al., 2008)—given the incomplete preservation of the cranial cervical series, this cannot be ruled out in *Ambiortus*. An opisthocoelous condition, like that present in some neornithines (potentially plesiomorphic to the clade), also cannot be ruled out. The costal processes are delicate and rod-like, fully fused and nearly as long as the vertebral centra. The caudal cervicals appear to be in ventral view; this surface is not strongly keeled (as in most enantiornithines and some ornithuromorphs, *Apsaravis* and *Gansus*) and developed carotid processes appear to be absent.

The proximal three to four thoracic vertebrae are preserved in articulation with the cervical vertebrae (Figs. 1, 2). They are preserved completely in articulation, not revealing the morphology of their articular surfaces. Although poor preservation makes it hard to assess morphological details, deep, broad fossae are visible excavating the lateral surface of the centra, as in other ornithuromorphs; similar fossae are present in enantiornithines, however in this group they are more narrow and deep than broad.

Coracoid. The left coracoid is nearly complete (right not preserved); only the medial angle is incomplete (Figs. 1, 2). The acrocoracoid is short, straight and slightly tapered inward (medially) proximally. The ventromedial surface of the acrocoracoid bears a proximodistal groove (also visible in *Archaeorhynchus*, specimen IVPP, no. V17091 and *Gansus* (specimen CAGS-IG-04-CM-003) and just proximal to the glenoid, the acrocoracoid bears a small oval-shaped concave facet interpreted as the impression of the acrocoracohumeralis ligament (also present in *Yixianornis*) (Kurochkin, 1985, 1999). The presence of the well-developed facet for the attachment of the acrocoracohumeral ligament strongly indicates that the modern-type ligament-based force balance system of the shoulder joint (Baier et al., 2007) was present in the Early Cretaceous ornithuromorphs. The glenoid is nearly flat; its ventral margin forms a labrum, separating the facet from the neck. Just distal to the head (slightly overlapping with the distal margin of the glenoid facet), a well-developed procoracoid process is present (Kurochkin, 1982, 1985, 1999); this feature may be an synapomorphy of Ornithuromorpha (Fig. 3; absent in *Apsaravis*; (Clarke and Norell, 2002). The procoracoid is located approximately 30% from the proximal end on the proximodistal axis, as in *Yixianornis* (32%) and *Gansus* (30%), however it is slightly more proximally located in *Yanornis* (26%) and more distally located in *Archaeorhynchus* (40%) and
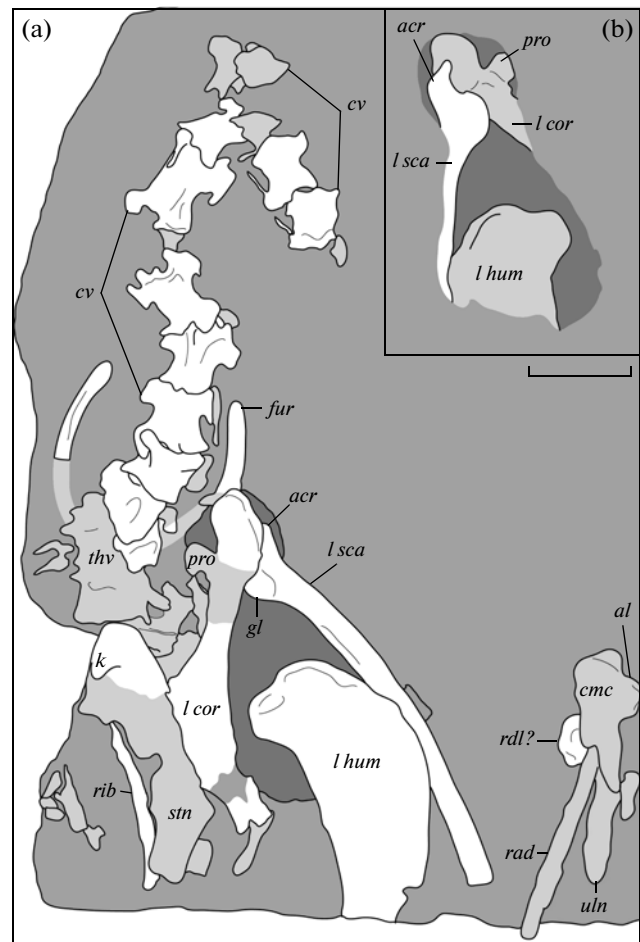

Fig. 2. Interpretive drawing of the holotype of *Ambiortus dementjevi* PIN, no. 3790/271 in dorsal (a) and ventral (b) views. Dark grey indicates where the slab is perforated (allowing some bones to be viewed in both views); medium grey indicates matrix; light grey indicates poorly preserved bone. Designations: (*al*) alular metacarpal; (*acr*) acromion; (*cmc*) carpometacarpus; (*cv*) cervical vertebrae; (*l cor*) left coracoid; (*gl*) glenoid facet; (*l hum*) humerus; (*k*) sternal keel; (*pro*) procoracoid process; (*rad*) radius; (*rdl?*) carpal bone; (*rib*) sternal ribs; (*l sca*) scapula; (*stn*) sternum; (*thv*) thoracic vertebrae; (*uln*) ulna. Scale bar, 1 cm.

