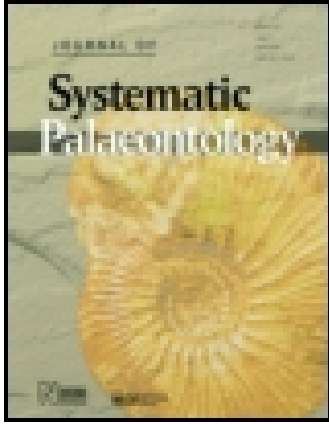


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A historical specimen of enantiornithine bird from the Early Cretaceous of Mongolia representing a new taxon with a specialized neck morphology

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We describe *Holbotia ponomarenkoi* gen. et sp. nov., the first articulated specimen of an enantiornithine bird from Mongolia, unearthed in 1977 from Early Cretaceous deposits and formerly thought to be a pterosaur. The specimen shows a series of morphological details that are either unique to the new taxon or very poorly known for Enantiornithes. A previously unobserved specialized cervical morphology, the development of a crest on the caudal surface of the distal tibia, and the presence of unusually widely spaced small teeth in the lower jaw are unique features of *Holbotia*. The results of a phylogenetic analysis indicate that *Holbotia* is more closely related to the Late Cretaceous edentulous *Gobipteryx* than to the Early Cretaceous enantiornithines with reduced dentition (Longipterygidae), which implies a different evolutionary pathway for the loss of teeth in Enantiornithes, as compared with Ornithuromorpha. The only preserved cervical vertebra of *Holbotia ponomarenkoi* displays partly ventrally facing prezygapophyseal articular surfaces, otherwise found only in the darters (Anhingidae), which implies an unusually increased degree of neck mobility. Morphology of the palate, described in detail for an Early Cretaceous enantiornithine bird for the first time, is roughly similar to that of *Archaeopteryx* and non-avian paravians. It shows that the evolution of specialized rostral morphology in Early Cretaceous enantiornithines was possible with retention of the primitive palatal structure, in contrast to modern birds (Neornithes), where the diversification of skull types was coupled with the evolution of several types of palate.

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Keywords: Enantiornithes; Mongolia; Early Cretaceous; teeth; bony palate; cervical vertebra

Introduction

The Enantiornithes are a diverse clade of Cretaceous birds first established in 1981 based on a collection of disarticulated bones from the Late Cretaceous El Brete locality of the Lecho Formation in Argentina (Walker 1981). For a long time enantiornithine birds were known primarily from isolated bones (see review in O'Connor 2009), and only in the early 1990s were some articulated specimens referred to this clade (Chiappe & Calvo 1994; Martin 1995; Zhou 1995). A number of important Early Cretaceous avian fossils discovered in the late 1980s or early 1990s and now accepted as members of the Enantiornithes (e.g. *Iberomesornis*, *Concornis* and *Sinornis*) were initially placed outside this clade. The same was true for the first unearthed partly articulated specimen of an enantiornithine bird, collected in the late 1970s and described below for the first time.

The specimen (PIN 3147-200; Fig. 1) comes from lacustrine deposits of the Early Cretaceous Andaikhudag

Formation at the Kholboot locality (Fig. 2) in the Mongolian Altai Mountains (Bayankhongor Aimag, Mongolia). It was collected by Soviet palaeontologist A. G. Ponomarenko in 1977, the same year that he collected the holotype and currently only known specimen of *Ambiortus dementjevi*, which was described as the oldest carinate bird in 1982 (Kurochkin 1982, 1985) and is now generally regarded as a member of Ornithuromorpha outside Ornithurae. Specimen PIN 3147-200 was found just 10 km to the west of the Khurilt Ulaan Bulag locality, where the holotype of *Ambiortus dementjevi* was found. A photograph of PIN 3147-200 was published in a popular paper by Kurochkin (1991, p. 44) accompanied with the handwritten label '*Holbotia ponomarenkoi* Kurochkin, 1982'. The skeleton was identified as a 'tiny pterosaur' preserved within an organic residue with two bird feathers alongside. Kurochkin (1991) provisionally interpreted the specimen as the regurgitated pellet of an unknown animal.

The avian nature of specimen PIN 3147-200 was not recognized until the mid-1990s when it was studied by

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Figure 1. *Holbotia ponomarenkoi* gen. et sp. nov., holotype, PIN 3147-200. Overall views of **A**, the slab; and **B**, counterslab.

D. Unwin and N. Bakhurina (Unwin 1993; Bakhurina & Unwin 1995) who rejected the identification of the fossil as a pterosaur and concluded instead that it was a bird, possibly related to *Ambiortus* (simply because it was found in such close proximity). Bakhurina & Unwin (1995, p. 226) also cited a personal communication from Kurochkin, in which he suggested that PIN 3147-200 'is a small, toothed, possibly enantiornithid bird' (see also Kurochkin 1995a, pp. 51–52). This bird was referred to as '*Kholbotiaka*' [nomen nudum] in an abstract (Kurochkin 1994, p. 332). In a review of Mesozoic birds from Mongolia and the USSR, Kurochkin (2000, p. 544) identified PIN 3147-200 as belonging to a new family within his order Euornithiformes (Enantiornithes). He noted two enantiornithine

characters of this specimen: V-shaped furcula with a long hypocleidium, and metatarsals that are fused only proximally. Padian (2004, p. 214) later cited '*Holbotia ponomarenkoi*' as a possible synonym of *Ambiortus dementjevi*, although he provided no evidence.

Here we provide a detailed description of PIN 3147-200, which apparently historically represents the first discovered associated skeleton of an enantiornithine bird. We validate the name *Holbotia ponomarenkoi*, and place this taxon within a phylogenetic context. This new taxon is the only known Early Cretaceous bird from Mongolia; previously only Late Cretaceous enantiornithines were described from the Gobi Desert (Elzanowski 1974, 1976; Kurochkin 1996, 1999; Chiappe *et al.* 2007b; Kurochkin

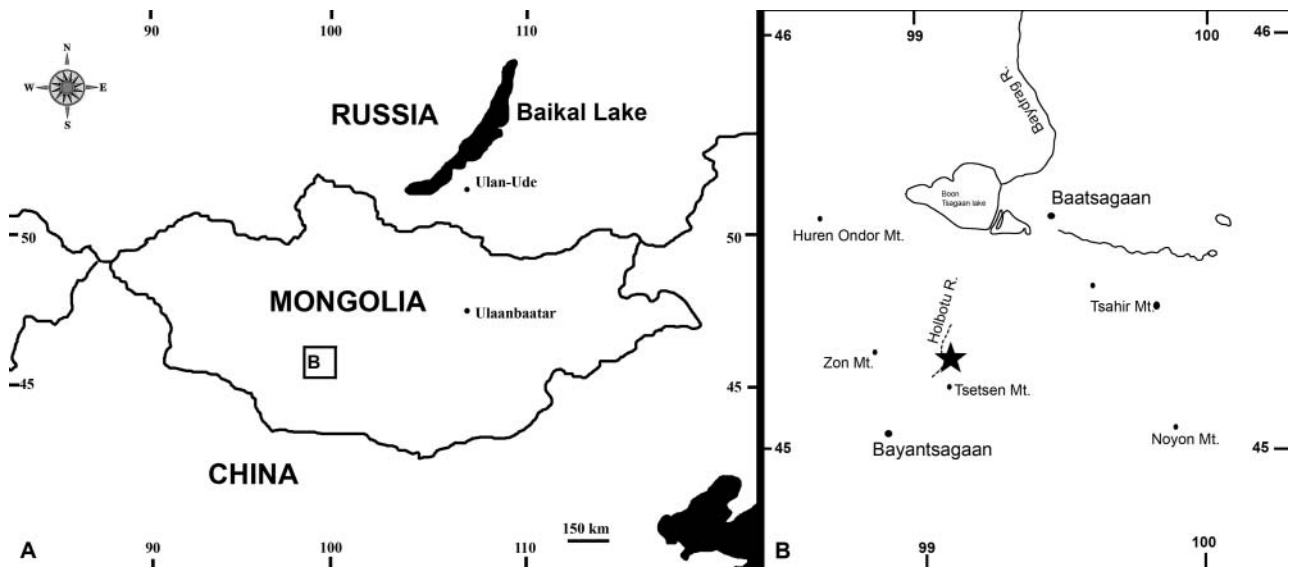


Figure 2. Map showing the geographical position of the locality Kholboot, 10 km west of Khurilt Ulaan Bulag; **A**, large scale map of Mongolia; **B**, detailed map of the central part of the Govi Altay region; star indicates the position of the locality.

et al. 2013). The specimen is stored at the Borissiak Palaeontological Institute of the Russian Academy of Sciences in Moscow (PIN).

Systematic palaeontology

Aves Linnaeus, 1758

Enantiornithes Walker, 1981

Holbotia gen. nov.

Type species. *Holbotia ponomarenkoi* gen. et sp. nov.

Derivation of name. After the locality name in Russian transliteration (Holbot).

Diagnosis. As for type and only species.

Holbotia ponomarenkoi sp. nov.

(Figs 1, 3–12)

Derivation of name. In honour of palaeontologist Alexander G. Ponomarenko, who found the holotype in 1977.

Holotype. PIN 3147-200, a partial skeleton including jaws, a cervical vertebra, furcula and hind limb bones, preserved in a slab and a counterslab (Figs 1, 3).

Occurrence and age. Kholboot (Holbotu), Holbotu-gol, south of Boon Tsagan nuur, north of Tsetsen uul Mountain, Bayankhongor Aimag, Mongolia. Khorilt layers, Andaikhudag Formation; Lower Cretaceous, Hauterivian-Barremian (Sinita 1993; Shuvalov 2000). According to Sinita (1993), the so called ‘pterosaur remains’ came

from the north-western shore of a rather large Early Cretaceous lake. These sediments represent an initial stage of this lake, reflecting a period when it was shallow and productivity was very low.

Diagnosis. Enantiornithine bird diagnosed by the following unique combination of characters: premaxilla low with subparallel dorsal and ventral margins; dentary with widely spaced small teeth; at least one cervical vertebra with the most cranial part of the prezygapophyseal articular surface facing ventrally (autapomorphy); caudal surface of the distal tibia with laterally located robust crest (autapomorphy); metatarsus elongate (at least eight times longer than wide proximally). Size small, comparable to extant Common Starling.

