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Anatomy of the Early Cretaceous enantiornithine bird *Rapaxavis pani*

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The exquisitely preserved longipterygid enantiornithine *Rapaxavis pani* is redescribed here after more extensive preparation. A complete review of its morphology is presented based on information gathered before and after preparation. Among other features, *Rapaxavis pani* is characterized by having an elongate rostrum (close to 60% of the skull length), rostrally restricted dentition, and schizorhinal external nares. Yet, the most puzzling feature of this bird is the presence of a pair of pectoral bones (here termed paracoracoidal ossifications) that, with the exception of the enantiornithine *Concornis lacustris*, are unknown within Aves. Particularly notable is the presence of a distal tarsal cap, formed by the fusion of distal tarsal elements, a feature that is controversial in non-ornithuromorph birds. The holotype and only known specimen of *Rapaxavis pani* thus reveals important information for better understanding the anatomy and phylogenetic relationships of longipterygids, in particular, as well as basal birds as a whole.

Key words: Aves, Enantiornithes, Longipterygidae, *Rapaxavis*, Jiufotang Formation, Early Cretaceous, China.

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Introduction

Recently, another new enantiornithine bird was discovered and described from the fossiliferous Early Cretaceous Jiufotang Formation of northeastern China (Morschhauser et al. 2009). The holotype of *Rapaxavis pani* (DNHM D2522) is one of the best-preserved and most complete enantiornithine specimens described to date (Morschhauser et al. 2009); unfortunately, it did not until more recently receive thorough preparation, and thus many preserved details were not clear at the time of the original study (Morschhauser et al. 2009). This specimen reveals new information about enantiornithine anatomy, including an intriguing pair of unidentifiable ossifications, so far only known in this taxon and the Early Cretaceous Spanish enantiornithine *Concornis lacustris* (holotype specimen LH 2814; Sanz et al. 1995; Morschhauser et al. 2009), among fossil or extant birds. The homology, development, and function of these paired bones present an intriguing biological puzzle that requires further investigation.

The original study of specimen DNHM D2522 preceded any formal preparation (Fig. 1A; Morschhauser et al. 2009). The specimen was later prepared by an amateur, during which the fossil was damaged (CLG, personal observation 2007; JKO'C, personal observation); subsequently, the specimen was further prepared by staff from the Natural History Museum of Los Angeles County, during which new information was revealed and the effects of earlier preparation were somewhat mitigated (Fig. 1B). We have been fortunate enough to study the specimen before and after its preparation, and are thus able to provide a complete description, including details both originally hidden in the matrix as well as those lost during preparation. This redescription of the holotype of *Rapaxavis pani* focuses primarily on the new morphological information available and interpretations that differ from the original publication (Morschhauser et al. 2009).

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

Institutional abbreviations.—CAGS, Chinese Academy of Geological Sciences, Beijing, China; DNHM, Dalian Natural History Museum, Dalian, Liaoning, China; GMV, National Geological Museum of China, Beijing; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; LH, Las Hoyas collection of the Unidad de Paleontología, Universidad Autónoma de Madrid, Spain.

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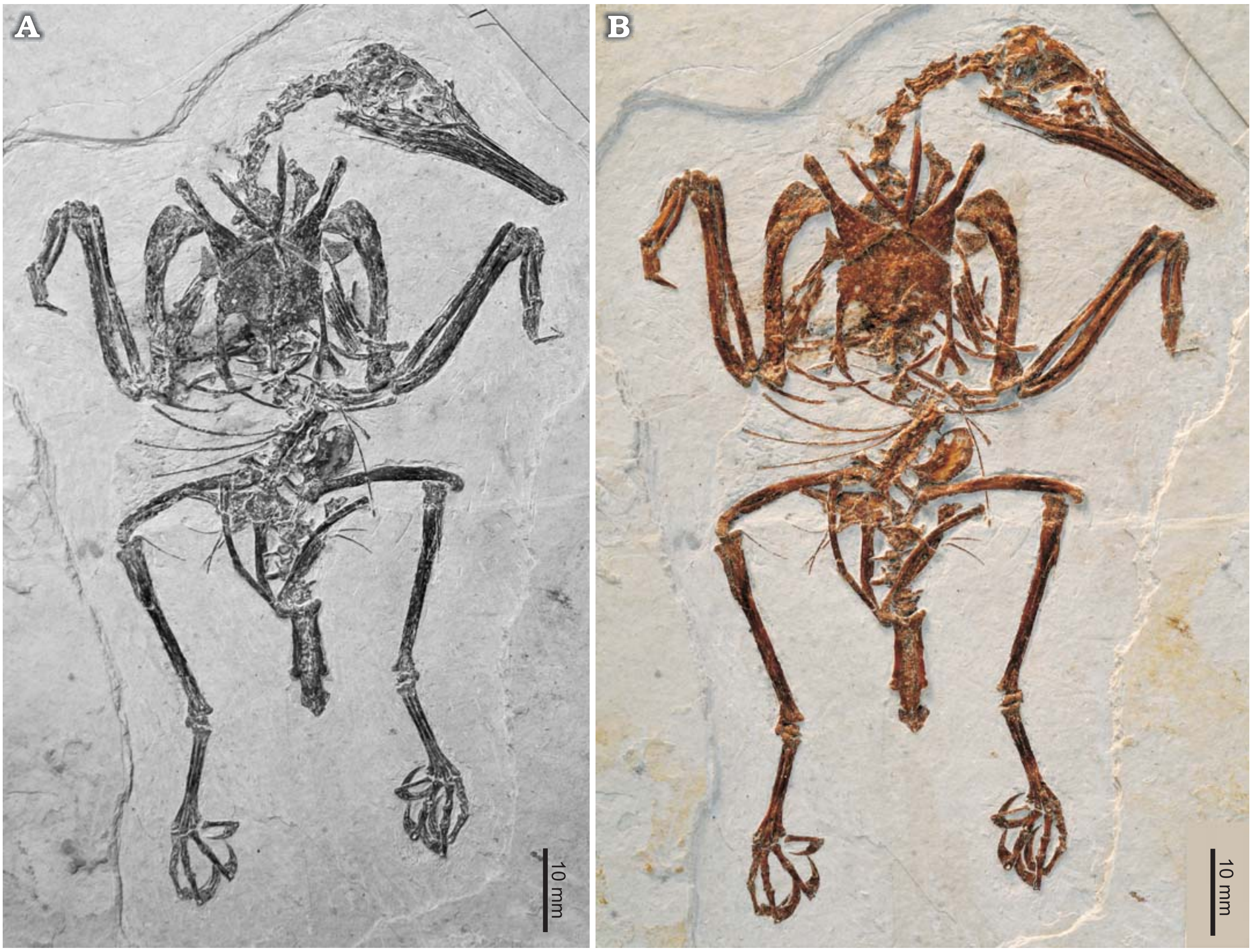

Fig. 1. Photographs of enantiornithine bird *Rapaxavis pani* Morschhauser, Varricchio, Gao, Liu, Wang, Cheng, and Meng, 2009 from the Early Cretaceous Jiufotang Formation in northeastern China. **A**. DNHM D2522 (holotype), prior to preparation. **B**. DNHM D2522 after preparation.

Systematic paleontology

Aves Linnaeus 1758

Enantiornithes Walker 1981

Family Longipterygidae Zhang, Zhou, Hou, and Gu, 2000

Genus *Longipteryx* Zhang, Zhou, Hou, and Gu, 2000

Type species: *Longipteryx chaoyangensis* Zhang, Zhou, Hou, and Gu, 2000, Qidaoquanzi, Chaoyang City, Liaoning Province, Jiufotang Formation.

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

Phylogenetic definition.—The common ancestor of *Longipteryx chaoyangensis* (see Zhang et al. 2000) and *Longirostravis hani* (see Hou et al. 2004) plus all its descendants.

Included taxa.—*Boluochia zhengi* (see Zhou 1995); *Longipteryx chaoyangensis* (see Zhang et al. 2000); *Longirostravis hani* (see Hou et al. 2004); *Shanweiniao cooperorum* (see O'Connor et al. 2009); *Rapaxavis pani* (see Morschhauser et al. 2009).