Schizooura (49%) (Fig. 3). The process is damaged but appears to be dorsomedially oriented and quadrangular with a flat medial margin. A similar morphology of the procoracoid is also observed in *Ganus* (specimen CAGS-IG-04-CM-004, 012), *Yixianornis* (IVPP, no. V13631) and *"Yanornis"* sp., specimen IVPP, no. V13278 (Fig. 4). The basal ornithuromorphs *Schizooura* and *Archaeorhynchus*, have more disparate procoracoid morphologies: long and craniomedially tapered in the former and small, short, and medially tapered in the latter (Figs. 3a, 3b) (Zhou et al., 2012; Zhou et al., 2013). The procoracoid process is reduced in the neornithine lithornithids. The sulcus of the triosseal canal (sulcus m. supracoracoidei) is not exca-
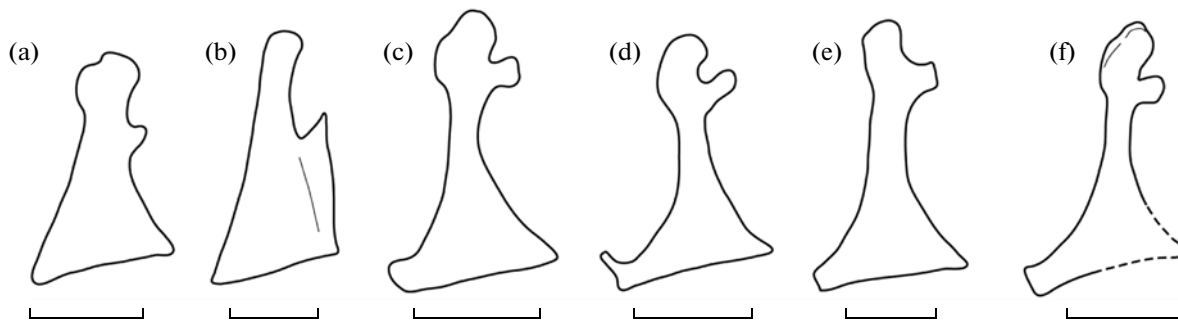
Fig. 3. Comparative drawings of ornithuromorph coracoids (right, ventral view): (a) *Archaeorhynchus spathula*; (b) *Schizooura lii*; (c) *Yixianornis grabaui*; (d) *Gansus yumenensis*; (e) *Yanornis martini*; (f) *Ambiortus dementjevi*—reconstructed portion marked with dash line. Scale bars, 1 cm.

vated in *Ambiortus*; it is almost flat and might have been very slightly concave. The articular facet for the scapula is located on the dorsal surface, lateral to the procoracoid process; although obscured by articulation with the scapula, the surface appears to be a small, circular, and deeply concave. A slit is visible between the shaft and the basal (dorsal) part of the procoracoid process; this may be due to crushing but it is also possible that a slit-like foramen n. supracoracoidei was present (as in storks, for example; the foramen is plesiomorphically present in Neornithes, including Lithornithidae). In *Ambiortus*, the lateral margin of the coracoid is strongly concave, while the medial margin is only gently concave, as in *Gansus*. The distal half of the lateral margin expands to form a lateral process (Kurochkin, 1999). This feature is widespread within Ornithuromorpha (present in *Gansus, Yanornis, Yixianornis, Songlingornis, Longicrusavis, Ichthyornis*), but absent in basal taxa (e.g. *Schizooura, Jianchangornis* and *Archaeorhynchus*). In *Gansus*—and possibly *Ichthyornis* (Marsh, 1880; Clarke, 2004)—the lateral

corner of this process bears a delicate omal projection (specimen CAGS-IG-04–CM-004, Fig.3d; absent in specimen 04-CM-012), similar to the morphology observed in some neornithines with aquatic habits (e.g. *Puffinus, Scolopax*). This feature does not appear present in *Ambiortus*. The dorsal surface of the coracoid, although not visible, is inferred to be nearly flat, lacking the deep, narrow excavation present in *Apsaravis* and some enantiornithines (e.g. *Enantiornis*) (Clarke and Norell, 2002; O'Connor, 2009); the presence of a broad and shallow fossa for the m. sternocoracoidei, like that in *Gansus, Yixianornis*, and *Yanornis*, cannot be determined in *Ambiortus*.

Scapula. The left scapula is incomplete in *Ambiortus*, missing the distal end (Figs. 1, 2); the scapular shaft is elongate and curved (Kurochkin, 1999), typical of Ornithuromorpha (e.g. *Longicrusavis, Yixianornis, Yanornis, Gansus*; Fig. 5). The shaft is mediolaterally compressed and the distal half of the lateral surface bears a slight groove interpreted for muscle attachment (Kurochkin, 1999) that is also present in *Gansus, Hongshanornis* and *Yanornis* (absent in *Yixianornis*). The acromion is well-developed; the caudal (proximal) portion is robust while the cranial (distal) half is sharply tapered in mediolateral view. The longitudinal axes of the caudal and cranial halves of this process have different orientations (craniodorsal and cranial, respectively) so that the dorsal margin of the acromion is not straight but bent. As was first noted by Kurochkin (1985), this is very similar to the morphology observed in Lithornithidae (Fig. 4d; Houde, 1988). *Apsaravis* also shows a similar morphology but the two taxa differ in that the bend in the acromion demarcates an acute angle in *Apsaravis* (obtuse in *Ambiortus* and *Lithornis*) and the process is untapered cranially (Clarke, Norell, 2002). In dorsal view, the tapered portion of the acromion is spatulate, interpreted as the articular facet for the furcula (Fig. 2b). The acromion process in *Gansus* is similar in that it is well-developed, however this taxon differs in that the process is rectangular, unbent and untapered (in lateral view, specimen CAGS-IG-04-CM-017) (You et al., 2006); these taxa greatly differ from the short
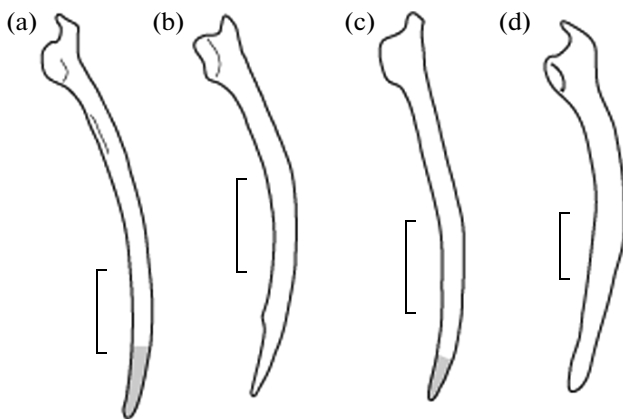