Differential diagnosis. *Holbotia* differs from all other enantiornithines by the autapomorphic structure of at least one cervical vertebra and the distal tibia (see Diagnosis). The characteristic dentition (widely spaced dentary teeth) distinguishes *Holbotia ponomarenkoi* from all other enantiornithines except long-snouted taxa sometimes referred to as Longipterygidae (Chiappe *et al.* 2007b; O’Connor *et al.* 2009; Wang *et al.* 2014; but see O’Connor & Zhou 2013). Amongst the Longipterygidae, *Holbotia* is most similar to *Boluochia* and differs from the long-snouted forms *Longipteryx*, *Longirostravis* and *Rapaxavis* by the proportionally shorter premaxillary portion of the premaxilla. *Holbotia* differs from *Boluochia* by the rounded rostral margin of the external nares; narrow and almost straight rostralmost premaxillary tooth; considerably longer metatarsus (in *Boluochia*, the metatarsus is about five times longer than wide proximally); metatarsal I without perpendicularly orientated hallux articulation. *Boluochia*

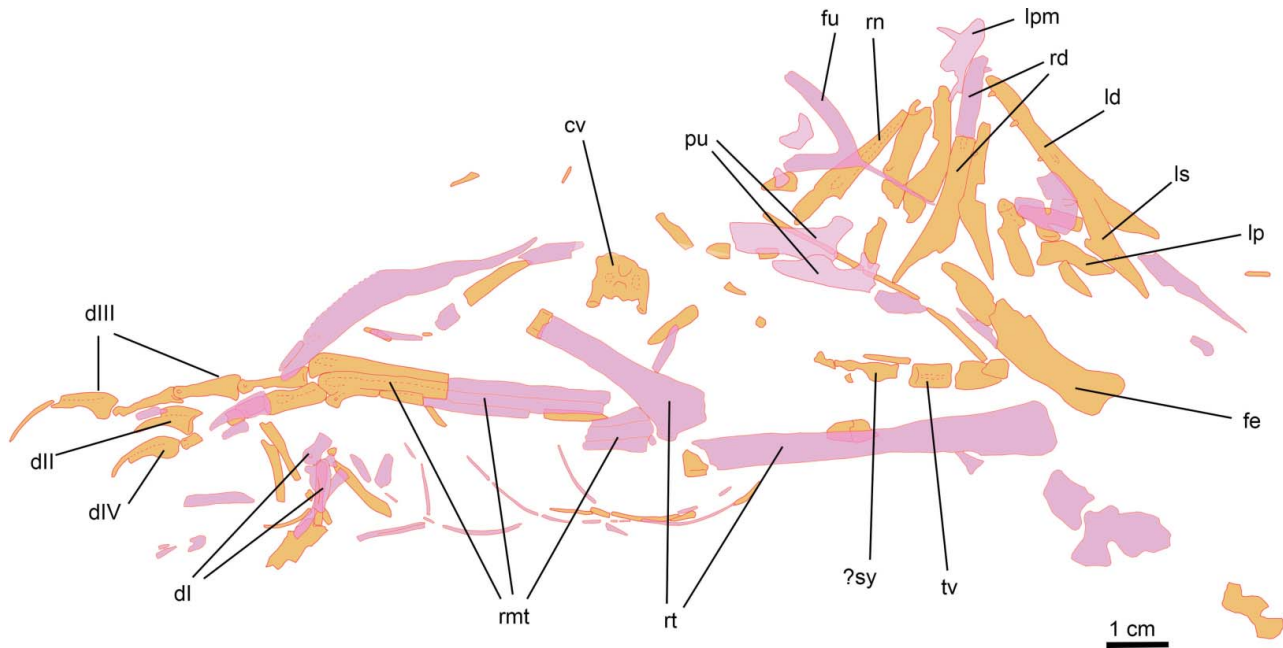


Figure 3. *Holbotia ponomarenkoi* gen. et sp. nov., composite outline drawing of main bones preserved on the slab (orange) and counterslab (pink). Abbreviations: cv, cervical vertebra; dI–IV, digits I–IV; fe, femur; fu, furcula; ld, left dentary; lp, left palatine; ls, left splenial; pu, pubic bones; rd, right dentary; rmt, right metatarsus; rn, right nasal; rs, right splenial; rt, right tibiotarsus; tv, thoracic vertebra; sy, synsacrum.

further differs from all Enantiornithes in that its metatarsal IV protrudes further distally than the other metatarsals (O'Connor *et al.* 2011a). Although this character is unknown in *Holbotia*, the condition similar to *Boluochia* seems very unlikely (see Description).

Description. Most of the jaw elements, the right nasal, the right frontal, an incomplete cervical and femur, fragments of the wing, the distal part of the right metatarsus and most of the pedal digit phalanges are preserved on the slab (Figs 1A, 3). On the counterslab are preserved the rostral parts of the right dentary, premaxilla, the furcula, a tibia broken into two pieces, proximal and central fragments of the right tarsometatarsus, and a hallux (Figs 1B, 3).

Skull. The prenarial portion of a premaxilla with partial maxillary and nasal processes is preserved on the counterslab near to the fragment of a dentary (Fig. 4). The premaxilla is interpreted here as the left one exposed in medial view. The dorsal and ventral margins of the prenarial portion are nearly parallel as in longirostrine enantiornithines (*Rapaxavis*, *Boluochia*, *Longipteryx*, *Longirostravis*; O'Connor *et al.* 2011a, b; O'Connor & Chiappe 2011), but the prenarial portion is notably shorter than those of *Rapaxavis*, *Longipteryx* and *Longirostravis*, being comparable to that in *Boluochia* (O'Connor *et al.* 2011a). The rostralmost tip of the premaxilla is blunt as in other enantiornithines; the sharp tip of the premaxilla in *Boluochia* may represent a preservational artefact (O'Connor *et al.* 2011a). There is

an indication of one probably enlarged premaxillary tooth, located roughly in the middle of the prenarial portion. The poor preservation of this area allows equivocal interpretations of the length of this tooth. Only the apex of the tooth is preserved, but an imprint of its proximal part allows reconstruction of the tooth outline. Judging from the imprint, the tooth was rather narrow and straight for its proximal two-thirds and the distal third was slightly curved caudally. A crushed depression, obviously representing a poorly preserved alveolus, is located on the premaxilla just where the root of the tooth should have been positioned. As this tooth is preserved outside its alveolus, its natural length cannot be unequivocally determined. It is not clear if there were other premaxillary teeth.

Only the rostral part of the nasal process of the premaxilla is preserved (Fig. 4). The process is wider than those of the relatively short-snouted enantiornithines *Pengornis* and *Shenqiornis* (Zhou *et al.* 2008; Wang *et al.* 2010) and is more similar to the widened nasal process of long-snouted forms, including *Boluochia* (Zhou 1995; O'Connor *et al.* 2011a). The rostral margin of the external naris is rounded as in *Archaeopteryx* and many enantiornithine birds. In *Longipteryx* and other long-snouted enantiornithines, nares are slit-like with a sharp rostral end (O'Connor & Chiappe 2011). The maxillary process of the premaxilla is broken and thus its length and exact shape cannot be discerned.

A series of poorly preserved bone fragments and imprints near the premaxilla (Fig. 4) possibly represent

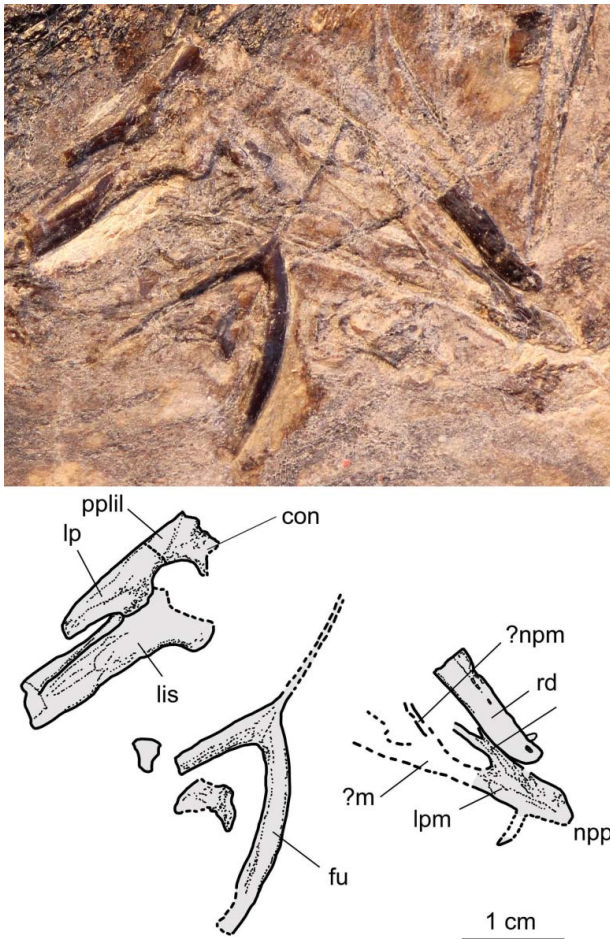


Figure 4. Close-up photograph (above) and interpretative drawing (below) of the counterslab of *Holbotia ponomarenkoi* gen. et sp. nov. showing details of the skull, furcula and pelvis. Abbreviations: con, concave area of preacetabular ilium; fu, furcula; lis, left ischium; lp, left pubis; lpm, left premaxilla; ?m, alleged imprints of maxilla + maxillary process of premaxilla; ?npm, alleged nasal process of maxilla; npp, nasal process of premaxilla; pplil, pubic peduncle of left ilium; rd, right dentary.

the remaining bones of the upper jaw. A groove continuous with the ventral margin of the premaxilla is interpreted as the maxilla. No traces of teeth are present either in this groove or in the adjacent matrix, but the absence of the maxillary teeth cannot be confirmed due to the poor preservation of this region. A poorly preserved inclined bony bar may represent the ascending nasal process of maxilla. If correctly identified, this would imply a short premaxillary process of the maxilla in *Holbotia*, in contrast to the strongly elongated premaxillary process of maxilla in the long-snouted *Longipteryx*, *Rapaxavis* and *Longirostravis* (O'Connor & Chiappe 2011).

An elongated bone on the slab adjacent to the supposed wing skeleton is interpreted here as the right nasal exposed in ventral view (Fig. 5). The most rostral end of the bone is missing. The lateral margin (facing right on

Fig. 5) is slightly concave rostrally and straight caudally (the bone becomes wider towards the caudal end). The rostral concavity is similar to the narial margin in *Shenqiornis* (O'Connor & Chiappe 2011, fig. 2G) and likely represents the narial margin in *Holbotia* as well. The lateral margin is formed by a distinct ridge rostrally. Caudally the ridge gradually flattens. Along the caudal part of the lateral margin there is an elongated shallow depression which is most likely a facet for the lacrimal (Fig. 5). Amongst known theropods, only in therizinosaurs (e.g. *Erlikosaurus*; see Clark *et al.* 1994; Lautenschlager *et al.* 2014) does the caudal part of the nasal contact the facial ramus of the maxilla, whereas in non-avian paravians (Xu & Wu 2001; Norell *et al.* 2006), *Archaeopteryx* (Wellnhofer 2009) and neornithine birds (e.g. Pycraft 1900; Balanoff & Rowe 2007) the caudal part of the nasal contacts the lacrimal. A slightly convex medial margin is formed by two distinct parallel ridges separated by a groove. This is evidently the pocket-like facet for the nasal process of the premaxilla. It could not be a facet for the collateral nasal because of its orientation: articulation with the nasal at this joint would require an unusually low angle between the nasals, which is unlikely. The orientation of this facet precludes the nasal processes of the premaxillae completely separating the nasal bones, as in *Longirostravis* (O'Connor & Chiappe 2011). There is no maxillary process on the nasal, and there is also no indication of the lateral extension of the nasal, which forms the caudal margin of the external nares in many enantiornithines (Zhou *et al.* 2005; Wang *et al.* 2014). If correctly identified, the structure of the nasal in *Holbotia* is consistent with either schizorhinal or 'atypical holorhinal' skull types and thus implies rhynchokinesis (see Zusi 1984). Schizorhinal nares were apparently present in the long-snouted and some other enantiornithines (O'Connor & Chiappe 2011). There is a large hole at the caudal end of the nasal, a probable preservational artefact. Just caudal to this hole the nasal is covered ventrally by the narrow rostral end of the right frontal (Fig. 5). The preserved left frontal was evidently not fused with the collateral bone.

