New Species of Enantiornithes (Aves: Ornithothoraces) from the Qiaotou Formation in Northern Hebei, China

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Abstract: We report on a new species of enantiornithine bird from the Lower Cretaceous Qiaotou Formation of northern Hebei, China. The new taxon, *Shenqiornis mengi* gen. et sp. nov., possesses several enantiornithine synapomorphies but is unique from other known species. The specimen has a well-preserved skull that reveals new information about enantiornithine cranial morphology. The new taxon possesses a large postorbital with a long tapering jugal process indicating that some enantiornithines may have had a fully diapsid skull, as in *Confuciusornis*. The tooth morphology of the specimen is unique and likely represents a previously unknown trophic specialization within Enantiornithes.

Key words: Aves, Enantiornithes, diapsid, teeth, Jehol, Qiaotou Formation

1 Introduction

Since their establishment as a clade less than three decades ago, Enantiornithes has become the most diverse group of Cretaceous birds known to science (Chiappe, 2007). The Lower Cretaceous (c.131–120 Ma) Jehol Group deposits of northeastern China (Wang et al., 2003; Zhou, 2006; Zhu et al., 2007) have held an important role in revealing a large portion of this diversity by producing more complete specimens than any other lithological unit in the world (Swisher et al., 2002; Zhang et al., 2003; Li et al., 2006, 2008; Zhou and Zhang, 2006). Many of these specimens, although complete, are poorly preserved with the bones split between two slabs. Thus as the known diversity of enantiornithines has rapidly increased, many anatomical details, especially those regarding the skull, vertebral column and pelvic girdle, have remained enigmatic.

Chinese enantiornithines from correlative deposits are lesser known, limited to the Xiaogou Formation, which is suggested to be comparable to the Jiufotang Formation (Zhou, 2006). Here we describe a new well-preserved specimen from the older Qiaotou Formation, a unit stratigraphically lower than the Yixian Formation of the Jehol Group (Ji et al., 2005). The exact age of this formation is currently under study (Ji et al., 2005) and it is unknown whether it correlates with the Dabeigou Formation, the oldest unit of the Jehol Group, from which the primitive enantiornithine *Protopteryx* is known (Zhang and Zhou, 2000; Zhou, 2006). The new specimen represents a new taxon and contributes to our understanding of enantiornithines by increasing known morphological diversity, providing new anatomical information, and expanding the known range of trophic specialization.

2 Systematic Paleontology

Aves Linnaeus, 1758
  Pygostylia Chiappe, 2002
    Ornithothoraces Chiappe, 1995
      Enantiornithes Walker, 1981

Shenqiornis mengi gen. et sp. nov. (Figs 1, 2)