Fig. 4. Comparative drawings of ornithuromorph scapulae: (a) *Ambiortus dementjevi*; (b) *Yixianornis grabaui*; (c) *Gansus yumenensis*; (d) *Lithornis plebus*, USNM, no. 336534 (from Houde, 1988). Scale bars, 1 cm. Grey areas not preserved.
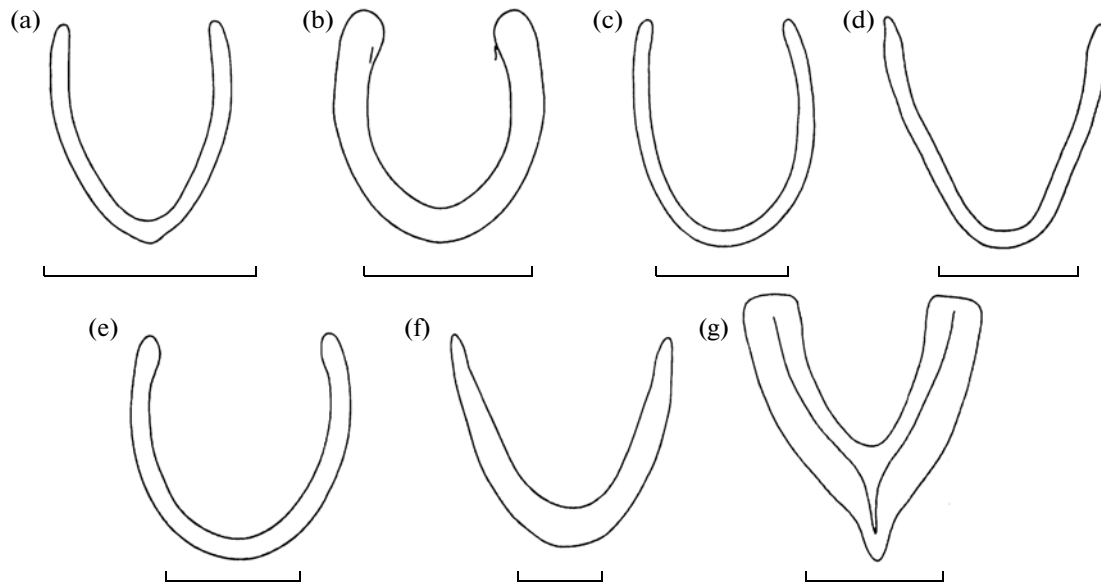
Fig. 5. Comparative drawings of ornithuromorph furcula: (a) *Longicrusavis houi*; (b) *Archaeorhynchus spathula*; (c) *Gansus yumenensis*; (d) *Yixianornis grabaui*; (e) *Ambiortus dementjevi*; (f) *Yanornis martini*; (g) *Schizooura lii*. Dark grey indicates matrix; light grey indicates poorly preserved bone or heavily reconstructed areas. Scale bars, 1 cm.

and bluntly tapered morphology in *Yixianornis* (extremely reduced in *Ichthyornis*; Clarke, 2004), or the short and sharply tapered morphology in *Hongshanornis*. The glenoid facet is flat, as in *Gansus* and *Hongshanornis* (slightly concave in *Ichthyornis*) and its plane is somewhat inclined in relation to the plane of the shaft, as in most neornithines, including Lithornithidae (Kurochkin, 1999). The coracoidal tubercle, not visible in *Ambiortus* (contra Kurochkin, 1999), is developed as a slight convexity proximomedial to the glenoid in other Early Cretaceous taxa (e.g. *Gansus*, *Yixianornis, Hongshanornis*), contrasting with the condition in *Ichthyornis* (Clarke, 2004).

Furcula—only the omal halves of the clavicular rami are preserved in *Ambiortus* (Figs. 1, 2). The rami are delicate and have oval cross-sections, with the long axis lateroventral-mediodorsally oriented. The omal tips are slightly medially oriented and the rami are somewhat curved throughout, suggesting the furcula was u-shaped (Fig. 5). The distal ends are blunt and not developed into distinct acromial or acrocoracoid processes (Kurochkin, 1999). According to Kurochkin (1999), before preparation there existed a void of the inter-clavicular symphysis that indicated the presence of a small boss where otherwise there might exist a hypocleidium (furcular apophysis). Ornithuromorpha encompasses a large range of furcular morphologies (Fig. 5); *Ambiortus* is most similar to *Gansus* (Fig. 5c; specimen CAGS-IG-04-CM-012) and the hongshanornithids (Fig. 5a). *Archaeorhynchus* (Fig. 5b) and *Jiuquanornis* Wang et al., 2013 (specimen FRDC-05-CM-021) from the Xiagou Formation (You et al., 2010) are also overall very similar, only

more robust and with well-developed acromial processes (tapered in the former, blunt and caudally projecting in the latter) (Zhou et al., 2012). *Yixianornis* and *Songlingornis* both possess a straight (as opposed to curved) sternal (ventral) margin (Clarke et al., 2006), and the omal tips of the clavicular rami distinctly taper into small acromial processes in *Yixianornis* (Fig. 5d). Although contacting the matrix, it appears the dorsal surface of the omal tips may have bore a flat articular surface, which would fit interpretations regarding the flat facet on the acromion process of the scapula (Kurochkin, 1999). The furcula is robust in *Yanornis* (Fig. 5f) and *Zhongjianornis yangi* Zhou et al., 2009, and *Schizooura* has a V-shaped furcula with a hypocleidium (Fig. 6g), very different from other ornithuromorphs but similar to enantiornithines (especially *Pengornis*) (Zhou et al., 2012).