On the slab between the right and left mandibles there is a set of poorly preserved bones which are interpreted here as palatal bones (Fig. 5). The palate of Enantiornithes is poorly known being reported only for *Gobipteryx* (including *Nanantius*; Elżanowski 1977; Kurochkin 1996; Chiappe *et al.* 2001; O'Connor & Chiappe 2011). A partial poorly preserved palate exposed in lateral view is also known in the holotype of *Longusunguis kurochkini* (Wang *et al.* 2014). In *Holbotia*, the vomers are only partially preserved: their rostral portions are missing, and thus the degree of fusion and their full length cannot be reconstructed. The vomers are fused throughout their medial portions, forming a rod-like central element, which is partly hidden beneath the right splenial (see below). There is a gap between the medial and caudal portions of the vomers, where two

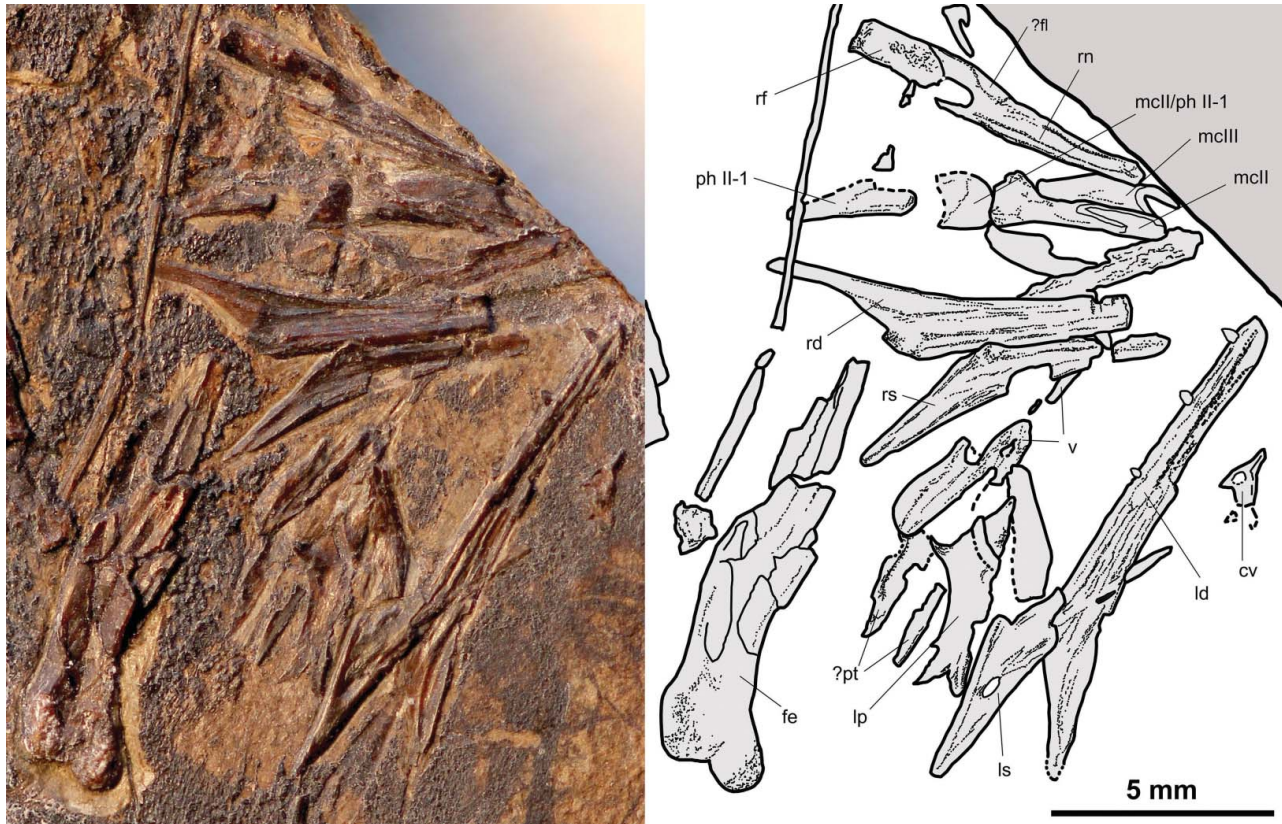


Figure 5. *Holbotia ponomarenkoi* gen. et sp. nov., details of the skull and femur on the slab. Abbreviations: cv, cervical vertebra; fe, femur; ?fl, facet to lacrimal; ld, left dentary; lp, left palatine; ls, left splenial; mclI, metacarpal II (major metacarpal); mclIII, metacarpal III (minor metacarpal); ph II-1, proximal phalanx of digit II; ?pt, pterygoids; rd, right dentary; rf, right frontal; rn, right nasal; rs, right splenial; v, vomer.

adjacent parallel grooves are still visible in the matrix. These grooves are continuous with the preserved medial and caudal portions of the vomers and thus are interpreted as imprints of the dorsal keeled surface of the caudal part of the rod-like central element. The vomers diverge caudally forming a narrow fork (Fig. 5) as in *Gobipteryx* (Chiappe *et al.* 2001, fig. 2). A small but distinct oval-shaped foramen is present on the midline of the vomers slightly rostral to the bifurcation point. This foramen is also present in some Neornithes, for example Tinamidae (McDowell 1948), where it is distally continuous with the intervomerine slit. The presence of such a slit just caudal to the intervomerine foramen in *Holbotia* cannot be confirmed. The caudal forked portions of the vomers are broken and thus their shape cannot be reliably reconstructed.

The right unfused part of the vomers (interpreted as being visible in ventral view) is preserved in contact with a flat bone fragment, which may represent either a fragment of vomer or a portion of another palate element (?palatine).

An elongate bone preserved in contact with the left unfused portion of the vomers is interpreted as a caudally displaced left palatine exposed in ventral view (Fig. 5).

The maxillary process of the palatine is pointed as in *Archaeopteryx* (Elżanowski & Wellnhofer 1996; Mayr *et al.* 2007), non-avian theropods and neornithine birds (Livezey & Zusi 2006). In *Gobipteryx* the maxillary process of the palatine is a paddle-like lamina broadly overlapping the maxilla and there is a dorsal process that bounds the caudal extension of the caudomedial process of the maxilla (Chiappe *et al.* 2001, p. 9, fig. 2). The maxillary process is partly broken in *Holbotia* and appears to be folded close to the main body of the bone, so its visible length is not natural. Rostrally, the maxillary process overlaps a narrow partly broken unidentified bone. The medial margin of the palatine forms a moderately developed, slightly rostrally curved choanal process. This process is present in many non-avian theropods and birds (Elżanowski & Wellnhofer 1996; Livezey & Zusi 2006) but is vestigial in *Gobipteryx*. The caudal portion of the palatine is forked so the bone is tetra-radiate as in many non-avian theropods and *Archaeopteryx* (Livezey & Zusi 2006; Mayr *et al.* 2007). The caudal portion of the palatine in *Gobipteryx* is not known (Chiappe *et al.* 2001). Two bone fragments preserved medial to the palatine are likely to be the pterygoids.

The dentaries are not fused in the symphysis or with the postdentary bones (Fig. 5). The shape of the dentary is typical for Enantiornithes (O'Connor & Chiappe 2011), with a straight alveolar ramus and unforked ventrally sloping caudal articulation with the surangular. The dentary is also straight in the parasagittal plane, with the mandibular symphysis not recurved medially, as in other enantiornithines and most basal birds. The dentary is not as strongly elongated as it is in the longirostrine enantiornithines (O'Connor & Chiappe 2011). The dentary is very shallow for the rostral two-thirds of its length, with subparallel dorsal and ventral margins, and slightly deepens ventrally at the beginning of the caudal process contacting the surangular. The caudal dorsal process is not developed, although there is a small notch along the sloping caudal margin of the bone weakly separating the incipient dorsal process (Fig. 5). On the medial side the Meckelian groove is very thin (as in *Archaeopteryx*: Wellnhofer 2009), filiform, and deep between the rostral end of the dentary and an oval depression located somewhat rostral to the middle of the bone (Fig. 5). Caudal to this depression the groove is wider and gradually widens towards the caudal end of the bone. In this part of the bone the Meckelian groove is bordered by a thick alveolar margin dorsally and a thin bony floor ventrally. The morphology of the Meckelian groove is reminiscent of that in *Hebiornis*, but in the latter taxon the groove appears to be notably wider (Zhang *et al.* 2004). In the bohaiornithids *Longsunguis*, *Sulcavis* and *Parabohaiornis*, the Meckelian groove does not approach the rostral margin of the dentary (O'Connor *et al.* 2013; Wang *et al.* 2014).

The lateral surface of the dentary is known only from the rostral end of the right bone exposed on the counter-slab (Fig. 4). This end is slightly sinusoidal in profile, with the rostral symphyseal part somewhat deeper than the more caudal part. Along the dorsal border there is a series of vascular foramina. The rostral foramen is most prominent, located rostral to the first tooth. Similar large, rostrally placed foramen have not been previously reported for Enantiornithes. It is followed by a tiny oval foramen and a larger, slit-like foramen (Fig. 4). The foramina are not located in a common groove.

The lower dentition is extremely sparse, consisting of three teeth. On the left dentary all the three teeth are preserved (Fig. 5). Between the first two teeth (roughly in the middle of the rostral interdental space) there is a matrix infilling which may represent the alveolus for an additional tooth, but this is uncertain. The teeth are preserved in individual sockets, and the dorsal margin of the dentary does not have a row where other teeth may have been originally located. Thus we suppose that only three to four teeth were originally present in the lower jaw of *Holbotia*. The first tooth is placed at some distance from the rostral end of the dentary. The last tooth is positioned approximately in the middle of the bone just above the depression

within the Meckelian groove (Fig. 5). On the right dentary there are only two teeth preserved, the most rostral tooth and the tooth above the middle depression. On the left dentary the space between the second and third teeth is slightly greater than between the first and second teeth. These spaces exceed the mesiodistal tooth length five to six times. The teeth are very small, mediolaterally compressed, unserrated and roughly similar in size, with relatively higher crowns in the more rostral teeth. The constriction between the crown and root cannot be observed in any specimen, but could be present in the hidden alveolar part of the tooth. There are no interdental plates between the teeth.