2.1 Holotype
A nearly complete and largely articulated individual preserved in a slab (DNHM D2950; Figs. 1a, 2a) and
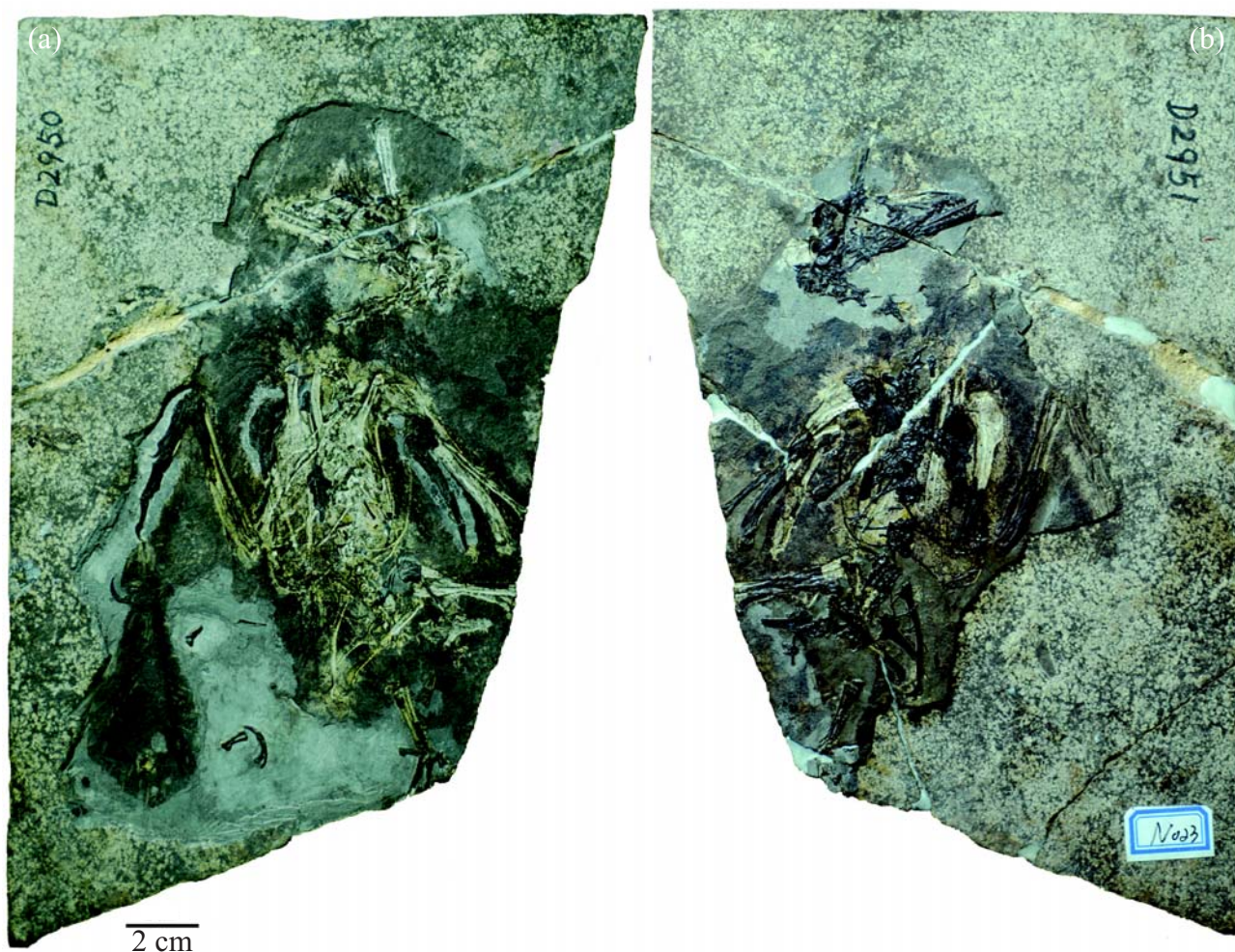
Fig. 1. Photographs of (a) DNHM D2950; (b) DNHM D2951.

counter slab (DNHM D2951; Figs. 1b, 2b). The bones are primarily preserved in DNHM D2951 (DNHM - Dalian Natural History Museum) and are exposed mainly in ventral view. The manus are preserved in DNHM D2950 along with voids of the remainder of the skeleton. Feathers are preserved as carbonized traces concentrated around the head, wings and tail. Despite the lack of fusion present in several of the compound bones (absence of tibiotarsus and carpometacarpus), this specimen is considered not to be an early juvenile based on the size and proportions of the skull and orbit and the absence of any pitted periosteal surfaces, and is here regarded as an subadult/adult.

2.2 Locality and horizon

Senjitu Area, Fengning County, Hebei Province, China. Qiaotou Formation, Late Jurassic–Early Cretaceous (Ji, 2004; Ji et al., 2005).

2.3 Etymology

The generic name, "*Shenqiornis*," celebrates the successful launch of the Shenzhou 7, China's third human mission into space. The species name is in honor of Meng Qingjin for his contribution to the study and protection of Liaoxi fossils as former Director of the Dalian Natural History Museum.