Geographic and stratigraphic range.—Lingyuan, Chaoyang, and Yixian, Liaoning Province, northeastern China; Lower Cretaceous Yixian and Jiufotang formations, Jehol Group (He et al. 2004; Yang et al. 2007; Fig. 2).

Rapaxavis pani Morschhauser, Varricchio, Gao, Liu, Wang, Cheng, and Meng, 2009

Figs. 1, 3–9.

Holotype: DNHM D2522, a nearly complete, largely articulated sub-

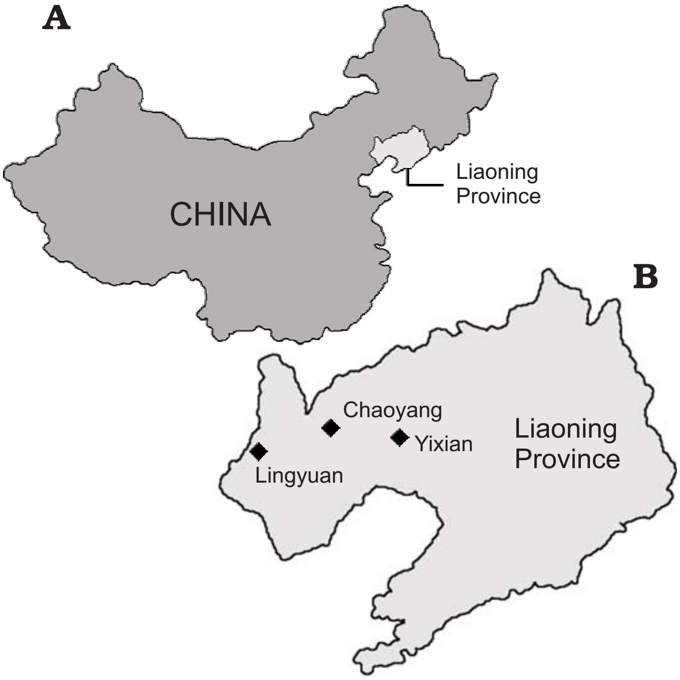

Fig. 2. A map of Liaoning province, China (**A**), indicating the approximate location of longipterygid bearing deposits (**B**).

adult individual preserved in a single slab of buff tuffaceous shale. The bones are preserved primarily in ventral view. No feathers are preserved.

Type locality: Lianhe, Chaoyang, Liaoning Province, China.

Type horizon: Jiufotang Formation, Lower Cretaceous (Swisher et al. 1999, 2002).

Emended diagnosis.—A small longipterygid enantiornithine bird characterized by the unique combination of the following morphological characters: rostrum approximately 60% skull length; dentition rostrally restricted; premaxillary process of maxilla approximately three times longer than the jugal process; nasals lacking maxillary process, external nares schizorhinal; furcula with short interclavicular symphysis and interclavicular angle of 50°; body of coracoid lateral and sternal margins straight; coracoidal facets of sternum defining an obtuse angle of approximately 110°; paracoracoidal ossifications present; sternal lateral trabecula distally forked; first phalanx of alular digit and second phalanx of major digit reduced to sharply tapering triangular splints (all manual claws absent); femur 80% the length of the "tibiotarsus"; and penultimate pedal phalanges longer than the preceding phalanges.

Description

Skull.—The skull of DNHM D2522 (Fig. 4) is crushed and preserved in right lateral view. The rostral half of the rostrum appears imperforate; however, the external nares are slit-like (schizorhinal) and may have been quite long but, due to the slight disarticulation of cranial elements, the external nares is only visible where it widens distally in the caudal half of the rostrum.

The premaxilla is similar to that of *Longirostravis*; the maxillary process is long but relative to the length of the facial margin its contribution is restricted rostrally. The maxillary process of the premaxilla articulates laterally with the maxilla; the exact length of this articulation is not clear due to overlap and the delicate nature of this process. The premaxillary process of the maxilla tapers rostrally while the premaxilla tapers caudally (Fig. 4). The premaxilla preserves three teeth on the right side, which are large compared to *Longirostravis* but still much smaller than those of *Longipteryx*. All teeth are restricted rostrally, as in other longipterygids, located in the premaxillary corpus, before the premaxilla diverges into maxillary and nasal processes (Fig. 4C). The nasal (frontal) processes of the premaxilla are elongate and extend to the caudal margin of the antorbital fossa, but appear not to completely exclude the nasals from the midline or dorsal margin of the skull (Fig. 4). The nasal processes are unfused along their entire lengths but it is unclear if the premaxillae were fused rostrally.

The maxilla forms a majority of the facial margin; the articulation with the premaxilla is elongate (Fig. 4). The caudodorsally directed nasal process is very delicate and appears not to be lined medially by a recessed bony wall as in *Pengornis* (Zhou et al. 2008). The premaxillary process is much longer (approximately three times) than the jugal process. The caudal articulation with the jugal is unclear. The strap-like jugal, preserved with the rostral end slightly displaced dorsally (figured in Morschhauser et al. 2009), was lost during the preparation of this specimen (Fig. 4A). As in other longipterygids, the maxilla is edentulous; nutrient foramina are also absent from the maxilla.

The nasals are exposed in two views, the right in lateral view and the left in ventral view (Fig. 4B, C). The nasals lack a maxillary process; they are elongate, rostrally tapering to a needle-like point and caudally expanding to form a rounded caudal margin. The nasals articulate medially with the nasal processes of the premaxillae for more than half their entire length. The nasal may have been perforated caudally by small, rostrocaudally elongate oval foramina, as in *Pengornis* (JKO'C personal observation).

The orbit and postorbital regions are poorly preserved. No lacrimal is identifiable. A small L-shaped bone at the caudoventral corner of the skull may represent the quadratojugal or the distal end of the jugal. It appears to contact a triangular bone that may represent a postorbital. This triangular bone is broad proximally, with a dorsally concave margin. It tapers ventrally toward the contact with the L-shaped bone (Fig. 4). The poor preservation of the caudal region of the skull prevents unequivocal interpretation of the region; it cannot be said whether *Rapaxavis* definitively possessed either a supra or infratemporal fenestra.

A quadrate is preserved, displaced towards the cervicals (Fig. 4B, C). We interpret the bone as in caudal view; if this is correct, then a pneumatic foramen is absent. The otic process is single-headed; the medial condyle of the mandibular process is approximately twice the size of lateral condyle. The