The almost complete right splenial is exposed in lateral view, while the caudal half of the left splenial is exposed in medial view and attached to the left dentary (Fig. 5; the orientation of the bone is according to the sagittal plane of the body, not the parasagittal line of the mandible). The most rostral part of the right splenial is probably missing. The splenial is triangular in shape, similar to that of *Archaeopteryx* (Elżanowski & Wellnhofer 1996, fig. 12), but with a relatively shorter caudal ala. A short caudal ala is also present in the enantiornithine *Hebeiornis* (Zhang *et al.* 2004). The splenial covered more than half of the dentary, leaving exposed only the most rostral part of the Meckelian groove. In the middle of the caudal part of the splenial there is a small oval foramen fully exposed in the left bone and filled by the matrix in the right bone (Fig. 5). This foramen apparently corresponds to the rostral mylohyoid foramen of theropods for the exit of the mylohyoid nerve (Currie 1995; Rauhut 2003). On the lateral side of the splenial there is a relatively deep Meckelian groove corresponding to the opposing groove on the dentary and together encircling the Meckelian cartilage (Fig. 5). The splenial is a flat bone without a ventral projection.

Axial skeleton. The axial skeleton is represented by a fragment of a cervical vertebra, at least two thoracic vertebrae, a fragment of the synsacrum, one caudal vertebrae, and fragments of thoracic and sternal ribs.

The cervical vertebra is preserved on the slab (Fig. 6). This fragment is interpreted as the neural arch exposed in ventral view and missing the dorsal roof of the neural canal, and the prezygapophyses which extend cranially about 0.7 mm beyond the cranial margin of the neural arch and bear partially preserved prezygapophyseal articular surfaces. On the neural arch cranially and caudally there are two depressions which may correspond to the interspinous recesses. Two other lateral holes could be chambers of the vertebra pneumatic system. The prezygapophysis is slightly curved in the parasagittal plane and the prezygapophyseal articular surface partially faces ventrally, as in extant darters (Anhingidae). The vertebra

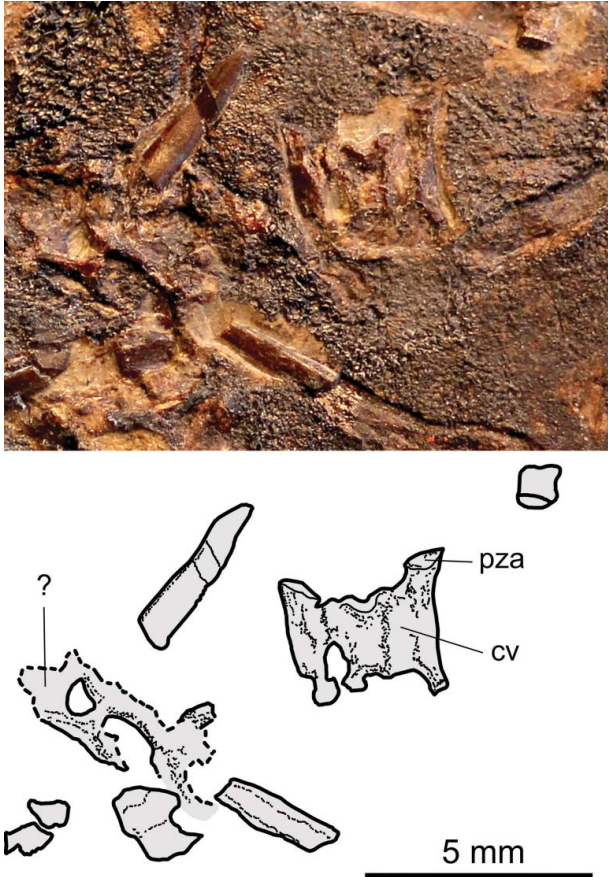


Figure 6. *Holbotia pomarenkoi* gen. et sp. nov., details of the cervical vertebra on the slab. Abbreviations: cv, cervical vertebra; pza, ventrally facing part of prezygopophyseal articulation.

appears to be almost square in shape, as wide as long or wider.

Between the femur and the imprint of the proximal tibiotarsus on the slab there is a series of poorly preserved bones (Fig. 7). The cranial piece (adjacent to the femur) may represent one or two thoracic vertebrae bearing almost no morphological information. Behind this there is a better preserved centrum of the last caudal thoracic vertebra exposed in lateral view. The centrum is quite elongated and evidently amphicoelous. The entire lateral surface of the centrum is excavated by a longitudinal depression, similar to *Halimornis* (Chiappe *et al.* 2002). This centrum is followed by a poorly preserved synsacrum fragment bearing at least two sacral transverse processes along the right side (Fig. 7).

One crushed free caudal vertebra is visible on the slab near the mandible (Fig. 5). Only one elongate process is preserved which may be either a transverse process or chevron. The exact shape of the vertebral canal is unclear but it is undoubtedly occupied a considerable portion of the cross-section of the vertebra.

On the slab alongside the femur there is a long and slender bone which is probably the anterior thoracic rib

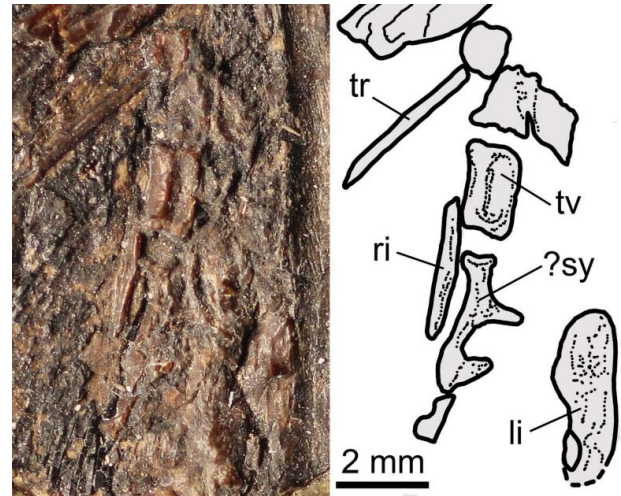


Figure 7. *Holbotia pomarenkoi* gen. et sp. nov., details of the axial skeleton and pelvis on the slab. Abbreviations: li, left ilium; ri, right ilium; tr, thoracic rib; tv, thoracic vertebra; sy, synsacrum.

(Fig. 7). The preserved length of this rib is about 14 mm. Its proximal end is hidden beneath the possible thoracic vertebra. There is no uncinat process co-ossified with the rib shaft on the preserved part. Mainly on the counterslab and partially on the slab there are several even more slender rib-like curved elements. These are best interpreted as the posterior thoracic ribs which are probably single-headed. In the area around the first pedal digit there are at least four relatively short and flattened rod-like elements which are interpreted here as the sternal ribs (Fig. 11). The sternal ribs are associated with a small flat bone most probably representing a fragment of the sternum (Fig. 11). If correctly identified, this fragment has three closely spaced articulation surfaces for the sternal ribs (costal facets).

Pectoral girdle and forelimb. On the counterslab there is a well-preserved furcula with a long hypocleidium exposed in ventral (cranial) view (Fig. 4). The furcula is the typical enantiornithine robust Y-shape. The right ramus is completely preserved while the left ramus is missing its omal end. The interclavicular angle is 52°. The ventral surfaces of the rami are slightly convex near the hypocleidium attachment and form a moderately pronounced ridge more distally. These ridges are placed very close to the inner margin of the rami. The inner and outer margins of the rami differ in the curvature, the inner being straighter while the outer is markedly convex, as in *Pengornis*. The length of the hypocleidium is at least 73% of the rami length.

A series of poorly preserved bone fragments on the slab between the right mandible and the nasal is interpreted here as the fragmented manus (Fig. 5), but it should be

noted that poor preservation of this area precludes equivocal interpretation of these bone fragments. If correctly interpreted, the metacarpals II and III are hollow bones positioned closely to each other as in many other Enantiornithes. The proximal portions of these metacarpals are broken, so the distorted cross-sections of both are visible. Metacarpal III appears to be subequal to metacarpal II in cross-section. The distal end of metacarpal II widens distally towards metacarpal III; however, this part of the bone is crushed so the degree of widening cannot be unambiguously defined. There is a crack in this part of the specimen which may be conjoint with the distal margin of the metacarpal II. A piece of bone preserved just distal to this crack may represent either a basal part of the phalanx II-1 or a distal part of metacarpal II. The distal half of phalanx II-1 is well preserved and its cranial margin is straight. This fragment seems to be tapered distally but this may be also a preservational artefact. The distal most margin of metacarpal III is not discernible.

Pelvic girdle and hind limb. A rod-like piece of bone adjacent to the right side of the synsacrum and the last thoracic vertebra might be a fragment of the right ilium (Fig. 7). The fragmentary left ilium is preserved on the opposite side of the synsacrum and is exposed in medial view. These bones do not preserve any anatomical details. A fragment of the left pelvic girdle, including the acetabular portion and pubic peduncle of the preacetabular ilium, partial pubis and ischium, is preserved on the counterslab near the furcula (Fig. 4). Poor preservation of this area makes interpretation tentative. The pubis was not fused to the ilium and ischium, as in *Sinornis* (Zhou *et al.* 1992; Sereno *et al.* 2002). Right and just ventral to the acetabulum, there is a visible suture between the pubis and the pubic peduncle of the ilium. Because of this suture, the bone positioned caudal to it cannot be a postacetabular portion of the ilium. The area just cranial to the acetabulum is moderately concave, and the bone identified as the pubis has a strongly convex surface. The area of contact between pubis and ischium is poorly preserved, but fusion was probably absent here. The caudal preserved part of the pubis is at least twice the width of the ischium. The ischium may be exposed either in lateral or in medial view. A process on the ischium, which is opposed to the presumed pubis, may be an iliac peduncle, a pubic peduncle or a dorsal process of the ischium, depending on the orientation. Unequivocal interpretation of this structure is impossible due to poor preservation of the adjacent part of the bone.

The hind limb is represented by a reasonably complete right leg including a fragment of the distal femur, the tibiotarsus broken in two pieces, fibula (?), the metatarsus, and most of the pedal phalanges. The distal femur is preserved on the slab and is most likely exposed in caudal view, as evident from the presence of a depression (fossa

poplitea?) just proximal and lateral to the condylus medialis (Fig. 5). The distal end is relatively complete but the hollow shaft is heavily compacted and partially broken into small pieces. Some pieces of the femoral shaft are also preserved on the counterslab. The condylus lateralis is notably more distally protruding than the condylus medialis. The condylus lateralis is also strongly protruding laterally relative to the shaft, although the latter effect may be partly explained by the orientation of the bone. The condylus lateralis may as well have been protruding notably caudally, as in *Alexornis* (Brodkorb 1976). The margin of the shaft adjacent to the lateral condyle is concave, whereas the margin of the shaft adjacent to the condylus medialis is almost straight. The condylus medialis is also slightly protruding medially relative to the shaft. In the middle part of the condylus lateralis there is a prominence which is likely a partially preserved crista tibiofibularis. There is also a moderately developed concavity in the distal outline of the bone apparently corresponding to the sulcus patellaris of extant birds.