2.4 Diagnosis

Medium sized enantiornithine bird with the following unique combination of characters: narrow nasal lacking maxillary process; postorbital with elongate, straight jugal process (local autapomorphy); robust teeth with circular cross-sections and slightly recurved apices (autapomorphy); omal tips of furcula expanded; distal third of coracoid lateral margin convex; sternum with fan-shaped expansion of outermost trabecula; unreduced and unfused manus with claws on the alular and major digits; dorsally projecting tubercle on caudodorsal surface of semilunate carpal; strap-like ischium lacking obturator process; pubis bearing boot-like distal expansion; J-shaped metatarsal I lacking lateral compression with laterally directed facet for the articulation with metatarsal II and caudally oriented facet for the articulation with digit I.

Fig. 2. Camera lucida drawings of (a) DNHM D2950; (b) DNHM D2951.

Anatomical abbreviations: al, alular metacarpal; al I, alular phalanx I; al II, alular phalanx II; cau, caudal vertebra; cor, coracoid; crv, cervical vertebra; den, dentary; dt, distal tarsals; ebc, external basicranium; fem, femur; fro, frontal; fur, furcula; hum, humerus; ili, ilium; isc, ischium; jug, jugal; ma, major metacarpal; ma I, major digit phalanx I; ma II, major digit phalanx II; ma III, major digit phalanx III; mi, minor metacarpal; mi I, minor digit phalanx I; mtI, metatarsal I; nas, nasal; par, parietal; pcl, pedal claw; pmx, premaxilla; po, postorbital; pph, pedal phalanx; pub, pubis; qd, quadrate; rad, radius; rib, ribs; sca, scapula; scl, scleral; stn, sternum; sur, surangular; syn, synsacrum tbt, tibiotarsus; tmt, tarsometatarsus; tth, thoracic vertebra; uln, ulna.

3 Anatomy

Anatomical nomenclature mainly follows Baumel and Witmer (1993) using the English equivalents of the Latin terms.

3.1 Skull

The skull is preserved primarily in DNHM D2951 (herein referred to as D2951) with voids in DNHM D2950 (herein referred to as D2950). The skull is preserved in right lateral view, although the external basicranium is also visible due to the largely disarticulated nature of the postorbital region (Fig. 3a). There are four robust teeth present in the premaxilla, typical of theropods and other toothed birds, such as *Sapeornis* and *Eoenantiornis* (Zhou and Zhang, 2002; Zhang et al., 2004). Based on the tooth distribution, the premaxilla is interpreted as restricted rostrally forming only a small portion of the facial margin. The nasal processes of the premaxilla (syn. frontal process; Baumel and Witmer, 1993) are relatively short, extending beyond the rostral margin of the antorbital fenestra but not

reaching the level of the lacrimal. The distal third of the nasal processes forms a wedge-like articulation with the nasals. The nasals are long and narrow, expanding caudally; a maxillary process is absent.

The maxilla has a long and slender dorsal process that extends caudodorsally to contact the nasal. Unlike the condition preserved in *Pengornis* (Zhou et al., 2008), the antorbital fossa is entirely occupied by the antorbital fenestra in D2950/1. The maxilla possesses at least four teeth (Fig. 3b).

The jugal is a straight bar, forked distally, as in *Archaeopteryx* and the Montsec nestling (Sanz et al., 1997; Elzanowski, 2002). There is no evidence of a postorbital process on the jugal and no quadratojugal is preserved.