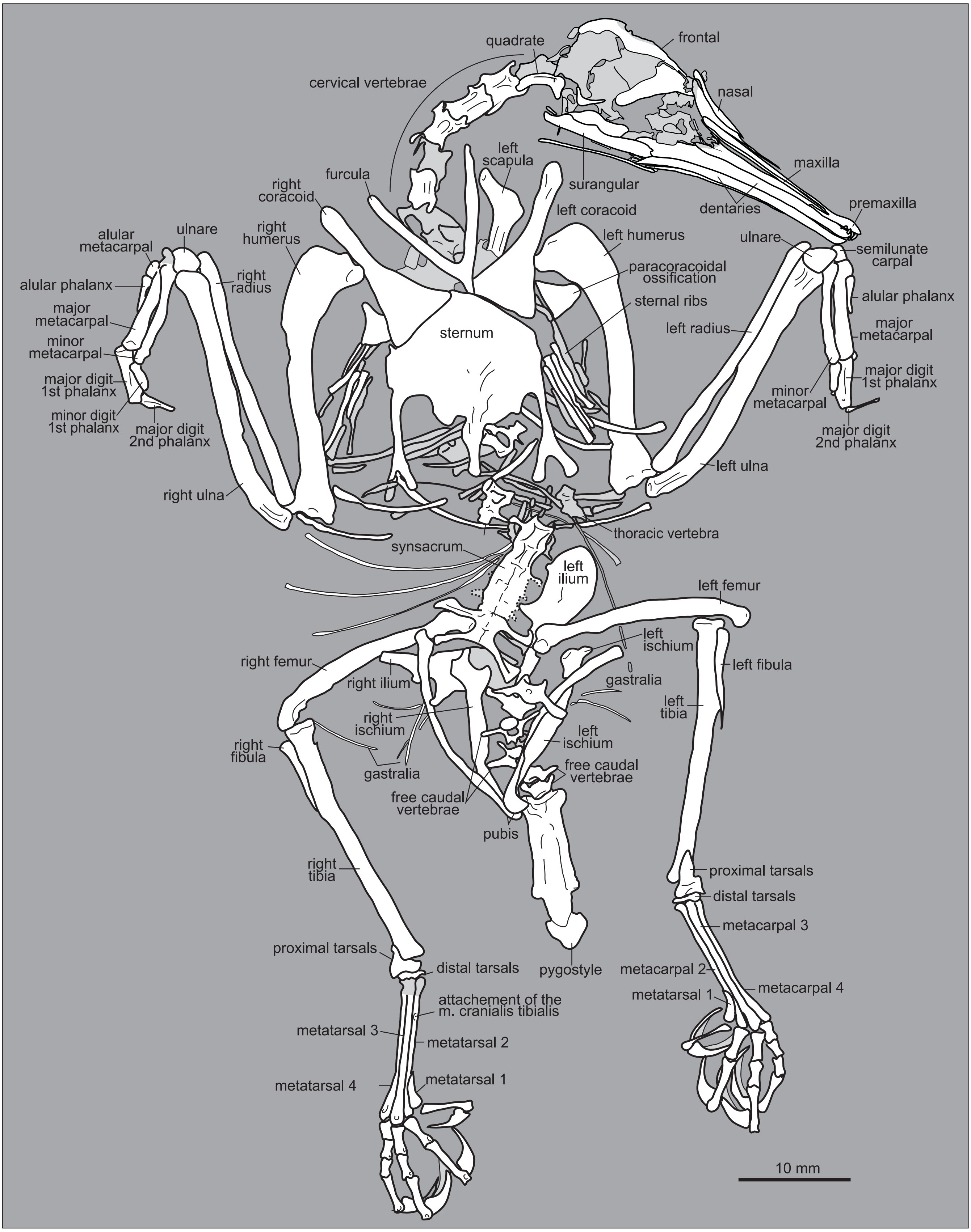

Fig. 3. Enantiornithine bird *Rapaxavis pani* Morschhauser, Varricchio, Gao, Liu, Wang, Cheng, and Meng, 2009 from the Early Cretaceous Jiufotang Formation in northeastern China. Camera lucida drawing of DNHM D2522 (holotype), after preparation. In all interpretive drawings light grey indicate areas of very poor preservation (dark grey indicates matrix).

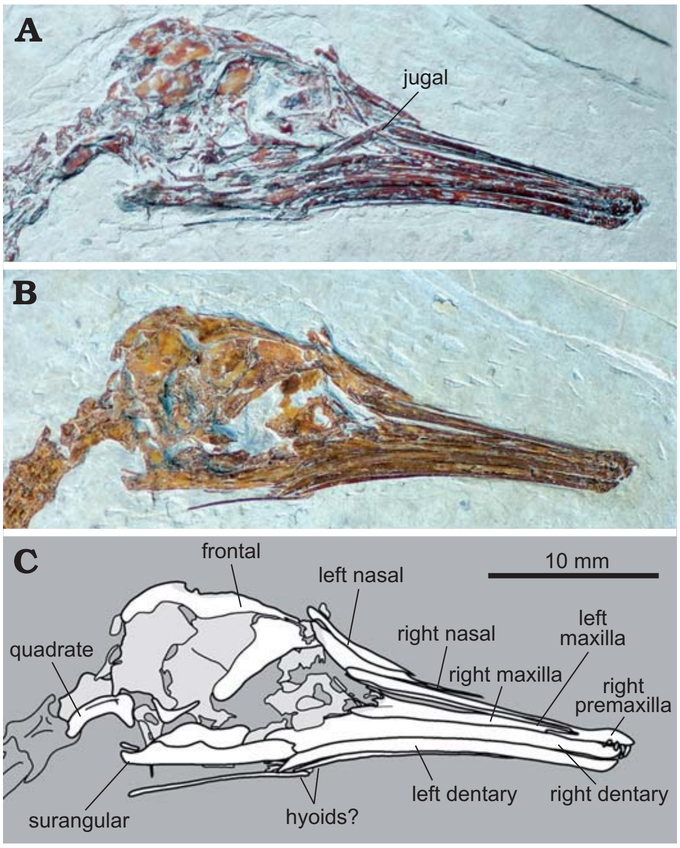

Fig. 4. Enantiornithine bird *Rapaxavis pani* Morschhauser, Varricchio, Gao, Liu, Wang, Cheng, and Meng, 2009 from the Early Cretaceous Jiufotang Formation in northeastern China. Close up of the skull of DNHM D2522 (holotype). **A**. Photographed before preparation. **B**. Photographed after preparation. **C**. Camera lucida drawing based on prepared specimen.

quadrate appears similar to that of *Pengornis*; interpretations of the bone are equivocal but if correct, the quadrate in these taxa is bowed craniocaudally (it appears straight in *Eocathayornis* and *Shenqiornis*; Zhou 2002; Wang et al. 2010).

The frontals are rostrocaudally elongate, and may have articulated rostrally with the convex caudal margins of the nasals. Although not entirely clear, the caudoventral margin forms a ventrocaudally concave unfused contact with the parietals. The parietals are poorly preserved; they appear quadrangular.

Mandible.—The mandibular bones remain unfused (Fig. 4). The dentary and surangular are both straight. The dentary expands caudoventrally so that the ventral margin is concave. The surangular tapers rostrodorsally to articulate with the caudoventrally tapering distal end of the dentary. In lateral view, the surangular bears two dorsal convexities, the proximal of which may be a coronoid process, and the distal of which represents the poorly preserved articulation with the quadrate (lateral mandibular process). Mandibular fenestrae are absent, although a few slit-like nutrient foramina are visible. Two teeth are preserved in the dentary, located rostrally as in other longipterygids.

Axial skeleton.—The cervicals preserve little information and the thoracic vertebrae are mostly covered by the sternum (Fig. 3). Approximately eight cervicals are visible, preserved in articulation; the caudal-most cervicals are poorly preserved, making it difficult to identify the cervical-thoracic transition. The most proximally preserved cervical is covered by the quadrate, obscuring its morphology, so it cannot be determined if it is the axis; no atlas is visible. The total number of cervicals is thus estimated to be nine or ten. Given the articulated and flattened nature of the cervicals, whether or not the articulations of the proximal vertebrae are heterocoelous cannot be determined (contra Morschhauser et al. 2009), although the morphology of the proximal most cervicals do differ from that of the caudal two-thirds of the series. A few disarticulated thoracic vertebrae reveal elongate spool-like centra with amphyplatan articular surfaces. The synsacrum is composed of six or possibly seven fully fused vertebrae (Fig. 5A; six in Morschhauser et al. 2009); the count is uncertain due to fusion and the poor preservation of the transverse processes. The synsacrum appears dorsoventrally flattened distally and the transverse processes of the fused sacral vertebrae enlarge caudally, but do not appear to contact one another. A ventral groove persists along the entire surface but is more pronounced from the third to fifth vertebrae (Figs. 3, 5A). The cranial articular surface is only slightly concave; the caudal articular surface appears flat; however, given the preserved view, this cannot be determined unequivocally.

There are six free caudals; dorsally each bears a small neural spine. The transverse processes exceed the centrum in mediolateral length and appear to become increasingly caudally deflected distal in the series. The articular surface is approximately equal in size to the vertebral foramen.