The right tibiotarsus is preserved in two pieces on the counterslab, both exposed in caudal view (Figs 8, 9). The distal fragment is rotated by about 320° compared with the proximal fragment, so both articulation surfaces are orientated towards the right side of the counterslab (Fig. 1). Consequently, the medial and lateral sides of both fragments are opposite facing. The tibiotarsus is a long bone, approximately 33 mm in length, which is about 1.6 times greater than the length of metatarsus. The proximal end is somewhat expanded compared to the shaft. The proximal articulation surface is oblique in profile, the medial margin is being elevated compared to the lateral margin, as in some other enantiornithines (Molnar 1986; Sanz *et al.* 1995, fig. 3; Kurochkin 1996; Chiappe & Walker 2002, fig. 11.13A). The fibular crest is inferred to be present along the lateral bone side proximally. Opposite to the presumed fibular crest, partially covered by the medial surface of the tibiotarsus, there is a short wedge-like element (Fig. 8), which is interpreted here as a proximal fibula in caudal view. It is much smaller than the proximal end of the tibiotarsus; the similarly thin fibula is present in some other enantiornithines, e.g. *Sulcavis* (O'Connor *et al.* 2013). The distal end of the tibiotarsus is slightly more expanded than the proximal end. On the medial margin of the caudal surface of the tibia there is a distinct medially projecting tubercle (Fig. 9), not reported in any other enantiornithine. There is a clear suture with the astragalus distally and medially (Fig. 9). Distally the astragalus appears to be broken, with two smaller fragments closely pressed to the proximal part of the bone. The calcaneum is a small oval bone with a round depression on its surface (Fig. 9). It is fused or partially fused to the tibia; possibly it is somewhat displaced post-mortem from its anatomical position. A similar unfused calcaneum with a round depression was documented in a juvenile

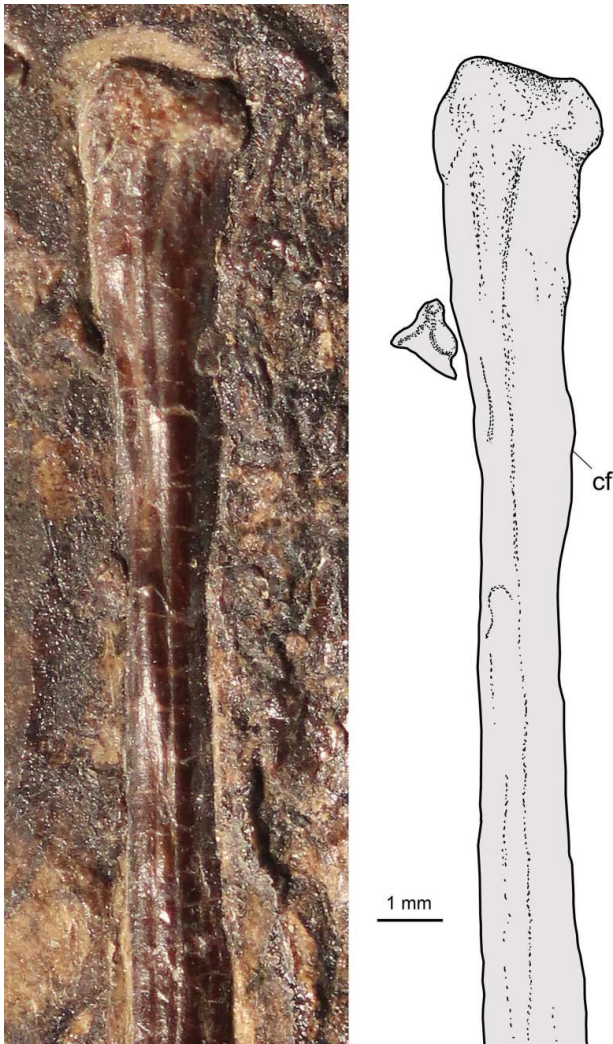


Figure 8. *Holbotia ponomarenkoi* gen. et sp. nov., close-up view of the proximal tibiotarsus on the counterslab. Abbreviation: cf, crista fibularis.

enantiornithine from the Early Cretaceous of China (Chiappe *et al.* 2007a). The calcaneum is about four times narrower mediolaterally compared with the astragalus. Thus the medial condyle is much wider than the lateral condyle, as is typical for Enantiornithes (Walker 1981; Molnar 1986; Kurochkin 1996; Chiappe & Walker 2002). Proximal to the calcaneum on the tibia there is a short but very robust crest extending along the bone lateral margin (Fig. 10). This crest topographically corresponds to the lateral crest of the trochlea cartilaginosa tibiotarsi of Neornithes (Baumel & Witmer 1993) and thus may be homologous to that structure. Medially the crest is flanked by a triangular depression (Fig. 10), but a distinctive trochlea cartilaginosa tibiotarsi is not discernible.

One small distal tarsal is preserved between the calcaneum and the proximal end of metatarsal II. Free distal tarsals are sometimes present in subadult

enantiornithines, e.g. *Iberomesornis*, *Rapaxavis* and *Shenqiornis* (O'Connor 2009; Wang *et al.* 2010; see Discussion).

The metatarsus is preserved completely between the slab (distal one-third) and counterslab (proximal two-thirds; Figs 1, 3, 9, 11). The proximal part is exposed in plantar view on the counterslab, and the distal part is exposed in dorsal view on the slab. The proximal end was broken off and displaced from the remaining bone. The metatarsus incorporates three metatarsals (II to IV), which are closely adpressed but not fused, except for potentially a very short area of fusion between metatarsals II and III at their proximal ends, but this remains uncertain. The sutures separating the metatarsals can be traced until the proximal end of the bone (Fig. 9). The metatarsals are not fused with the distal tarsals, which are preserved as separate elements (see above). The proximal end of the metatarsus is slightly expanded compared to the shaft, which is roughly uniform in width. At the proximal edge of the metatarsus, on the plantar surface of metatarsal II there is a shallow groove (Fig. 9, fg) similar to that observed in *Evgenavis* (O'Connor *et al.* 2014), which is presumably a prerequisite of the hypotarsal sulci and grooves of Neornithes. The shaft of metatarsal II narrows shortly below the proximal end, so that near the proximal end metatarsal II is approximately half the width of metatarsal III. The proximal end of metatarsal IV is only slightly narrower than metatarsal III but distally it narrows so that it is half the width of this metatarsal at mid-shaft. For the most of the metatarsus length, metatarsals II and IV are roughly equal in width.

On the plantar surface of the proximal part of metatarsal II there is a longitudinal ridge possibly representing a small medial plantar crest (Fig. 9). This plantar ridge is positioned near the medial margin of the bone. A more distal short portion of the bone is missing on the counterslab but represented on the slab where it is exposed in dorsal view. The next preserved fragment of the metatarsal II on the counterslab is the middle third of the bone (Fig. 9). Its plantar surface is almost flat, and a longitudinal groove running along the lateral side of the distal half is evidently the result of crushing.

The proximal two-thirds of metatarsals III and IV are exposed in plantar view on the counterslab (Fig. 9). On the broken-off proximal fragment the plantar surface of both metatarsals has a laterally positioned ridge and medial flat area. On the plantar side of metatarsal III the lateral ridge is present along the entire fragment and another, medial ridge appears shortly after the proximal breakage (Fig. 9). Both ridges are separated by a wide groove, which is likely a preservational artefact. On the plantar surface of metatarsal IV the lateral ridge extends approximately to the middle point of the bone, continuously decreasing in height distally.

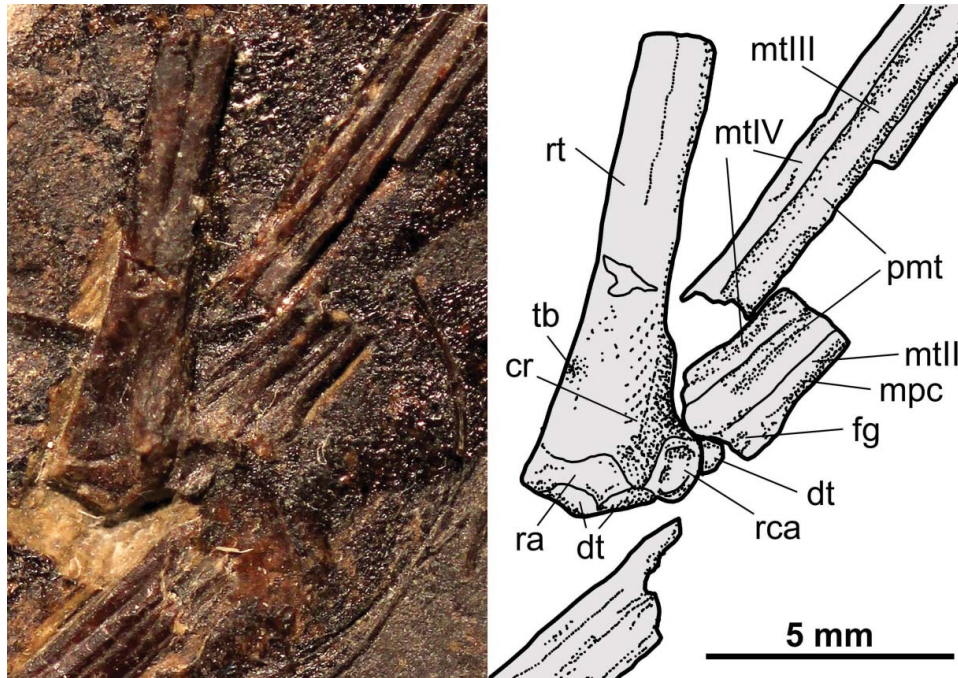


Figure 9. *Holbotia ponomarenkoi* gen. et sp. nov., details of distal tibiotarsus and proximal metatarsus on the counterslab. Abbreviations: cr, crest on the caudal surface of tibia; dt, distal tarsals; fg, flexor groove; mpc, medial plantar crest; mtlII–IV, metatarsals II–IV; pmt, proximal half of metatarsus; ra, right astragal; rca, right calcaneus; rt, right tibiotarsus; tb, tuberculum on the mediocaudal surface of the distal tibiotarsus.

Metatarsal I is preserved on the medial surface of the metatarsus and appears to be displaced distally from its typical position. It is J-shaped in dorsal view with a medially deflected distal end (Fig. 11). The distal articular surface of metatarsal I is badly preserved. The middle part of the dorsal margin of metatarsal I is somewhat deflected medially, thus expanding above the dorsal surface of metatarsal II. Exactly the same morphology is observed in

Nanantius and in *Sulcavis* and may be a common feature of Enantiornithes.