The postorbital is T-shaped with a large tapering jugal process, as opposed to the reduced postorbital in the Montsec nestling and *Pengornis*; the bone is disarticulated so it cannot be determined unequivocally whether or not it contacted the jugal. While the postorbital clearly did not fully separate the infratemporal fenestra from the orbit in the former taxa, the length of the jugal process of the
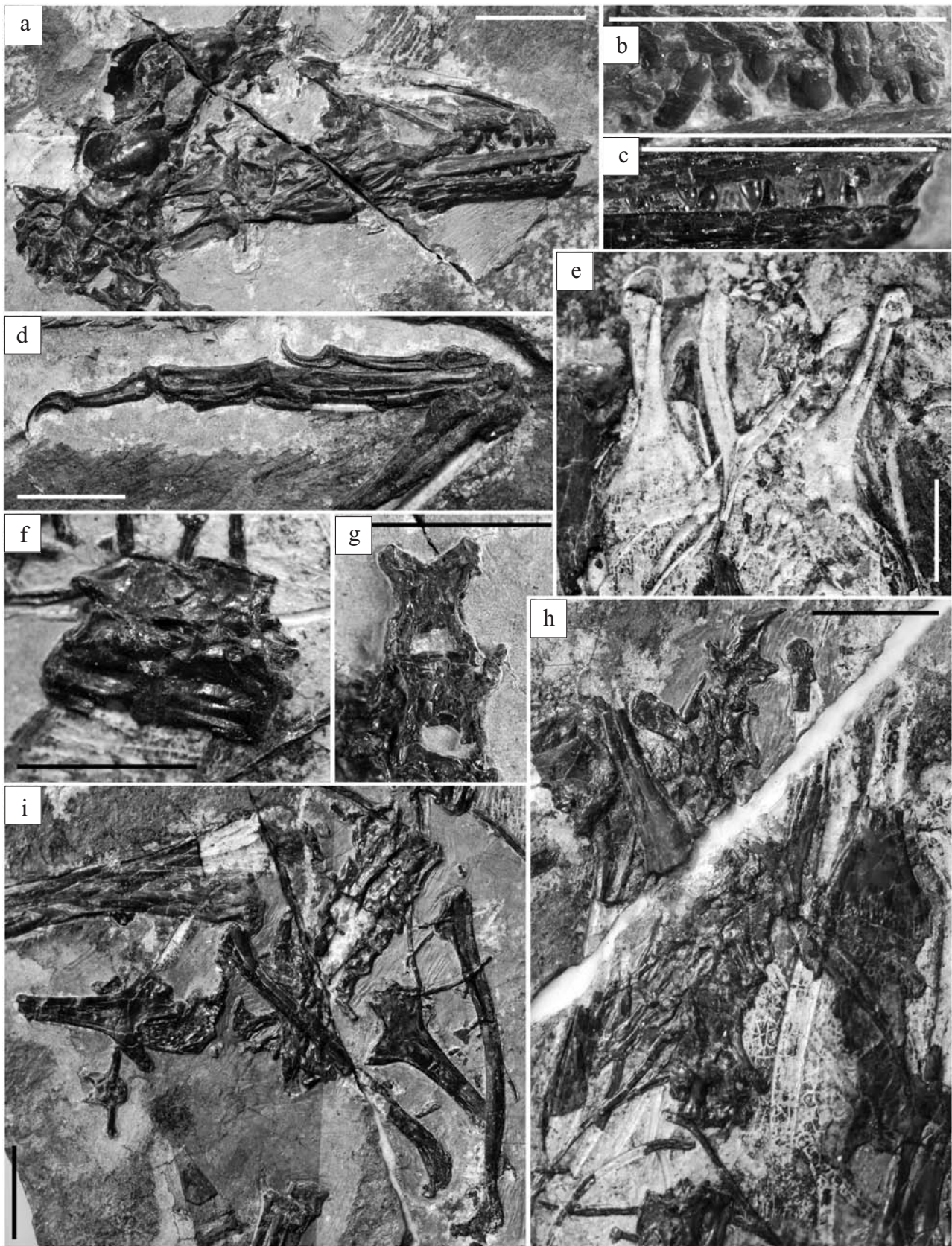
Fig. 3. Detailed photographs of DNHM D2950/1.
All scale bars represent 1 cm. (a) Skull in right lateral view; (b) upper dentition; (c) lower dentition; (d) left manus; (e) thoracic girdle, D2950; (f) thoracic vertebrae; (g) cervical vertebrae; (h) thoracic girdle, D2951; (i) pelvic girdle.