The pygostyle (Fig. 5B), preserved in ventral view, is excavated which we interpret as the presence of ventrally directed lateral processes, as seen in the longipterygids and other enantiornithines (*Halimornis*, *Cathayornis*, *Dapingfangornis*; Zhou et al. 1992; Chiappe et al. 2002; Li et al. 2006; JKO'C and LMC personal observations). Where the caudal excavation ends, the pygostyle constricts mediolaterally in a step-like fashion, before forming a bluntly tapered caudal margin, also consistent with longipterygids and some other enantiornithines (Chiappe et al. 2002; Sereno and Rao 1992; Hou et al. 2004). A dorsal fork, also characteristic of enantiornithine pygostyle morphology (i.e., *Halimornis*, *Cathayornis*, *Longipteryx*), is not visible. The pygostyle is robust and approximately 10% longer than the tarsometatarsus; the relative size and robustness of the pygostyle is consistent with other longipterygids, which typically possess a proportionately large pygostyle (most extreme in *Longipteryx*, with the pygostyle exceeding the tarsometatarsus in length by 20%; O'Connor et al. 2011).

Thoracic girdle.—The furcula of DNHM D2522 is Y-shaped; an elongate hypocleidium nearly 50% the length of the furcular rami was lost during preparation (Figs. 1, 3, 6, 7A, B).

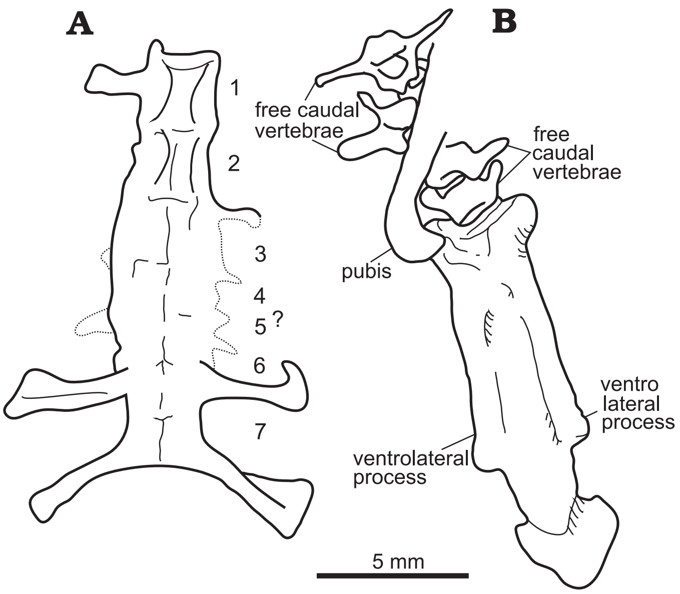

Fig. 5. Enantiornithine bird *Rapaxavis pani* Morschhauser, Varricchio, Gao, Liu, Wang, Cheng, and Meng, 2009 from the Early Cretaceous Jiufotang Formation in northeastern China. Detail drawings of DNHM D2522 (holotype) from the Early Cretaceous Jiufotang Formation in northeastern China: synsacrum (**A**) and pygostyle (**B**).

The clavicular symphysis is short, as in *Longipteryx*. The ventral margin of the furcula does not form a keeled surface or bear a ventral ridge as in some enantiornithines (e.g., *Dapingfangornis*, *Shenqiornis*; JKO'C personal observation). The omal tips (proximal ends of the clavicles) taper bluntly and extend slightly further than originally published (Fig. 7A, B; omal tips covered in matrix).

The lateral margin of the strut-like coracoid is essentially straight (Fig. 6), as in *Longipteryx* and *Iberomesornis*, lacking the strong convexity that typically characterizes enantiornithines (Chiappe and Walker 2002). A procoracoid process is absent, as in most enantiornithines (Chiappe and Walker 2002). No medial groove or supracoracoideum nerve foramen is visible. The dorsal surface of the coracoid may have been slightly excavated, as evidenced by a gentle convexity of the ventral surface, but a deep dorsal fossa like that of *Enantiornis* and some other enantiornithines was definitely absent (Chiappe and Walker 2002). The inner angle formed by the medial and sternal margins is slightly more acute than the lateral, however a distinct median process (angulus medialis; Baumel and Witmer 1993) is not considered present (contra Morschhauser et al. 2009).

Only the left scapula is preserved with its proximal half visible in medial view (Fig. 6). The acromion is large and straight with a kidney shaped articular surface; the tubercle described on the acromion (Fig. 7A; Morschhauser et al. 2009) with matrix removed and given its position is reinterpreted as the dorsomedial margin of the articular surface of the acromion (Fig. 5B). The scapular blade appears to have a costal excavation, as in *Elsornis* (Chiappe et al. 2006) and some other enantiornithines (Chiappe and Walker 2002).

The sternum is quadrangular; the rostral margin forms a caudally obtuse angle (110°) defined by the coracoidal sulci (Fig. 6). There is no rostral midline notch as in *Eoalulavis* (Sanz et al. 1996). The coracoidal sulci are adjacent, separated by a distance no greater than half the width of the sternal margin of the coracoid. There are no costal facets visible; five sternal ribs are preserved tightly associated on the left side (four on the right), however because there are numerous associated rib fragments, the total number of sternal ribs may have been greater (estimated 5–7). The lateral margin of the sternum is straight; the lateral trabecula is strongly forked distally (Fig. 6). A third process was described on the lateral trabecula by Morschhauser et al. (2009); the authors correctly postulated that this may represent a displaced fragment of bone, however still considered the morphology an autapomorphy of the taxon. Additional preparation confirms that the third process is indeed a small rib fragment (Fig. 7C, D); it is has the same dorsoventrally compressed morphology of a rib, unlike the more robust sternal processes. The intermediate trabecula is small and triangular. The caudal margin of the sternum forms a wide V from the medial margin of the intermediate trabecula before constricting into a short xiphoid process (Fig. 6). The distal ends of the lateral trabeculae extend caudally beyond the xiphial region. The xiphoid process bears a low ventral ridge inferred to be the caudal portion of the carina. The sternum bears a short ventral ridge that diverges cranially from the xiphoid process, reminiscent of the sternal carina in some enantiornithines (Chiappe et al. 2007; Zhou 2002). This feature may be a diagenetic artifact in DNHM D2522, resultant from the underlying thoracic vertebrae as the ridge is only clearly preserved diverging left (this ridge was considered absent by Morschhauser et al. 2009). However, the presence of a proximally forked keel in other enantiornithines (e.g., *Concornis*, *Elsornis*) suggests that the elongate hypocleidium of enantiornithines, possibly including *Rapaxavis*, may have articulated with the V-shaped notch formed by the proximal divergence of the keel, similar to the extant hoatzin.

The thoracic girdle of this specimen includes an additional pair of ossifications of indeterminate function and homology. These bones, here named the paracoracoidal ossifications, are acute triangles, located lateral and dorsal to the articulation of the coracoids with the sternum (Fig. 8A). The surface of these elements is porous (Morschhauser et al. 2009); even after preparation there is still matrix embedded on the surface, which highlights the pitted surface of these bones. Since this element is new and no previous information is known on its origin or function, it cannot be determined if the porous surface is indicative of incomplete ossification or simply the nature of the element in this taxon; however, comparisons with the Early Cretaceous enantiornithine *Concornis* (Fig. 8B) suggest that these bones may be incompletely ossified in DNHM D2522.

Gastralia are preserved scattered near the pelvic girdle (Fig. 3); no uncinate processes are observed.