Sternum—the left half of the rostral most portion of the sternum is preserved in the main slab of *Ambiortus*, specimen PIN, no. 3790/271 (Figs. 1a, 2a), and the left caudal half of the sternum is preserved as an impression in the specimen PIN, no. 3790/273 (previously undescribed; Fig. 6a, 6c). The rostral margin is parabolic; the single preserved coracoidal sulcus is strongly angled laterocaudally so that the rostral margin of the sternum would have formed a tall arch (Fig. 2a) (Kurochkin, 1999). The sternal rostrum in *Gansus* is similar with an inner angle estimated at 110° (specimen CAGS-IG-04-CM-012). The relative position of the coracoidal sulci is unclear and it cannot be determined if they were crossed, as in *Ichthyornis* (Clarke, 2004). The well-developed coracoidal sulci in *Gansus* and *Yixianornis* were certainly closely spaced
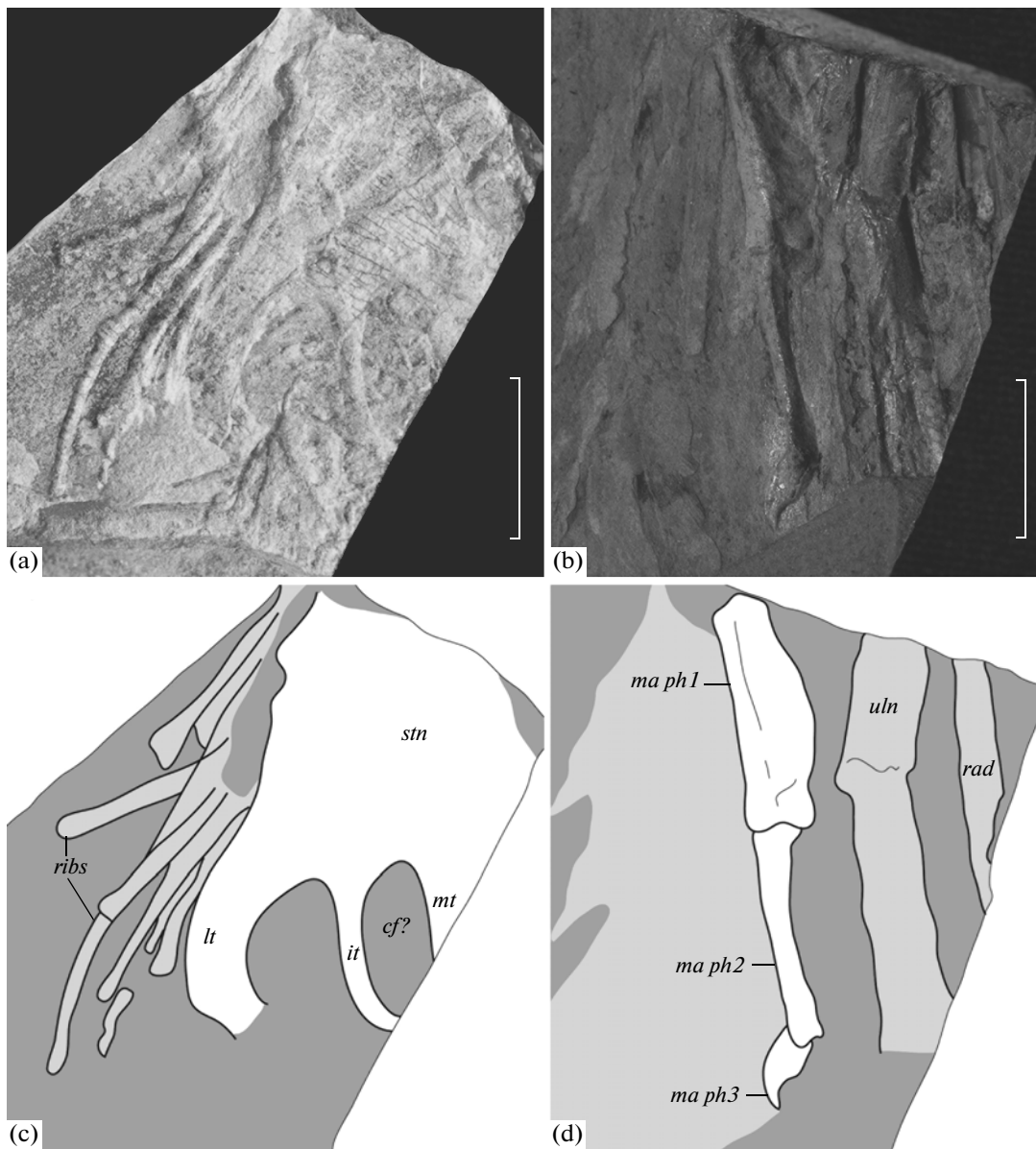
Fig. 6. Counter slabs of the holotype of *Ambiortus dementjevi*: (a), photograph PIN 3790/272; (b) photograph of PIN3790/273; (c), interpretive drawing of PIN 3790/272; (d), interpretive drawing of 3790/273. Designations: (*cf?*) caudal fenestra; (*it*) intermediate trabecula; (*lt*) lateral trabecula; (*ma ph1*) major digit first phalanx; (*ma ph2*) major digit second phalanx; (*ma ph3*) major digit ungual phalanx; (*mt*) median trabecula; see also Fig. 2. Dark grey indicates matrix; light grey indicates poorly preserved bone. Scale bars, 1 cm.

and potentially may have crossed each other medially although this also cannot be confirmed in either taxon. The proximal portion of the base of the keel is preserved in *Ambiortus* (Fig. 2a), although the extent of the ventral projection of the keel is unknown; the base of the keel does not reach the rostral margin, although the cranioventral margin of the keel may have been level with the rostral margin, as in *Yixianornis* and *Lithornis*. The keel extends to the rostral margin in *Gansus* (specimen CAGS-IG-04-CM-003), *Yanornis* (specimen IVPP, no. V13278), and *Archaeorhynchus* (specimen IVPP, no. V17091).