postorbital in D2950/1 suggests that some contact or overlap with the jugal was present. Given the distribution of elongate postorbitals outside Ornithothoraces (*Sapeornis*, *Confuciusornis*), the morphological variation within Enantiornithes, and the apparent absence of a postorbital within Ornithuromorpha (*Ichthyornis*, *Hesperornis*), it is difficult to determine whether the elongate jugal process in D2950/1 is a derived morphology (Chiappe et al., 1999). The absence of a large postorbital process on the jugal indicates that the condition in other non-avian theropods, in which the two bones articulated for an extended length, was not present. The presence of a bony postorbital bar in D2950/1 would preclude this taxon from any form of cranial kinesis, present in all modern birds.

The quadrate is preserved in caudal view; the caudal surface is excavated, similar to that of *Archaeopteryx,* and perforated by a pneumatic foramen as in *Pengornis* and the Montsec nestling. The medial condyle of the mandibular process of the quadrate is much larger than the lateral condyle.

The frontals are craniocaudally long, slender rostrally, caudally expanding into domed structures. The parietals are oval and vaulted; they are unfused to the frontals and occipital bones. The basicranium is preserved disarticulated and caudoventral to the rostrum and orbit. The occipital bones are fully fused with the exception of the basioccipital and where the two exoccipitals meet on the midline to each form a dorsal quarter of the occipital condyle. The supraoccipital forms a cerebral prominence, more pronounced than that of *Neuquenornis* (Chiappe and Calvo, 1994). Large fossae excavate the exoccipital lateral to the foramen magnum; ventrally the exoccipital bears two foramina. These may represent the *canales n. hypoglossi* (XII), the location of which in modern birds typically opens through the exoccipital (Zusi, 1993). The foramen magnum is a pentagonal opening, mediolaterally wider than it is craniocaudally tall, and more than 4× the size of the occipital condyle; the foramen magnum is proportionately much larger than the occipital condyle in *Neuquenornis*, closer to 10 times the size of the latter. The basioccipital forms the caudal half of the occipital condyle; basal tubera project caudolaterally giving the basioccipital a ventrally concave caudoventral margin.

Both dentaries are preserved in lateral view. There were at least seven teeth in each dentary (Fig. 3c). The caudal-most tooth is smaller than the rest. A row of nutrient foramina runs parallel to the dorsal margin of the dentary, possibly for the veins that supplied the robust teeth. The dentary is straight; caudal to the dentigerous region, the ramus expands ventrally. The articulation with the surangular appears unforked, typical of other Early Cretaceous enantiornithines, such as *Eoenantiornis* and

Shanweiniao (O'Connor et al., 2009).

The cranial and dentary teeth are nearly the same in size and morphology, with the one exception noted in the dentary (Fig. 3b, c). The teeth are bulbous with a circular cross section near the root. Distally they bulge slightly along the rostral margin and then taper quickly into a slightly caudally directed point.

3.2 Axial skeleton

The cervical series is incomplete; seven vertebrae, including the atlas and axis, are preserved. The atlantal hemi-arches appear unfused. The post-axial cervicals are disarticulated and displaced so that both dorsal and ventral surfaces are visible. The cranial-most post-axial cervicals appear incipiently heterocoelous. The prezygapophyses project cranially beyond the articular surface; the postzygapophyses are elongate, twice as long as the prezygapophyses (Fig. 3g). The postzygapophyses become more robust distally through the series. Ventrally, the posterior cervicals possess carotid processes and a small ventral process but appear unkeeled. Costal processes are unfused to the vertebral bodies; they are robust proximally, tapering sharply at their distal ends (Fig. 3h).

The amphyplatan thoracic vertebrae have elongate and spool-like centra, typical among enantiornithines (Chiappe and Walker, 2002; Fig. 3f). The vertebrae possess tall neural spines very similar to those of *Iberomesornis* (Sanz and Bonaparte, 1992); the postzygapophyses are slightly longer than the prezygapophyses, and both extend beyond the caudal/cranial margin of the centrum. The parapophyses are centrally located and the centra bear a deep lateral groove, both features typical of enantiornithines (Chiappe and Walker, 2002).