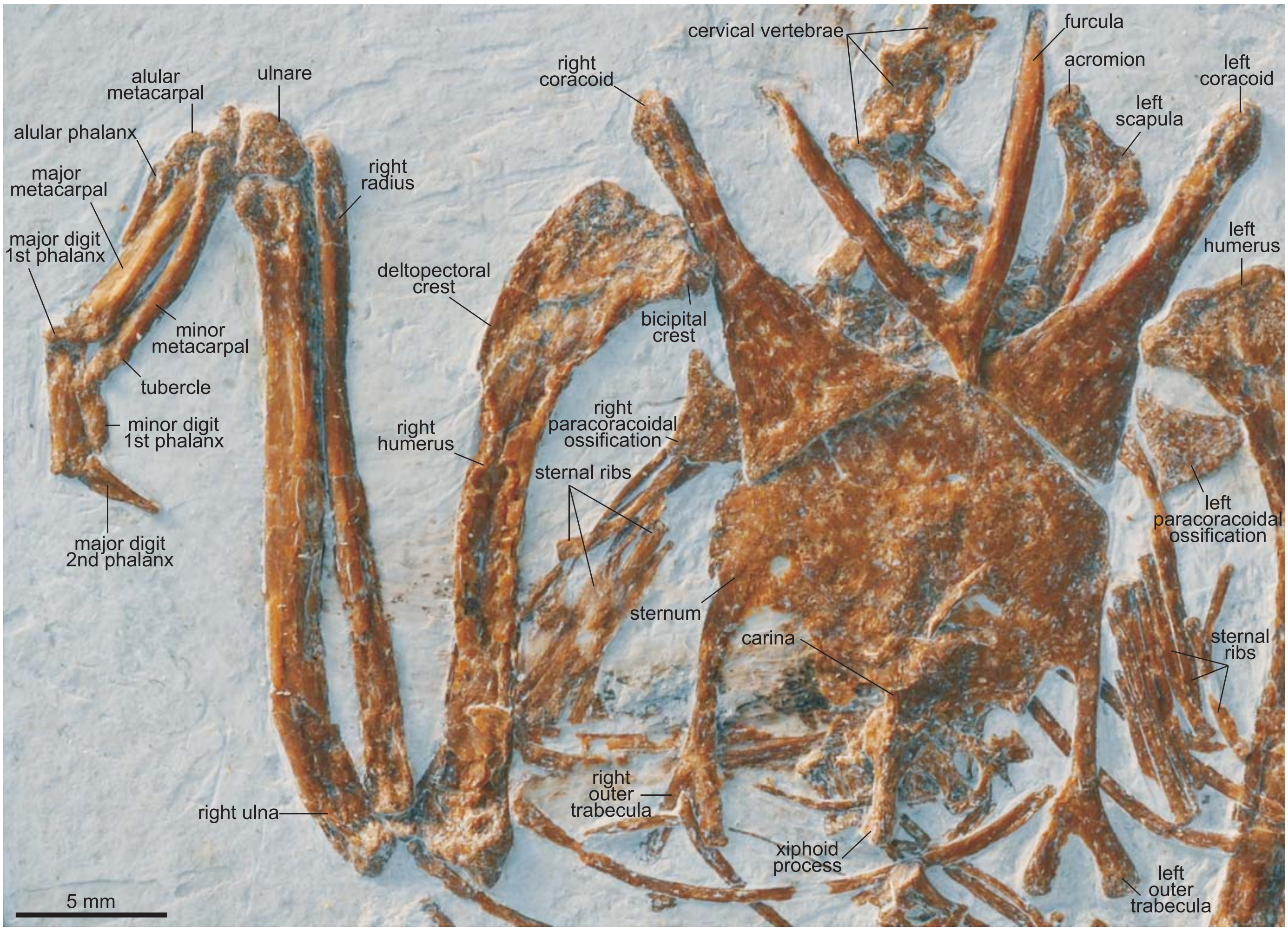

Fig. 6. Enantiornithine bird *Rapaxavis pani* Morschhauser, Varricchio, Gao, Liu, Wang, Cheng, and Meng, 2009 from the Early Cretaceous Jiufotang Formation in northeastern China. Close up of the pectoral girdle and wing of DNHM D2522 (holotype), from the Early Cretaceous Jiufotang Formation in northeastern China.

Thoracic limb.—Both humeri are preserved in cranial view (Figs. 3, 6; medial view according to Morschhauser et al. 2009). The proximal margin in cranial view is concave on the midline, rising dorsally and ventrally, as in other enantiornithines (Chiappe and Walker 2002). The bicipital crest forms a cranial projection relative to the shaft, but is not hypertrophied as in other enantiornithines (i.e., *Eoalulavis, Enantiornis*). The deltopectoral crest is narrow, less than the shaft width, and tapers distally; it appears projected dorsally, contra Morschhauser et al. (2009) (Fig. 6). Given that both humeri are preserved in cranial view, the presence of a dorsal tuberculum as proposed by Morschhauser et al. (2009) is equivocal. Distal on the humerus, the dorsal condyle is smaller than the ventral, which is a transversely elongate oval (Fig. 6). The distal end possesses a small flexor tubercle so that the distal margin is angled relative to the shaft width, but not as strongly as in some enantiornithine taxa (i.e., *Alexornis*; Brodkorb 1976).

The ulnae are preserved in ventral view; they are robust, subequal to the humerus in length and approaching it in mediolateral width (Fig. 6). The bone is bowed proximally and straight distally. The ventral cotyla is slightly concave. A short ridge extends distally from the proximal end representing the attachment of the m. biceps brachii tendon; cranioventral to this scar, the ulna is excavated by a shallow brachial impression that extends approximately one quarter the length of the bone. The paired ridges and tubercle described by Morschhauser et al. (2009) for the distal portion of the ulna are reinterpreted as artifacts resultant from postmortem crushing. The radius is rod-like and is nearly half the mediolateral width of the ulna. A large triangular bone preserved in articulation with the ulna on both sides is interpreted as the ulnare (as in Morschhauser et al. 2009).

The degree of proximal fusion of the carpometacarpus is difficult to discern due to poor preservation, but the individual bones can for the most part be distinguished, suggesting they were not completely fused. Distally, the major and minor metacarpals are clearly unfused as in other enantiornithines (Fig. 6). Proximally, the semilunate carpal does not overlap with the rectangular alular metacarpal. The latter appears to form a ginglymous articulation with the alular digit. The major metacarpal is thicker than the minor meta-