The impression of the distal portion of the sternum, not previously described, indicates the presence of two pairs of caudal trabeculae as in most Early Cretaceous ornithuromorphs (*Archaeorhynchus*, *Yanornis*, *Yixianornis*, *Gansus*, *Songlingornis*; reduced in *Jianchangornis* and *Schizooura*). The lateral trabecula is mediolaterally wide, with a concave medial margin and convex lateral margin (autapomorphy) so that the distal end of the process appears to curve medially (Figs. 6a, 6c). *Yanornis*, *Yixianornis*, and *Songlingornis* have a similar morphology (Clarke et al., 2006), with wide lateral trabeculae, however these taxa possess large distal
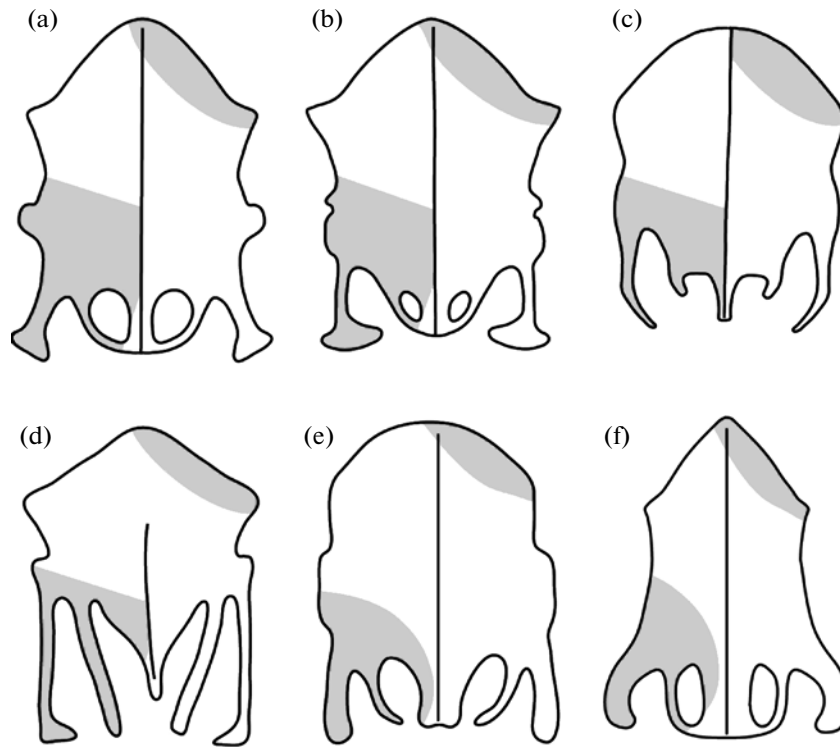
Fig. 7. Comparative drawings of ornithuromorph sterna: (a) *Yanornis martini*; (b) *Yixianornis grabaui*; (c) *Hongshanornis longicresta*; (d) *Archaeorhynchus spathula*; (e) *Gansus yumenensis* (subadult); (f) *Ambiortus dementjevi.* Grey indicates preserved areas in *Ambiortus.* Not to scale.

expansions and lack the distomedial curvature present in *Ambiortus* (Fig. 7). In *Gansus*, this process is more delicate, straight, and does not have strong lateral projection (specimen CAGS-IG-04-CM-003) (You et al., 2006). In *Hongshanornis* the lateral trabeculae are curved and lack distal expansions, but differ from *Ambiortus* in that they are very narrow and delicate. The intermediate trabecula in *Ambiortus* is as long as the lateral trabecula (consistent with other ornithuromorphs), although much thinner and less recurved. It appears to enclose a caudal fenestra like that present in *Songlingornis, Yanornis* and *Yixianornis* (Clarke et al., 2006), however the distal margin of the sternum, including the distal ends of the caudal trabeculae, are not fully preserved and the presence of a fenestra cannot be confirmed with absolute certainty (Figs. 6a, 6c). In *Gansus* the fenestra remains open mediodistally in the specimen CAGS-IG-04-CM-003 but is closed in the specimen IVPP V15076 (Li et al., 2011), indicating this feature is affected by ontogeny. The proximolateral margin of the sternum (costal margin) in *Ambiortus* is level (aligned) with the intermediate trabeculae (autapomorphy); in *Gansus*, the costal margin is level with the lateral trabeculae. In other taxa with laterally splayed trabeculae (e.g. *Songlingornis, Yixianornis*) the level of the costal margin is between the lateral and intermediate trabeculae—no other taxon displays the level of lateral projection present in *Ambiortus*. Although the lateral margin is incomplete, a short lat-

erally projecting "zyphoid" process (Clarke et al., 2006) cranial to the caudal trabeculae, like that present in *Gansus, Yixianornis* and *Songlingornis*, appears to be absent in *Ambiortus* (as in *Archaeorhynchus* and *Jianchangornis*) (Fig. 7).