Two distal trochleae are well preserved and may be equivocally interpreted either as trochleae metatarsorum II and III, or trochleae metatarsorum III and IV. We favour the first interpretation as this allows minimal deviation from typical enantiornithine morphology. If we were to assume that the large trochlea adjacent to metatarsal I is indeed a trochlea metatarsi III, then we would need to accept that trochlea metatarsi II was unusually narrow, being completely covered by metatarsal I. This is, however, very unlikely because trochlea metatarsi II is usually as broad as the trochlea metatarsi IV or even the broadest of the three trochleae in Enantiornithes (Chiappe 1993; Chiappe & Walker 2002; O'Connor 2009). Trochlea metatarsi II is also broad in other primitive non-ornithuromorph birds such as Confuciusornithidae (Chiappe *et al.* 1999) and *Mystriornis* (Kurochkin *et al.* 2011). According to our interpretations of the trochleae, the narrowest metatarsal is probably the deflected metatarsal IV, which is indeed the narrowest of the three in almost all enantiornithines (Chiappe 1993; Chiappe & Walker 2002).

Metatarsal II is the widest metatarsal at the distal end (Fig. 10). The distal trochlea of the metatarsal is ginglymoid and wider than the trochlea metatarsi III. There is a marked depression on the dorsal surface just proximal to the condyle, as in *Evgenavis* (O'Connor *et al.* 2014). Proximally it continues into the longitudinal groove, which is

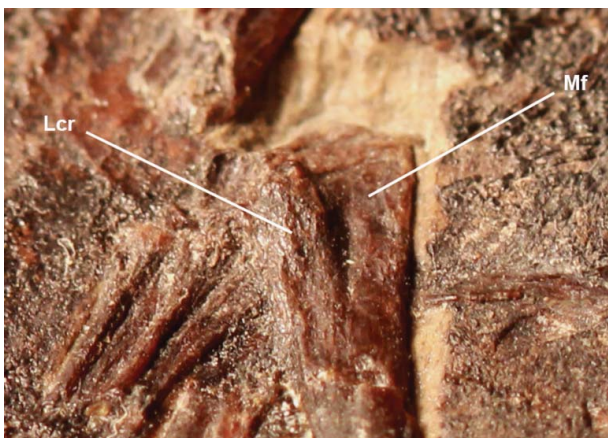


Figure 10. *Holbotia ponomarenkoi* gen. et sp. nov., close-up and angled view of the distal tibiotarsus showing the details of the caudal surface of tibia. Abbreviations: Lcr, lateral crest; Mf, medial flat surface/concavity.

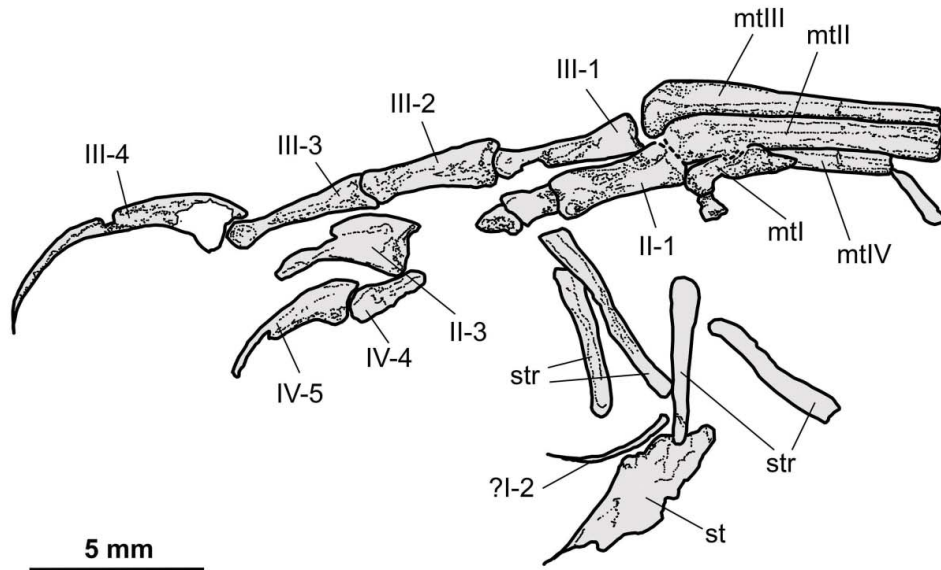


Figure 11. *Holbotia ponomarenkoi* gen. et sp. nov., details of the distal metatarsus and foot on the slab. Abbreviations: ?I-2, probable unguinal phalanx of digit I; III-1–4, phalanges of digit III; II-1, 3, phalanges of digit II; IV-4, 5, phalanges of digit IV; mtI–IV, metatarsals I–IV; st, sternum; str, sternal ribs.

probably a post-mortem artefact of bone compaction. The distal end of metatarsal III projects distally distinctly beyond the level of metatarsal II (Fig. 11), as in many Enantiornithes. Its condyle may have been weakly ginglymoid but this cannot be confirmed due to preservation. The dorsal surface of metatarsal III bears a depression just proximal to the distal trochlea. The shaft of metatarsal III is only slightly narrower than the shaft of metatarsal II.

The two phalanges of the first pedal digit are preserved on the counterslab in a reversed position so that the digit opposes the other digits (Fig. 12). The proximal phalanx

(I-1) is broken in two. The proximal part is preserved on the slab and has a somewhat expanded proximal end (Fig. 11), placed adjacent to the distal condyle of metatarsal I. The distal part of the proximal phalanx and the entire distal (ungual) phalanx are preserved on the counterslab in articulation (Fig. 12). The proximal phalanx is similar in length to the unguinal phalanx. Its distal condyle is rounded and expanded compared with the shaft and bears a distinct ligamentary pit which is placed closer to the dorsal side. The dorsal half of the medial surface of the shaft is more depressed compared with the ventral half. Only the

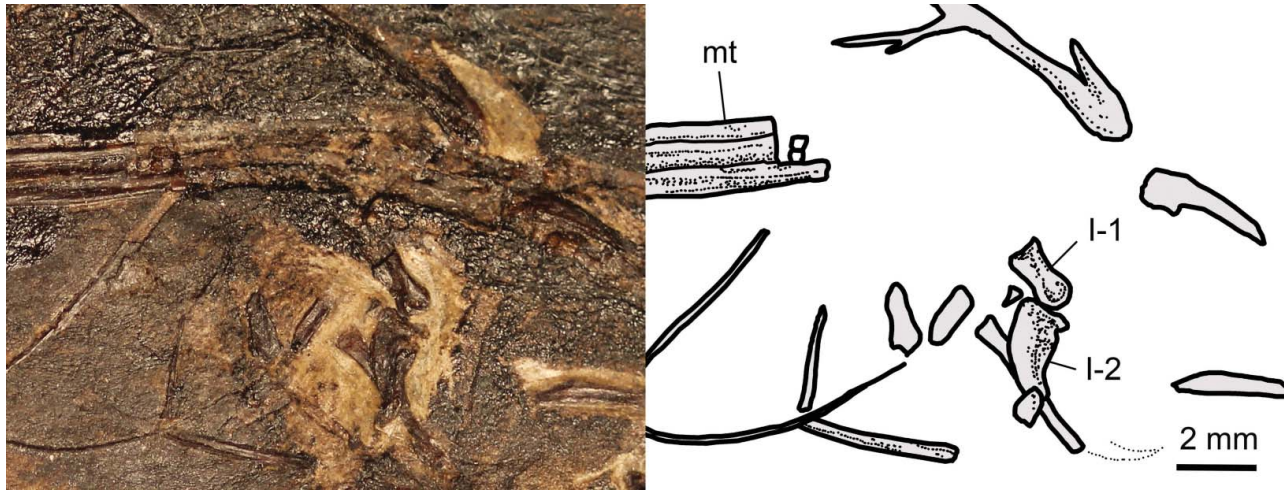


Figure 12. *Holbotia ponomarenkoi* gen. et sp. nov., details of the distal metatarsus and foot on the counterslab. Abbreviations: I-1, 2, phalanges of digit I; mt, metatarsals.

proximal half of the unguis phalanx (I-2) is preserved on the counterslab and bears a low ridge-like flexor tubercle (Fig. 12). The distal part of the unguis phalanx is apparently preserved on the slab near the alleged sternal fragments (Fig. 11). The imprint of the horny sheath of the hallux is partly preserved on the counterslab, and indicates that the claw was strongly curved. However, the exact degree of curvature is unclear because the unguis phalanx may be displaced relative to the imprint of the horny sheath.

Pedal digits II and IV are preserved roughly articulated with the corresponding trochlea. These two digits have typical enantiornithine morphology (in terms of robustness and number of phalanges), thus supporting our interpretation of the trochlea. The best preserved is pedal digit III having four phalanges exposed on the slab in medial view (Fig. 11). The three non-unguis phalanges are quite long, roughly similar in size, have robust proximal and slender distal ends, and shallow collateral ligament pits. These phalanges are considerably flattened dorsoplantarily. The unguis phalanx is almost completely preserved (the missing bone is outlined as the print), strongly curved, and has no distinct flexor tubercle. The imprint of the horny sheath of the claw is also partially preserved.

The second pedal digit is the most robust, as in some other enantiornithines (e.g. Bohaiornithidae: Wang *et al.* 2014) and has three phalanges. The proximal phalanx of digit II is articulated with metatarsal II (Fig. 11). It is the most robust pedal phalanx, exposed in dorsal view. On the dorsal surface there is a distinct pit proximal to the distal condyle and a less defined depressed area near the proximal end. The penultimate phalanx (II-2) is poorly preserved on the slab (Fig. 11) but is better preserved on the counterslab, exposed in lateral view; the distal end is

missing. It is shorter and less robust than phalanx II-1, and is dorsoplantarily compressed. The unguis phalanx (II-3) is preserved on the slab (Fig. 11) and also as a void on the counterslab. Digit IV is poorly preserved. Unguis phalanx IV-5 is preserved on the slab just near the unguis of digit II. It articulates with a thin piece of bone that is most likely represents a fragment of the penultimate phalanx (IV-4). A similarly thin penultimate phalanx is also present in the Bohaiornithidae (Wang *et al.* 2014). The other phalanges of the fourth digit are not preserved, although some fragments on the counterslab may represent their remains. Judging from the position of the unguis, the second digit was the shortest, followed by the fourth and then the third, as in Bohaiornithidae (Wang *et al.* 2014). The third digit was less than two-thirds of the length of the metatarsus, while digits II and IV were less than half the length of the metatarsus. The metatarsus is generally short in Enantiornithes (digit III is comparable in length to the metatarsus) but a similarly elongated metatarsus is present in *Concornis*.

The unguis are moderately curved. The unguis of digit IV is small, as in many enantiornithines. The presence of grooves on the side surfaces cannot be unequivocally established due to crushing, but the groove appears to be poorly developed at least on the unguis of digit I.

Plumage. Numerous feathers are visible on the slab and counterslab, none of which seem to be preserved in their anatomical position. In the majority of the feathers, the vanes are badly preserved so that the individual barbs are not distinguishable. However, one feather positioned near the claws (Fig. 1) can be interpreted as a modern-looking contour feather with a thin rachis and completely differentiated barbs. The other preserved feathers either lacked

completely differentiated vanes or, more likely, the individual barbs of these feathers were bound together post-mortem.