The number of vertebrae fused into the synsacrum cannot be discerned (Fig. 3i). The incorporated vertebrae possess transverse processes that increase in length and width distally; the processes expand distolaterally so that the ends of the distal-most transverse processes contacted each other as in *Pengornis* and *Cuspirostrisornis* (Hou, 1997). A single free caudal is preserved; the transverse processes are elongate, equal in length to the centrum width (Fig. 3i). No pygostyle is preserved.

No uncinate processes are preserved; several slender disarticulated elements near the pelvic girdle are interpreted as gastralia (Fig. 3i).

3.3 Thoracic girdle

The strut-like coracoids are flattened making it impossible to determine whether they bore a dorsal fossa as in some enantiornithines (*Eoenantiornis*, *Neuquenornis*; Fig. 3e, h). The acrocoracoid process is small and rounded; a procoracoid process is absent as in other enantiornithines

with the exception of *Protopteryx* (Zhang and Zhou, 2000; Chiappe and Walker, 2002). The medial margin of the right coracoid appears to have a groove (Fig. 3h) but it is impossible to determine if it is perforated by the foramen supracoracoideum, as in many other enantiornithines (Chiappe and Walker, 2002). The lateral margin is strongly convex along the distal quarter as in *Concornis* (Sanz et al., 1995); a lateral process is absent. The sternal margin is straight and slightly less than half the omal-sternal length.

The scapula is long, approximately 50% longer than the coracoid (Table 1; Fig. 3h). The scapular blade is straight and the distal end is blunt. The acromion (Fig. 3e) is long and straight, as in *Eoalulavis*, *Elsornis*, and *Shanweiniao* (Sanz et al., 1996; Chiappe et al., 2007).

The furcula is Y-shaped with an interclavicular angle of approximately 50° (Fig. 3e, h). The omal tips curve dorsally (visible in the right ramus) and bear bulb-like omal expansions in dorsal view (left ramus) as in *Shanweiniao*. The rami fuse over a broad area; the suture forms a ventral ridge that is visible along the entire length of the hypocleidium. The hypocleidium is long, approximately 70% the length of the rami; it is keeled dorsally and tapers distally. It cannot be determined if the furcula was laterally excavated as in other enantiornithines, such as *Longipteryx*, and *Eoenantiornis* (Zhang et al., 2001).

A large piece of the left sternum is preserved allowing a reconstruction of this structure (Fig. 3h). The rostral margin is rounded but the lateral corner is not preserved. The sternum ends in a simple xiphoid process, which is preserved as a void in both slabs (Fig. 3h). The sternum possesses at least one trabecula interpreted as the outer (lateral process) trabecula of other enantiornithines, for example, *Shanweiniao*, *Longipteryx*, and *Concornis*. It extends laterodistally from the rostrolateral margin of the sternum, as in *Concornis*, and ends in a simple fan-shaped expansion that is leveled with the distal end of the xiphoid process. The region between the outer trabecula and the xiphoid process is badly broken, so it cannot be determined with any degree of certainty whether an inner trabecula (medial process) was present. A small groove in the void of the sternum rostral to the xiphoid could represent a shallow keel (D2950).

3.4 Thoracic limb

The humerus is straight with a moderate deltopectoral crest, less than half the shaft width (Figs. 2, 3). The crest extends for one-third the length of the humerus before it ends abruptly (as in *Enantiornis, Longirostrais* and *Protopteryx*). The proximal cranial surface is convex and the caudal surface is concave; the midline of the proximal surface is concave as in other enantiornithines (Chiappe and Walker, 2002). The bicipital crest does not appear to

Table 1 Selected measurements of *Shenqiornis mengi* combined from both slabs of the holotype specimen (DMNH D2950/1) in mm