Humerus. Only the proximal half of the left humerus is preserved in *Ambiortus* (Figs. 1, 2). The humeral head is not as well-defined, proximodorsally forming a continuous convexity with the deltopectoral crest (as in *Gansus*). The articular surface of the humeral head is continuous with the proximal deltopectoral crest; the articular surface of the humeral head faces proximally and caudally, but not cranially as in more advance birds and thus the head is not completely globular. The bicipital crest shows very little cranial projection (Kurochkin, 1985, 1999) (hypertrophied in some enantiornithines), consistent with other basal ornithuromorphs (*Gansus, Ichthyornis, Yanornis*). In profile (cranial view), the bicipital crest is separated from the humeral head by a concavity (*Archaeorhynchus, Ichthyornis, Longicrusavis*); distally, the crest ends abruptly, as in *Ichthyornis* and *Zhongjianornis* (gradually diminishes in *Archaeorhynchus, Gansus, Jianchangornis, Longicrusavis, Schizooura* and *Lithornis*) (Zhou et al., 2012) (Fig. 8). The proximocranial surface of the bicipital crest bears a short, deep dorsoventrally oriented groove-like depression, also present in *Gansus* (specimen CAGS-IG-04-CM-012); this
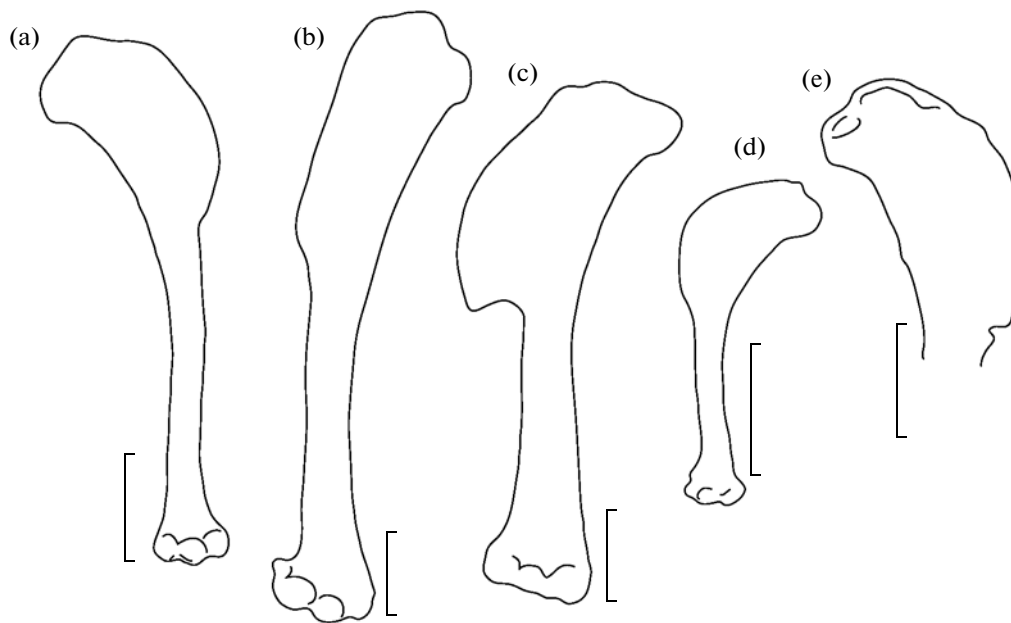
Fig. 8. Comparative drawings of ornithuromorph humeri: (a) *Gansus yumenensis*; (b) *Yanornis martini*; (c) *Schizooura lii*; (d) *Longicrusavis houi*; (e) *Ambiortus dementjevi*. Scale bars, 1 cm.

surface is interpreted as the transverse ligamental groove (Kurochkin, 1985, 1999). Some enantiornithines, including *Otogornis*, have a circular fossa excavating the cranial surface of the humerus (e.g. *Gurilynia, Martinavis* Martin et al., 2007, *Longipteryx chaoyangensis* Zhang et al., 2001, *Cathayornis yandica* Zhou et al., 1992) although a transverse ligamental groove is reportedly present in some enantiornithines (Chiappe, Walker, 2002). In basal ornithuromorph taxa, the humeral head is flat on the cranial surface (*Schizooura, Archaeorhynchus*); the cranial surface is convex forming a globe-shaped humeral head in more derived taxa (*Gansus, Ichthyornis*). In *Ambiortus*, the cranial surface is concave, but limited only to the most proximal portion, so that the proximocranial margin forms a labum that continues along the proximal quarter of the deltopectoral crest. This feature may be exaggerated by crushing. Just distal to this labum, the cranial surface is centrally concave.

The dorsally projecting deltopectoral crest in *Ambiortus* is subequal to the shaft in width, rounded (Kurochkin, 1999), and appears to taper into the shaft distally as in most ornithuromorph taxa (e.g. *Yanornis, Yixianornis, Hongshanornis, Longicrusavis, Jianchangornis, Gansus*); the crest projects cranially in *Lithornis* and other neornithine birds. The crest is proportionately wider in the hongshanornithids but narrower in *Yanornis; Schizooura* and *Zhongjianornis* share an unusual morphology in which the crest does not taper into the shaft distally, rather the dorsodistal corner of the crest forms a distinct projection (O'Connor and Zhou, 2013; Zhou et al., 2012). On the caudal surface the area of the ventral tubercle (and capital incision) is damaged although we interpret a ventral tubercle

would have been present (Kurochkin, 1999). A separated dorsal tubercle is absent (Kurochkin, 1999). Just distal to the humeral head the caudal surface of the bone is slightly convex.

Ulna and radius. Only fragments of the antebrachium are preserved in the holotype of *Ambiortus* (Figs. 1, 2, 6). The radius is much more narrow than the ulna.

Carpals and Carpometacarpus. Ambiortus preserves a single proximal carpal, preserved underlying the proximal end of the carpometacarpus (Figs. 1, 2). The exposed portion appears rectangular, not V-shaped, which may suggest that this is the radiale, however, its size is more consistent with the ulnare (as interpreted by Kurochkin, 1999); the surface is concave centrally with another concavity on the surface facing away from the carpometacarpus.

The hand is very poorly preserved in *Ambiortus*; the ventral aspect of the carpometacarpus is preserved in the main slab overlying the radius and ulna (Figs. 1a, 2a). The carpometacarpus is fully fused proximally, forming a well-developed carpal trochlea (Kurochkin, 1999), typical of Ornithuromorpha (fuses late in more basal birds and is often preserved unfused, e.g. *Rapaxavis pani* Morschhauser et al., 2009, *Shenqiornis mengi* Wang et al., 2010). An extensor process, present in *Gansus*, is reportedly present in *Ambiortus* (Kurochkin, 1999). This feature cannot be confirmed, although the dorsal and ventral profiles of the alular metacarpal are not symmetrical; the thickest region on the ventral surface is distally located, while it appears the thickest region on the dorsal surface is proximally located (visible even though the carpometacarpus is in ventral view). The cranioventral margin of the alular

metacarpal bears a facet that tapers proximally. Whether these are true morphologies or the result of poor preservation cannot be determined.