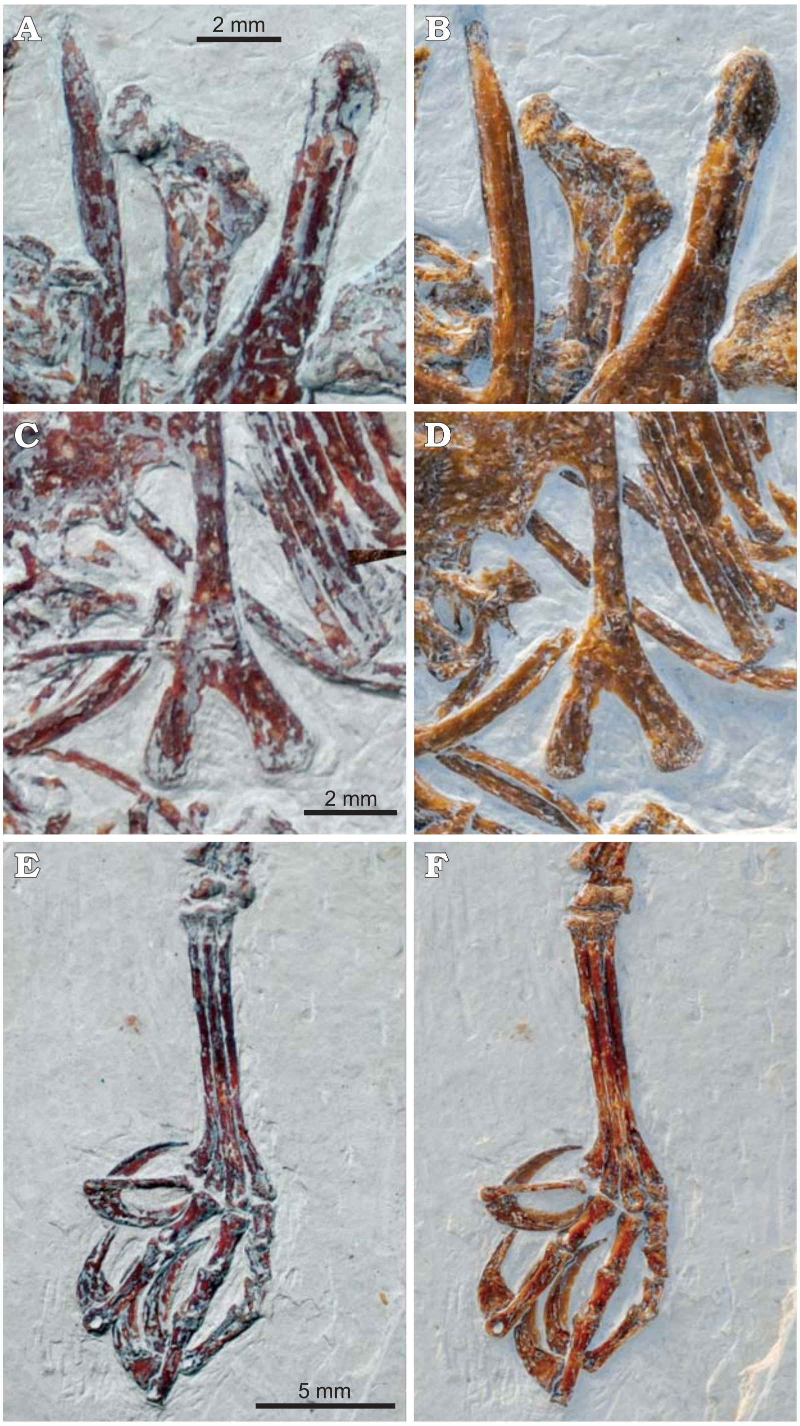

Fig. 7. Enantiornithine bird *Rapaxavis pani* Morschhauser, Varricchio, Gao, Liu, Wang, Cheng, and Meng, 2009 from the Early Cretaceous Jiufotang Formation in northeastern China. Detail photographs of DNHM D2522 (holotype). **A**, **B**. Close up of thoracic girdle before (**A**) and after (**B**) preparation. **C**, **D**. Close up of sternum left outer trabecula before (**C**) and after (**D**) preparation. **E**, **F**. Close up of left tarsometatarsus before (**E**) and after (**F**) preparation.

carpal; the two bones closely abut for their entire length, however, a small space is created mid-shaft where the cranial surface of the minor metacarpal is concave (Fig. 6). As in other enantiornithines (e.g., *Longipteryx, Pengornis, Hebeiornis*; Zhang et al. 2004), the minor metacarpal is contiguous with the pisiform process, forming a ridge on the ventral surface of the carpometacarpus (described as the major metacarpal diving under the minor proximally by Morschhauser et al. 2009). The minor metacarpal projects distally further than the major metacarpal, a synapomorphy of enantiornithines (Chiappe 1996; Chiappe and Walker 2002). Distally, the minor metacarpal bears a small tubercle on the caudal margin.

The digits of *Rapaxavis* are extremely reduced; the alular digit consists of a single short phalanx that tapers distally, ending far proximal to the distal end of the major metacarpal (Fig. 6). The major digit possesses only two phalanges; the first is cylindrical in shape, lacking the dorsoventral expansion of more advanced birds. The second phalanx is reduced, the distal third tapering rapidly; the cranial margin of the phalanx is much thicker than the caudal half so that the caudal margin of the phalanx is keeled. The minor digit bears two phalanges; the first is wedge-shaped, approximately half the width and thickness of the first phalanx of the major digit. The second phalanx is extremely reduced to a small fragment of bone (Morschhauser et al. 2009). The hand of *Longirostravis* is disarticulated and incomplete (alular digit not preserved) and thus it cannot be ascertained for certain if the manual morphology is similar between the two taxa (contra Morschhauser et al. 2009); the manus in *Longirostravis* is, however, clearly reduced relative to that of most other enantiornithines, in which the phalanges of the alular and major digits are long and bear claws (i.e., *Longipteryx, Cathayornis*).

Pelvic girdle.—The pelvic girdle is preserved completely unfused. Both ilia are preserved in lateral view; the right is disarticulated and slightly displaced (Fig. 9). The preacetabular process of the ilium has a broad, rounded cranial margin. The postacetabular process is strap-like and less than half the thickness of the preacetabular process. The caudal margin is not preserved on either side, but it is estimated that the postacetabular process was shorter than the preacetabular process by 25–35%.

The ischium is long, two-thirds the length of the pubis (Fig. 9). The iliac peduncle is narrow and longer than the broad pubic peduncle. The ischium possesses a stout dorsal process, visible on the right element, located on the proximodorsal margin of the shaft; it cannot be determined due to disarticulation if this process contacted the ilium as in some other enantiornithines (Sereno and Rao 1992; Chiappe and Walker 2002). As in other enantiornithines, an obturator process is absent (Chiappe and Walker 2002). The ischia are strap-like for most of their length (contra Morschhauser et al. 2009) and deflected dorsally only along their distal third. The distal end is covered but the two ischia curve medially, taper bluntly and appear to contact (Fig. 9). In medial view (visible on the right element) the ischium appears to have possessed a medially directed ventral flange that extended the distal half of the bone. The preserved morphology is distinct from that of the scimitar-like ischium of *Sinornis* (Sereno et al. 2002).

The pubes are retroverted and are unfused to each other, though they curve medially and would have formed a short symphysis; the distal end is expanded into a small boot as in some enantiornithines and most basal birds (e.g., *Longipteryx*, *Confuciusornis*, *Archaeopteryx*). Morschhauser et al. (2009) described the pubes as kinked but it appears they are caudodorsally concave throughout their length, rather than forming a distinct kink (Fig. 9).

Pelvic limb.—The femur is long, more than three-quarters (80%) the length of the tibiotarsus, and bowed craniocaudally (contra Morschhauser et al. 2009). The femora are both preserved in medial view (right element in craniomedial view) with the lateral margin embedded in the slab, making it difficult to describe the morphology of the trochanters (Fig. 9). The "tubercle on the trochanter" described by Morschhauser et al. (2009) appears to have been an artifact of the incomplete removal of matrix along the craniolateral margin of the right femur. The femoral head is separated from the shaft by a distinct neck; with the current preparation it appears that a fossa for the femoral origin of m. tibialis cranialis was absent.

There is no true tibiotarsus—the proximal tarsals are fused to each other but not to the tibia (Fig. 9). A small fibular crest extends laterally for approximately one third the total length of the tibiotarsus. Contra Morschhauser et al. (2009), two cnemial crests are not present; the cranial surface of the left tibia preserves what may be a single low cnemial crest, a morphology consistent with some enantiornithines (Chiappe and Walker 2002). As observed by Morschhauser et al. (2009), the distal fifth of the tibia bears a shallow cranial sulcus. The sulcus appears to be oriented distomedially; a similar morphology has been observed in the enantiornithine *Qiliania* (CAGS-04-CM-006) from the Early Cretaceous Xiagou Formation of Gansu Province and interpreted as the retinaculum extensorus (Baumel and Witmer 1993; Ji et al. 2011). The proximal tarsals are fused together, forming the distal condyles with a triangular ascending process (Fig. 9).