Discussion

Historical relevance of the specimen

Unearthed in 1977, the holotype specimen of *Holbotia ponomarenkoi* gen. et sp. nov. apparently represents the first discovered associated skeleton of an enantiornithine bird; no other specimens were reported in the literature prior to 1986 (Lacasa-Ruiz 1986). The first almost complete enantiornithine bird from the now famous Early Cretaceous sediments of China, *Sinornis santensis*, was only discovered in 1987 (Serenio & Rao 1992; Serenio *et al.* 2002; Zhou & Hou 2002). The holotype of *Cathayornis yandica* was unearthed in 1990 and was described the same year as *Sinornis* (Zhou *et al.* 1992; see O'Connor & Dyke 2010 regarding the taxonomy of these fossils). These finds were followed by a series of other important discoveries in Liaoning in the early 1990s and then by numerous finds in the 2000s, which are continuing (Zhou *et al.* 1992; O'Connor 2009). Skeletal remains of Early Cretaceous enantiornithine birds from Spain were also reported in the late 1980s (Lacasa-Ruiz 1986; Sanz *et al.* 1988). At this time enantiornithine birds were known mostly from isolated remains, preventing correct taxonomic assignment of a number of significant specimens. For example, the now classical enantiornithines *Sinornis*, *Iberomesornis* and *Concornis* were not initially recognized as such (Sanz & Bonaparte 1992; Sanz & Buscalione 1992; Serenio & Rao 1992). Unfortunately, the significance of the Mongolian specimen was also not recognized immediately after its discovery. Kurochkin (1979) first reported the specimen as a bird and later mentioned it in his description of *Ambiortus* (Kurochkin 1982). Soon after that, he appears to have changed his opinion regarding the taxonomic position of the fossil since it was subsequently mentioned as a pterosaur in one of his popular papers (Kurochkin 1991). By the time that the specimen was again re-established as a bird (Kurochkin 1994), understanding of Enantiornithes was much improved (Martin 1995).

Ontogenetic age

The preserved bones of the holotype of *Holbotia ponomarenkoi* lack the porosity which is found in juveniles and early subadult specimens of enantiornithines (Chiappe *et al.* 2007a). However, the proximal tarsals remain unfused to the tibia, and the distal tarsals, if correctly identified, are completely free from the metatarsus. The same condition (unfused compound bones and mature texture of bone surface) was found in smaller specimens

referred to the family Bohaiornithidae, whereas the largest specimens of this clade show complete fusion of the compound bones (Wang *et al.* 2014). Wang *et al.* (2014) considered the smaller bohaiornithid specimens with incomplete fusion in the compound bones as subadult, not fully grown individuals. Incomplete fusion of the tibiotarsus was also reported in juvenile enantiornithines (Chiappe *et al.* 2007a), *Longipteryx* (Zhang *et al.* 2001) and *Iberomesornis* (Sanz & Bonaparte 1992), as well as in an unnamed tibiotarsus from the Late Cretaceous of France (Buffetaut *et al.* 2000). The enantiornithine affinity of the latter specimen is, however, not obvious since the bone is notably different from tibiotarsi of other known enantiornithines.

Chiappe & Walker (2002) stated that no free tarsals have ever been reported in adult enantiornithines. Indeed, free distal tarsals are present in a juvenile *Longipteryx* specimen yet fused to metatarsals in adult specimens (Zhang *et al.* 2001; O'Connor 2009). Free distal tarsals are present in juvenile specimens of Early Cretaceous Chinese enantiornithines (Chiappe *et al.* 2007a) and also in the holotype of *Iberomesornis romerali* (Sanz & Bonaparte 1992), which is considered to be a juvenile by some authors (Kurochkin 1995; Martin 1995; Feduccia 1996) but an adult by others (Sanz *et al.* 2002). The holotype of the longirostrine taxon *Rapaxavis* also has unfused distal tarsals and is thought to be subadult (Morschhauser *et al.* 2009; O'Connor *et al.* 2011a). *Shenqiornis* displays complete absence of fusion in the distal tarsals although it has no other features of juvenile birds (O'Connor 2009). Thus the holotype of *Holbotia ponomarenkoi* was evidently a subadult. The small size of the specimen (comparable with the extant Common Starling) indicates that the fully grown individuals of this species were still small.

Geographical significance

Representatives of the clade Enantiornithes are now known to have had an almost global distribution in the Late Cretaceous, but the Early Cretaceous distribution of these primitive birds was probably more restricted. Early Cretaceous enantiornithines were previously known only from China, Spain and Australia (Molnar 1986; Chiappe 2007; O'Connor 2009; O'Connor *et al.* 2011). *Holbotia* is the first Early Cretaceous Asian enantiornithine bird from outside China, and it is remarkable that this find represents a distinct taxon, despite the fact that enantiornithine remains from China are known in large numbers. This may potentially indicate somewhat different environmental conditions in southern Mongolia.

New morphological data

The holotype of *Holbotia ponomarenkoi* preserves some morphological details not previously reported in

Enantiornithes. The specimen preserves a partial palate in ventral view which was previously described only in the Late Cretaceous edentulous genus *Gobipteryx* (Elzanowski 1977; Kurochkin 1996; Chiappe *et al.* 2001; O'Connor & Chiappe 2011). However, the cranial morphology of *Gobipteryx* was notably specialized compared to other Enantiornithes (O'Connor & Chiappe 2011), and thus its palatal structure is unlikely to be typical for enantiornithines. Indeed, the palate of *Holbotia* differs from that of *Gobipteryx* in the pointed maxillary process, well-developed hooked choanal process, and bifurcating caudal end of the palatine. All these features are obviously primitive as they are found in *Archaeopteryx* and theropod dinosaurs. This observation indicates that the morphology of the palatine was generally stable across the transition from Archaeopterygidae to Enantiornithes. Perhaps only advanced enantiornithines (*Gobipteryx*) evolved specialized palate morphologies. The differentiation of palate types is a well-known phenomenon in extant birds. It is interesting that *Holbotia* retains primitive palatal morphology yet has advanced dentition. The basal enantiornithine bird *Pengornis* had numerous small teeth and a fairly short rostrum (Zhou *et al.* 2008; O'Connor & Chiappe 2011; Hu *et al.* 2014), while *Holbotia* has a small number of dentary teeth, and probably only one premaxillary tooth, and a moderately elongated rostrum. Thus morphological specialization of the feeding apparatus in at least some Early Cretaceous enantiornithines was apparently possible without major modifications to the morphology of the palate.

'Longirostrine' enantiornithines with reduced dentition were previously referred to the families Longipterygidae and Longirostravisidae (both may form a natural group: O'Connor *et al.* 2009; Wang *et al.* 2014). The rostrum of *Holbotia ponomarenkoi* was somewhat more elongated than in the majority of Enantiornithes, as inferred from the premaxillary morphology of the holotype specimen, but this Early Cretaceous Mongolian taxon appears to be only distantly related to the other 'longirostrine' taxa. The lack of robust premaxillary teeth in *Holbotia* (present in Longipterygidae) may indicate that the elongation of the snout probably occurred in parallel with other long-snouted taxa (see below). Meanwhile the roundish rostral margin of the external naris and possibly short premaxillary process of maxilla suggest a shorter snout in *Holbotia* relative to Jehol 'longipterygids'.

Holbotia preserves an unusual morphology of the cervical vertebrae not known in any other fossil bird taxa. In extant birds and most reptiles, the prezygapophyseal articular surface of the cervical vertebrae faces dorsally while its cranialmost part is sometimes inclined and faces cranially. Only in darters (Anhingidae) does the cranialmost part of the prezygapophyseal articular surface of the eighth cervical vertebra face ventrally (Fig. 13), which is obviously related to increased mobility of the neck in these piscivorous birds. The same morphology is found in

the only preserved cervical vertebra of *Holbotia ponomarenkoi*. This feature however does not allow us to infer a similarity in the lifestyle of *Holbotia* and darters, because in the latter the cervicals are greatly elongated, which is not the case in *Holbotia*. However, it does imply increased neck mobility in this taxon, based on comparison with modern birds. Importantly, this conclusion may not be automatically extrapolated to other Enantiornithes. For example, the recently described holotype of *Sulcavis* preserved a series of cervicals in ventral view (Fig. 13), which seem to display no ventrally facing articular surfaces (O'Connor *et al.* 2013). However, the situation may be more complicated if such a morphology was present only in one of the cervicals in Enantiornithes (as in Anhingidae). Such a modified cervical vertebra may be simply not well preserved in *Sulcavis*.

In the hind limb, the robust and proximally extending lateral crest on the caudal surface of distal tibiotarsus is for the first time reported for enantiornithines. A pronounced but distally restricted crest is also visible in *Lectavis* (Chiappe & Walker 2002; Walker & Dyke 2010), though it was not formally described in that taxon. This crest is related to the tibial cartilage, a specialized avian soft-tissue structure. In the modern birds, the tibial cartilage is positioned in a sulcus (trochlea cratilaginis tibiotarsi) on the posterodistal surface of tibiotarsus, and is enclosed by two ridges, cristae trochlea (Baumel & Witmer 1993). The two cristae and the sulcus in between them vary from being extremely well developed (e.g. Strigiformes) to completely non-pronounced (Phalacrocoracidae). The morphology of this structure seems to be predominantly phylogenetically (and not ecologically) dependent because a similar deep trochlea is present in owls and swifts, on the one hand, while on the other hand, falcons and cormorants both have unusually flat trochlea. Hutchinson (2002) considered tibial cartilage a derived characteristic of ornithurine birds; it was evidently present already in the Early Cretaceous *Gansus*, as can be seen in some of the newly described specimens (Li *et al.* 2011). The trochlea and the corresponding cristae are also well developed in the primitive ornithurine *Apsaravis* (Clarke & Norell 2002). The cristae, however, were reported to be absent in the more primitive ornithuromorphs Hongshanornithidae (Chiappe *et al.* 2014) and *Patagopteryx* (Chiappe 2002). The tibial cartilage was definitively present in enantiornithines because the trochlea cartilaginis tibiotarsi is developed in various representatives of the clade (O'Connor & Zhou 2013).