The alular digit is not preserved in *Ambiortus*, nor is the minor digit. The major digit, preserved as an impression (Figs. 6b, 6d; specimen PIN, no. 3379/272), has three phalanges; the caudal margin is not very clear but the first phalanx does not appear as strongly dorsoventrally compressed and caudally expanded (Kurochkin, 1999) as in most other ornithuromorphs (*Yanornis, Yixianornis*). The cranial pila is well developed along the entire length of the phalanx. It appears a small internal index process (Stegmann, 1978) was present but it does not project past the distal articular surface as it does in *Ichthyornis* (Clarke, 2004). The intermediate phalanx is delicate, half the thickness of the first, and tapered slightly (Kurochkin, 1999). The ungual phalanx is small and relatively uncurved (more curved in *Yixianornis*; proportionately larger in *Longicrusavis* and *Yanornis*); the major digit ungual appears reduced in *Gansus* as well (specimen CAGS-IG-04-CM-004).

M a t e r i a l. Holotype.

Phylogeny

The dataset is a modified version of O'Connor and Zhou (2012); scorings for *Ambiortus* were modified based on this study of the specimen and *Lithornis* (scored for the genus) and several newly described ornithuromorph taxa (e.g. *Schizooura lii, Jianchangornis microdonta, Zhongjianornis yangi*) were added to the dataset. A total of 60 taxa were scored for 245 equally weighted characters, 31 of which were treated as ordered; Dromaeosauridae was used as the outgroup. The dataset was analyzed using TNT (Goloboff et al., 2008); we conducted a heuristic search retaining the single shortest tree from every 1000 trees (producing four trees 850 steps long) followed by an additional round of tree bisection and reconnection (TBR) branch swapping. This analysis produced 5760 most parsimonious trees (length = 850 steps; CI = 0.385; RI = 0.671; Fig. 9). The Nelson strict consensus tree is consistent with that published by O'Connor et al. (2011) in the non-ornithothoracine part of the tree. The enantiornithine clade shows greater resolution while the ornithuromorph clade shows less. Relationships are poorly supported, but notably *Liaoningornis* and *Eoalulavis hoyasi* Sanz et al., 1996 form a clade, 'longipterygidae' is resolved as *Boluochia zhengi* Zhou 1995 + *Longipteryx*, and *Rapaxavis* forms a clade with *Shanweiniao cooperorum* O'Connor et al., 2009 + *Longirostravis hani* Hou et al., 2004 ('Longirostravisidae'). Within Ornithuromorpha, *Archaeorchynchus* is resolved as the most basal taxon, with *Jianchangornis* and *Patagopteryx deferrariisi* Alvarenga et Bonaparte, 1992 forming successive outgroups to a clade formed by a dichotomy between a polytomy between *Schizooura, Zhongjianornis* and
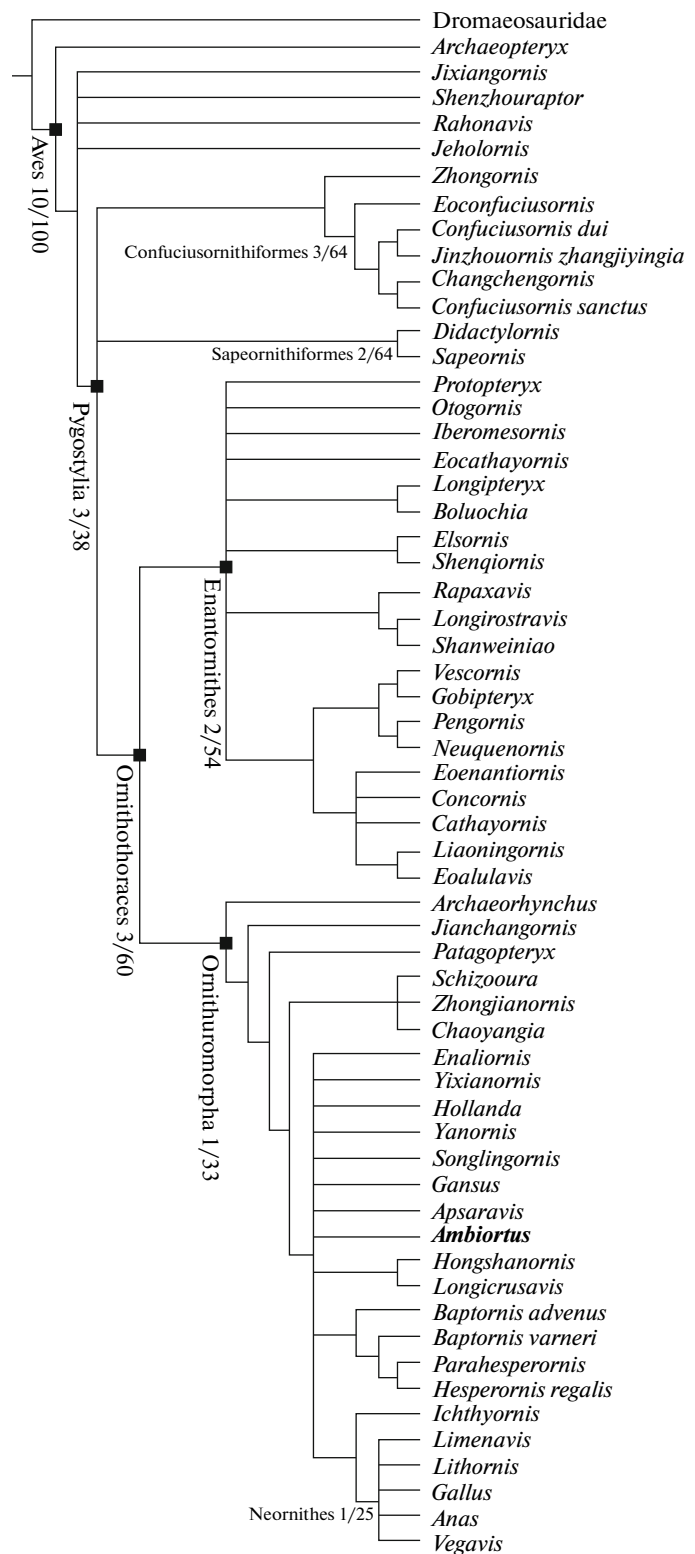