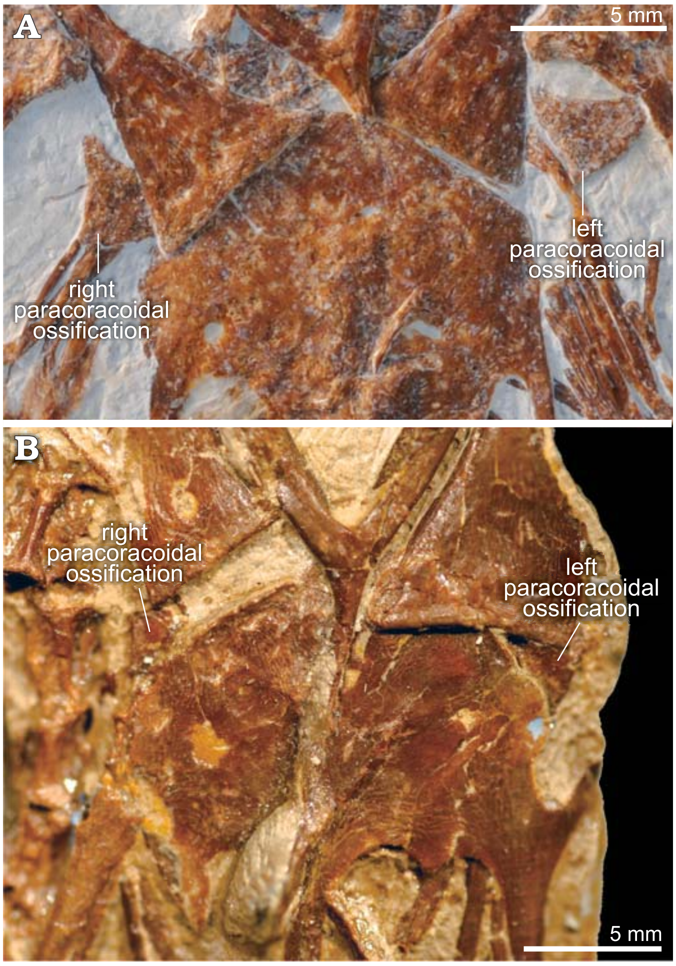

Fig. 8. Close up of the unidentified pectoral ossifications (paracoracoidal ossifications) in two enantiornithine birds. **A**. *Rapaxavis pani* Morschhauser, Varricchio, Gao, Liu, Wang, Cheng, and Meng, 2009, DNHM D2522 (holotype), from the Early Cretaceous Jiufotang Formation in northeastern China. **B**. *Concornis lacustris* Sanz and Buscalioni, 1992, LH 2814, from the Early Cretaceous Calizas de La Huérguina Formation of Spain. Ossifications identified by arrows.

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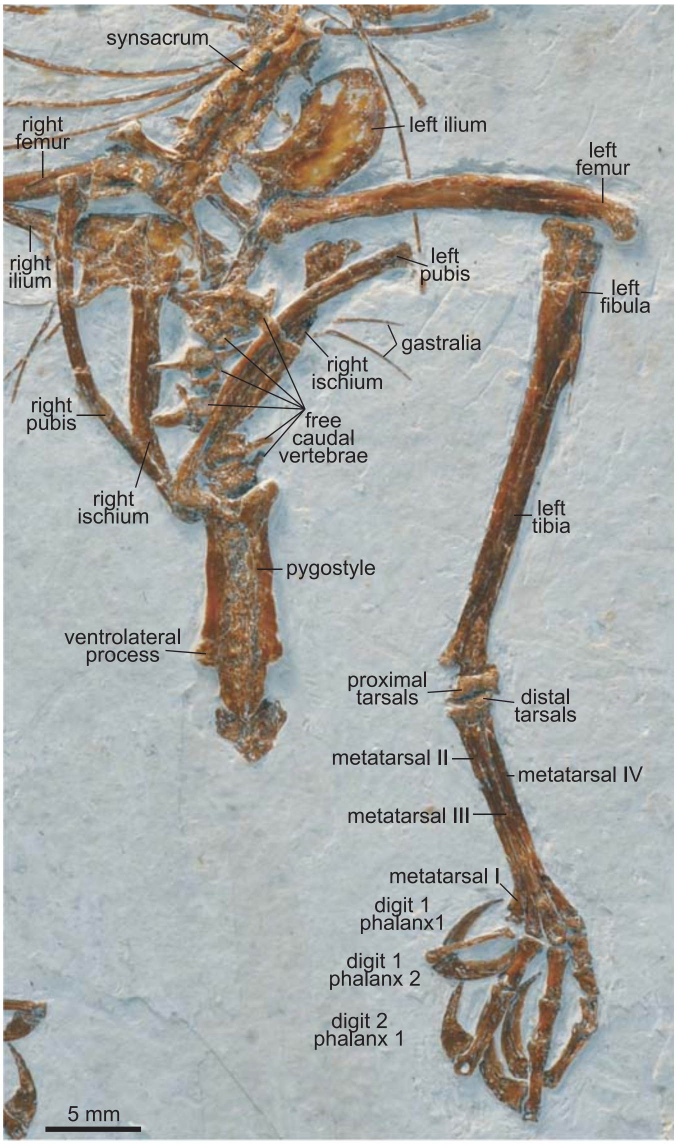

Fig. 9. Enantiornithine bird *Rapaxavis pani* Morschhauser, Varricchio, Gao, Liu, Wang, Cheng, and Meng, 2009 from the Early Cretaceous Jiufotang Formation in northeastern China. Close up of the pelvic girdle and hind limb of DNHM D2522 (holotype).

The condyles are subequal in size and taper toward each other; the lateral surface of the lateral condyle may have had a lateral epicondylar depression, as in CAGS-04-CM-006 and *Lectavis* (Chiappe 1993). The fibula is triangular and fat proximally, swiftly tapering to a splint, and only extending for the proximal third of the tibia.

A true tarsometatarsus is also absent; the distal tarsals are unfused to the metatarsals (Fig. 9). The tarsals and metatarsals are preserved in place; the tarsal bones are fused to one another (described as two unfused tarsals by Morschhauser et al. 2009) and form a cap that covers the proximal end of the metatarsals, thickest over the fourth. Proximal fusion between the metatarsals was reported by Morschhauser et al. (2009); although the metatarsals are preserved in tight articulation they are clearly unfused (Fig. 7E, F). Fusion of the tarsometatarsus is subject to ontogenetic change and, given the unknown developmental stage of DNHM D2522, it cannot be determined if this is the true morphology of the taxon or a juvenile feature of the specimen. Proximally, metatarsal II bears a poorly developed tubercle for the m. tibialis cranialis on its dorsolateral surface, contacting metatarsal III. Metatarsal III is slightly thicker than metatarsals II and IV, which are subequal. Metatarsal III is the longest, closely followed by metatarsal IV, which is longer than metatarsal II. The distal trochlea of metatarsal III is slightly wider than that of the other metatarsals. The sulci on the cranial surface of the distal end of metatarsals II–IV appear to represent crushing (Morschhauser et al. 2009). Metatarsal I is straight in medial view, medially concave in cranial view and between a quarter to a third the length of metatarsal III (Fig. 7F). The characteristic J-shape seen in the metatarsal 1 of some enantiornithines (e.g., *Neuquenornis*) is absent contra Morschhauser et al. (2009); in medial the hallux in DNHM D2522 is relatively straight.

The hallux is long and slender (Fig. 9). The first phalanx of the second digit is short and robust; the penultimate phalanx is long, approximately equal in length to the first phalanx of the hallux, but more robust. The third digit is the longest in the foot; the proximal two phalanges are subequal. The penultimate phalanx is 50% longer than the preceding phalanx. The first three phalanges of the fourth digit are approximately equal and are the shortest phalanges in the foot. The penultimate phalanx is nearly double the length of preceding phalanx. These pedal phalangeal proportions are consistent with advanced perching capabilities that may suggest an arboreal lifestyle (Hopson 2001; Morschhauser et al. 2009). All claws are hooked, broad proximally then curving distally. They possess laterally projecting ridges, also known in other enantiornithines (O'Connor et al. 2009). All pedal claws bear long horny sheaths.

Discussion

After studying the prepared holotype specimen of *Rapaxavis pani* (DNHM D2522), the following revisions are most notable from the original manuscript: absence of definitive evidence for heterocoelous vertebrae (the cervicals are in articulation); absence of a tubercle on the acromion of the scapula (reinterpreted as the poorly preserved margin of the acromion); absence of a third process on the distal lateral trabeculae (trabeculae distally forked and symmetrical); absence of cnemial crests on the tibiotarsus (no crests present); absence of a fully fused tarsometatarsus (tarsal cap unfused to the incompletely fused metatarsals); and the absence of the avisaurid J-shaped metatarsal I (relatively straight).

Rapaxavis belongs to the most diverse clade of Early Cretaceous enantiornithines, the Longipterygidae (junior synonyms: Longirostravisidae, Longipterygithidae; Zhou and Zhang 2006), known to consist of at least five taxa (Zhang et al. 2000; Hou et al. 2004; Morschhauser et al. 2009; O'Connor et al. 2009; O'Connor et al. 2011). Phylogenetic support for this clade comes from several cladistic analyses (Chiappe et al. 2006; Cau and Arduini 2008), including one analysis that included all longipterygid taxa recognized at the time (O'Connor et al. 2009). The results of this analysis suggest that *Longirostravis* and *Rapaxavis* form a more exclusive relationship within the clade (O'Connor et al. 2009), a conclusion not surprising given that DNHM D2522 was originally considered to be a new specimen of *Longirostravis* (Morschhauser et al. 2006).