Caudally protruding cristae trochlea have not been reported from non-avian theropods. Nevertheless, the distal surface of the tibia is notably concave in *Tarbosaurus* (pers. obs.), and thus the cartilage was presumably present at least in some Tyrannosauroidae. Brusatte *et al.* (2012) reported only laterally (non-caudally) protruding lateral crest ('lateral malleolus of tibia') in *Alioramus*

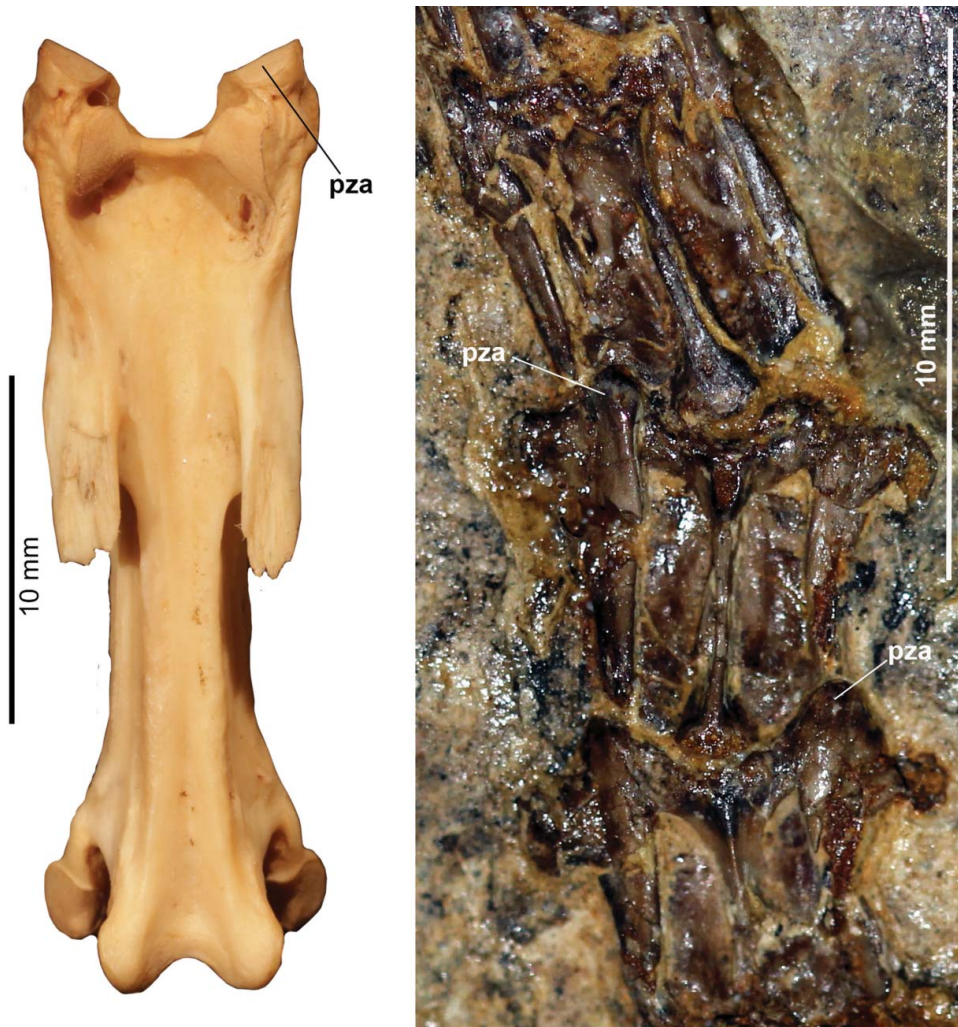


Figure 13. Eighth cervical vertebra of the living *Anhinga melanogaster* (left) and part of the vertebrate column of the Early Cretaceous enantiornithine bird *Sulcavis georum* (holotype Beijing Museum of Natural History Ph-000805; right), both in ventral view, showing the ventrally facing cranial parts of prezygopophyseal articulations (Pza) in *Anhinga*, and more usual condition in *Sulcavis*.

and other Tyrannosauroidae. The cartilage still was probably present in these taxa because in some modern birds (e.g. Phalacrocoracidae) the trochlea is almost completely flat, but the cartilage is nevertheless well developed.

Phylogenetic analysis and inferences for the evolution of Enantiornithes

For phylogenetic analysis, we used the dataset from Wang *et al.* (2014), which is now the largest published matrix for Mesozoic birds (57 taxa and 262 morphological characters, see Supplemental Material for the scorings of *Holbotia*). This dataset is itself based on the comprehensive matrix for Mesozoic birds of O'Connor & Zhou (2013). We performed the traditional heuristic and new technology algorithms using TNT software (Goloboff *et al.*

2008), with equally weighted characters and default settings (see also Wang *et al.* 2014). The shortest trees found by the new technology search algorithm have a tree length of 985 steps. The heuristic most parsimonious trees are 15 steps longer.

The character–taxon matrix was also analysed using PRAP (parsimony ratchet analysis using PAUP; Müller 2007) and PAUP* 4.0b10 (Swofford 2002). The equal-weight analysis with 1000 ratchet replications produced 133 most parsimonious trees with the tree statistics shown in Table 1. To increase resolution and recover any phylogenetic signal, a successive weighting analysis (Farris 1969) was conducted. Using PAUP, the characters were reweighted by the maximum value of rescaled consistency indices (RC), and a heuristic search with 1000 random sequence addition replicates and TBR (tree bisection and reconnection) branch swapping was performed. Tree

Table 1. Statistics for equal weight (PRAP and PAUP) and reweight (PAUP) analyses.

Parameters	Equal weight analysis	Reweight analysis 1	Reweight analysis 2	Reweight analysis 3
N, number of trees	133	1	1	1
L, tree length	1000	242.8	242.4	242.4
CI, consistency index	0.365	0.574	0.581	0.581
RI, retention index	0.675	0.824	0.830	0.830
RC, rescaled consistency index	0.246	0.473	0.481	0.481
HI, homoplasy index	0.635	0.426	0.420	0.420

statistics stabilized after three successive runs of the reweight analysis (Table 1). The single most parsimonious tree produced by reweight analysis is shown on Figure 14.

The resultant trees have generally similar topology but differ in the phylogenetic position of some enantiornithines (*Iberomesornis*, *Cathayornis*, *Eocathayornis*). The results of all analyses (Fig. 14) indicate that *Holbotia* falls within a clade that includes the Early Cretaceous Eurasian genera *Concornis*, *Vescornis*, *Eoalulavis* and *Qiliania*. The Late Cretaceous genera *Gobipteryx* and *Neuquenornis* were also recovered as members of this clade, which

was first found in the analysis by Wang *et al.* (2014). A previous analysis (O'Connor & Zhou 2013) placed the primitive enantiornithine genus *Pengornis* (Zhou *et al.* 2008; Hu *et al.* 2014) within this clade. This is not surprising given the relatively unspecialized morphology of the Early Cretaceous members of this group, which lack the strong feeding specializations characteristic of other clades (Longipterygidae + Longirostravisidae and Bohaiornithidae). However, the Late Cretaceous *Gobipteryx* shows remarkable specialization, including tooth reduction and complete fusion of the rostral bones. It is

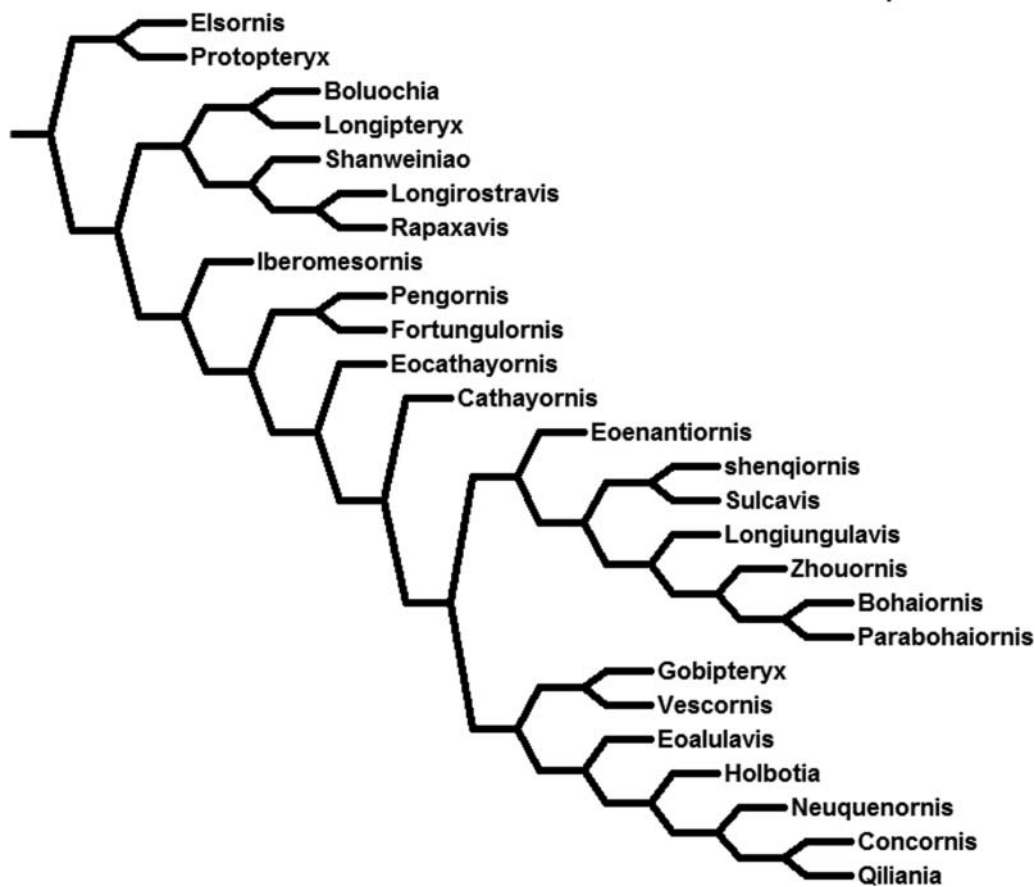


Figure 14. Part of the most parsimonious tree resulting from analysis using PAUP (see Table 1 for tree statistics), showing the phylogenetic position of *Holbotia ponomarenkoi* gen. et sp. nov. within Enantiornithes.

thus noteworthy that *Holbotia* shows a supposed tendency toward tooth reduction (although the exact number of teeth is unknown), implying that such an evolutionary pathway first began within this clade in the Early Cretaceous. The almost complete dentary of *Holbotia* shows that this bird lacked an elongate rostrum (as in Longipterygidae), and thus tooth reduction in this lineage probably followed a different evolutionary pathway from other enantiornithines (Longipterygidae + Longirostravisidae).

Edentulous enantiornithines (represented only by *Gobipteryx*) and ornithuromorphs most probably lost their teeth via different evolutionary pathways. Louchart & Viriot (2011) noted that tooth reduction in enantiornithines first started from the caudal parts of the premaxilla and maxilla, or both. Primitive members of the clade Ornithuromorpha, in contrast, show reduction of teeth in the rostral part of the snout, while the caudal part retained closely spaced teeth (Louchart & Viriot 2011). The premaxilla seems to be completely toothless already in the Early Cretaceous *Iteravis* (Zhou *et al.* 2014). It is noteworthy that no primitive ornithuromorphs are known to have possessed widely spaced teeth, as in *Holobotia*, and thus tooth reduction in Ornithuromorpha probably occurred via gradual caudal expansion of the initial edentulous (keratinized?) zone (Louchart & Viriot 2011). In enantiornithines close to the *Gobipteryx* lineage, the loss of teeth may have been achieved through the gradual increase of intratooth space.

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Supplemental material

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