Fig. 9. Cladogram of the strict consensus tree (5760 MPT's, length 850 steps) of the hypothetical phylogenetic relationships of these Mesozoic birds. Note that *Ambiortus, Gansus, Yixianornis* and the other 'songlingornthids' are grouped together in a polytomy of ornithuromorph taxa. Major nodes are marked with absolute/relative Bremer support values.

Chaoyangia, and the clade that includes all other more derived birds. This clade is a polytomy between *Ambiortus, Enaliornis* Seeley 1876, *Yixianornis, Gansus, Yanornis, Hollanda, Apsaravis, Songlingornis*, Hongshanornithidae, Hesperornithiformes, and a polytomy between *Anas, Gallus, Lithornis, Limenavis patagonica* Clarke et Chiappe, 2001 and *Vegavis* with *Ichthyornis* as the sister taxon.

DISCUSSION

Ambiortus preserves a number of features that firmly place the taxon within the derived ornithothoracine clade: rectangular medially projecting procoracoid; lateral process on coracoid; U-shaped furcula; curved scapula; rounded deltopectoral crest; and sternal keel nearly or reaching the rostral margin of the sternum. *Ambiortus* is the only definitive ornithuromorph from Mongolia and the most important Early Cretaceous specimen from outside China. Geographically, the next closest major fossil avifauna is that of the Xiagou Formation, which has yielded a large number of specimens of mostly *Gansus*. The Xiagou Formation, like the Mongolian Andaikhudag Formation (Shuvalov, 2000), is composed of continental deposits, as opposed to near-shore lacustrine like the Jehol Group. Ambiortus superficially resembles *Gansus*, although separated by differences in sternal, coracoidal, and scapular morphology. Although sharing many morphological features with certain Jehol taxa, these species show distinct differences in body plan, typically showing more robust body shapes. Given that the Xiagou Formation (115−105 Ma) and Andaikhudag Formation, (136−125 Ma) (Kurochkin, 2000) are separated by somewhere between 10 to 30 Ma, the superficial similarities in body-shape between *Gansus* and *Ambiortus* may be related to similar adaptations to comparable environments, suggesting that *Ambiortus* might have been waterbird as well. This is consistent with other Cretaceous ornithuromorphs, which tend to show aquatic niches (O'Connor et al., 2010).

Ambiortus shares features with a number of ornithuromorph taxa (*Yixianornis, Lithornis, Gansus*). The sternum possesses autapomorphies, but shows a high degree of similarity to the 'songlingornithids' *Yixianornis, Yanornis* and *Songlingornis*; these taxa share the presence of robust lateral trabeculae and caudal fenestrae (Fig. 7). Although sternal morphology was once thought to be fairly conservative, as more ornithuromorph specimens accumulate the range of sternal morphologies continues to rise (You et al., 2010); closely related species tend to show a relatively high degree of similarity to each other (e.g. Hongshanornithidae, Songlingornithidae), which may suggest *Ambiortus* is related to this clade. The shape of the acromion process of the scapula is very similar to that observed in Lithornithiformes (Fig. 4), which may also suggest a close relationship, although this group is considered to be fairly derived within Aves (Neornithes: Paleognathae) (Houde, 1988). As has been the case with the enantiornithines, the increase in ornithuromorph taxonomic diversity has not resulted in greater systematic clarity—rather the known diversity shows no clear pattern of character acquisition.

Because morphological comparison does not readily reveal relationships, we placed *Ambiortus* together with other similar taxa (*Lithornis*) into a cladistic analysis in order to test hypothetical relationships and previous hypotheses that this taxon may be a more derived paleognathous bird (Kurochkin, 1985, 2000). The results conform with our morphological observations, placing *Ambiortus* in a polytomy that includes morphologically similar taxa, *Yixianornis, Yanornis, Songlingornis* ('Songlingornithidae') and *Gansus* (Fig. 9). Seventeen character changes occur at the node that separates the *Ambiortus* polytomy from more derived birds (*Ichthyornis* + *Neornithes*). Although several of these features are homoplastic (characters 116, 134, 172, 191), the node is marked by: a higher degree of fusion (characters 1 and 47); increased pneumaticity (characters 36, 120); advances in the morphology of the quadrate (character 25: 0 ⟶ 1); the presence of a dorsal supracondylar process (character 134: 1 ⟶ 2); a well-differentiated ulnare (character 152: 0 ⟶ 1); the presence of a pisiform process (character 156: 1 ⟶ 2); the loss of the major digit claw (character 172); reduction of the pubis (character 197: 1 ⟶ 2); the presence of two proximal tarsometatarsal vascular foramen (character 226: 1 ⟶ 2); the presence of an intercotylar eminence (character 228: 0 ⟶ 1); and the presence of a well-developed facet for metatarsal I on the plantar surface of metatarsal II (character 234: 0 ⟶ 1). Although most of these features cannot be scored in the holotype of *Ambiortus*, this taxon does retain a manual claw on the major digit. The analysis confirms hypotheses that *Lithornis* is more derived, although the inclusion of this taxon resulted in a collapse of Ornithurae, Ichthyornithiformes and Neornithes. These results highlight an already recognized need to increase character sampling in Mesozoic bird datasets (O'Connor and Zhou, 2013).

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