Longipterygidae is characterized by cranial modifications associated with their presumed trophic specialization, namely an elongate rostrum and rostrally restricted dentition. The rostral proportions of the clade represent a distinct departure from the typical enantiornithine, which may have facilitated the diversification of the group by making new food sources available (O'Connor and Chiappe 2011). The longipterygid clade is so far known from both the Yixian (*Longirostravis*, *Shanweiniao*) and Jiufotang (*Longipteryx*, *Rapaxavis*, *Boluochia*) formations of the Jehol Group, northeastern China. The presence of the more basal *Longipteryx* in the younger Jiufotang Formation suggested the presence of a great deal of undiscovered diversity within the clade, and was subsequently confirmed by the discovery of two new longipterygids (Morschhauser et al. 2009; O'Connor et al. 2009). The primitive morphologies of the younger *Longipteryx*, however, suggests that there existed longipterygids with morphologies similar to *Longipteryx* (i.e., unreduced manus) in the Yixian Formation, yet undiscovered. *Boluochia zhengi* from the Jiufotang Formation has been recently identified as a longipterygid, with morphologies that suggest it is more closely related to *Longipteryx* than other longipterygids; however, there is no preserved wing material in the only known specimen of this taxon (O'Connor et al. 2011). Though *Rapaxavis* is considered closely related to *Longirostravis*, it comes from the younger Jiufotang Formation, while *Longirostravis* is from the Yixian Formation, indicating that the *Longirostravis* lineage persisted for at least five million years (125–120 Ma; He et al. 2004; Yang et al. 2007).

Unlike other longipterygids, *Rapaxavis* preserves an additional mysterious thoracic element; these features may simply not be preserved in other enantiornithines, however, multiple specimens of *Longipteryx* are known, none of which preserve these paired bones suggesting that, in this taxon at least, they were truly not present. This paired structure is of unknown significance and is also present in the holotype specimen of the Early Cretaceous Spanish enantiornithine *Concornis* (Fig. 8B). Contra Morschhauser et al. (2009), the ossifications are also paired in the Spanish taxon; the bones are damaged in this region so that the exact morphology of the structures cannot be discerned but their placement, dorsolateral to the coracoid-sternum articulation, is comparable to the condition in *Rapaxavis*. Based on their position, these bones may have served a similar function to the craniolateral processes of the ornithurine sternum; however, craniolateral processes are present on the sternum of *Concornis*. We have used the term paracoracoidal ossifications to refer to these elements. The homology, development, and function of these structures is yet unknown but their existence is further evidence of the disparity between the flight apparatus of modern and enantiornithine birds, as well as the diversity and experimentation within the enantiornithine clade.

The paracoracoidal ossifications have a porous texture in the holotype of *Rapaxavis*, but not in *Concornis* (surface texture appears comparable to other elements), suggesting that the individual represented by DNHM D2522 had not reached the final stages of development (Fig. 8). This inference is supported by the absence of fusion in the compound bones of the hindlimb, although the degree of ossification among compound bones is a weak assessment of precise ontogenetic stage. As is particularly evident in other specimens (e.g., *Shenqiornis*), given unknowns regarding the pattern of enantiornithine growth (Chinsamy and Elżanowski 2001; Cambra-Moo et al. 2006), any inferences regarding the ontogenetic stage of DNHM D2522 should await histological analysis.

The morphology of *Rapaxavis pani* is described as preserved in the only known specimen (DNHM D2522), however, ontogeny may affect features such as degree of fusion and proportions. In the absence of any well-documented growth series, to what degree fusion and proportions may change is unknown among enantiornithines. It may be that DNHM D2522 is an adult in size and skeletal morphology but not in skeletal maturation, a developmental strategy observed in the extant kiwi (Bourdon et al. 2009) and consistent with the pattern of slow, extended growth hypothesized for enantiornithines (Chinsamy et al. 1994, 1995). A juvenile *Longipteryx* (IVPP V12552) suggests that DNHM D2522 may fuse compound bones later in ontogeny, but not increase greatly in size. IVPP V12552 lacks many compound bones present in the *Longipteryx* holotype (IVPP 12325) although it is only roughly 10% smaller than the adult. Without further material and extensive histological analysis, there remain many unknowns regarding the morphology of *Rapaxavis pani*.

The absence of a fused tarsometatarsus in *Rapaxavis* may or may not represent the adult condition; however, the morphology of this taxon reveals important information regarding the formation of this compound bone in non-ornithuromorph birds. Among the latter, free distal tarsals are only known in a few specimens, likely a preservational bias given the small size of these bones. *Archaeopteryx* preserves two to three distal tarsals that are reportedly free in some specimens (Wellnhofer 1974) and partially fused to the metatarsals in others (Elżanowski 2002). The Late Cretaceous long-tailed *Rahonavis* preserves a single distal tarsal over the fourth metatarsal (Forster et al. 1998). A tarsal cap fused to the proximal ends of the metatarsals was reported in *Iberomesornis* (Sereno 2000), although Sanz and Bonaparte (1992) considered the tarsals in this subadult specimen to be separate, as they are interpreted here. A juvenile enantiornithine from Liaoning, GMV 2158, preserves a single small,

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free distal tarsal located between the proximal ends of metatarsals II and III (Chiappe et al. 2007). The enantiornithine *Shenqiornis mengi* also preserves a single distal tarsal element (Wang et al. 2010); this bone is larger than those typical of *Archaeopteryx* (Wellnhofer 1974); however, the element is disarticulated and it cannot be determined the extent to which it capped the metatarsals, or if additional distal tarsal bones were incorporated into the "tarsometatarsus". *Rapaxavis* preserves a distal tarsal cap separate from the unfused metatarsals. Although the individual distal tarsals inferred to form the tarsal cap cannot be distinguished, the preserved element entirely caps the proximal surfaces of metatarsals II–IV (Fig. 7E, F) and clearly differs from the small individual distal tarsals recognized in *Archaeopteryx* and other subadult enantiornithines (Chiappe et al. 2007). No free distal tarsals are recognized within Ornithuromorpha or the more exclusive Ornithurae; fossil specimens typically show greater degrees of tarsometatarsal fusion than even the most fused enantiornithines (i.e., the Late Cretaceous El Brete enantiornithines; Chiappe 1993). Tarsometatarsal development in fossil ornithuromorphs is assumed to have progressed similarly to modern birds, with a distal tarsal cap forming prior to its fusion with the proximal ends of metatarsals II–IV. This condition was used to support the argument that the early evolutionary history of birds was characterized by a basal dichotomy between "Sauriurae" (*Archaeopteryx*, Enantiornithes and other basal birds), on the one hand, and the Ornithurae (and non-ornithurine ornithuromorphs), on the other hand (Martin 1983, 2004; Feduccia 1996; Hou et al. 1996; Kurochkin 2006). Under this hypothesis, "sauriurine" birds are envisioned as having very small distal tarsals that are unincorporated into the tarsometatarsus (Kurochkin 2006) and metatarsal fusion that proceeds from the proximal end distally (Hou et al. 1996). Notwithstanding the fact that this hypothesis and the monophyletic nature of "Sauriurae" have been rejected numerous times on cladistic terms (Chiappe 1995, 1996; Zhou and Zhang 2002; Clarke and Norell 2002; Clarke et al. 2006; O'Connor et al. 2009; Bell et al. 2010), the holotype of *Rapaxavis pani* clearly demonstrates the presence of a tarsal cap—allegedly a fundamental difference between "Sauriurae" and Ornithurae—in a non-ornithuromorph (i.e., "Sauriurae") taxon. Despite this, the development of the tarsometatarsus within different clades of Mesozoic birds remains poorly understood.

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