	Right	Left
Skull, length	41.9[A]	41.6[A]
Dentary	20.9[A]	21.3
Furcula	25.7	28.9
Coracoid	(22.1)	26.2
Scapula	34.6[A]	39.3
Humerus	43	46.6
Ulna	44.8	46.8
Radius	39.6	45.8
Carpometacarpus	24.8[A]	25.5
Alular Metacarpal	4.1[A]	4.5
Phalanx 1	(8.9)	10
Claw	4[A]	5.9
Major Metacarpal	16.8[A]	21.7
Phalanx 1	10.1	11.1
Phalanx 2	8.4	8.7
Claw	4.7	5.5
Minor Metacarpal	18.4[A]	20.7
Phalanx 1	4.4[A]	6.9
Ilium	25[A]	
Ischium	18	17.5
Pubis	35	33.4
Femur		38.8[A]
Tibiotarsus	(33)	
Tarsometatarsus	25	24.8[A]
Metatarsal I		7
Phalanx 1	7	
Metatarsal II	22.4[A]	
Phalanx 1	5.6	
Phalanx	2	(7.8)
Metatarsal III	25	
Phalanx 1	(8.4)	
Metatarsal IV	22.8	
Phalanx 1	4.1	
Sternal midline	28.8[A]	

[A]Estimated lengths. Parentheses represent incomplete elements.

project strongly cranially. Similar to the condition in *Pengornis*, the ventral tubercle is separated by a shallow capital incision, unlike the deep groove that separates the ventral tubercle in the El Brete enantiornithines (Chiappe and Walker, 2002). The distal end of the humerus is poorly preserved; the condyles are located on the cranial surface as in other ornithothoracine birds. The distal margin does not appear angled ventrally as in some enantiornithines, for example, *Alexornis*, *Eoalulavis,* and *Vescornis* (Brodkorb, 1976; Zhang et al., 2004).

The ulna is proximally bowed and more robust than the straight distal half (Figs 1, 2). Remige papillae (quill knobs) are absent. Proximally, the olecranon process is small; distally, the dorsal condyle is large and rounded in profile. The radius is straight and approximately half the shaft width of the ulna – there is no evidence of the longitudinal sulcus present in some other enantiornithines (Chiappe and Walker, 2002).

A single proximal carpal is preserved; it cannot be determined if it is the ulnare or radiale. Two distal carpals are present, interpreted as the semilunate and carpal x (Chiappe et al., 2007); these remain free from the metacarpal bones, not fusing to form a carpometacarpus (Fig. 3d). The semilunate carpal has a semi-rounded profile

with a straight cranial margin. The caudodorsal surface of the semilunate bears a dorsally projecting tubercle. Carpal x is rectangular, and located proximal to the minor metacarpal, fitting with a notch on the caudodistal corner of semilunate carpal. A free carpal x is known in juvenile enantiornithines, and *Longipteryx* possesses distal carpals fused to each other but not the metacarpals (Chiappe et al., 2007). DNHM D2950/1 shares the basal condition of *Archaeopteryx* with carpals and metacarpals fully unfused in adults (Wellnhofer, 1974).

The proximal ends of the alular and major metacarpals are nearly aligned. The alular metacarpal is less than one quarter the length of the major metacarpal; it is wedge-shaped so that the cranial margin is angled craniocaudally, with the thicker end of the metacarpal articulating with the digit. The alular digit ends level with the distal end of the major metacarpal as in *Eoenantiornis*, *Longipteryx*, and *Eoalulavis*. The first phalanx is slightly bowed and tapers distally. The distal end possesses deep extensor pits and articulates with a recurved claw. The major metacarpal is robust and increases in craniocaudal thickness distally. The first phalanx is slightly less than half the length of the major metacarpal; it is robust and bar-like, with a straight cranial margin and slightly convex caudal margin. The second phalanx is much shorter than the proximal one; it is wedge-shaped, tapering distally. The third phalanx is a recurved claw, slightly smaller than that of the alular digit. The minor metacarpal is thinner than the major metacarpal but approximately the same length. The proximal end of the minor metacarpal is distal to that of the major metacarpal, offset by the carpal x, so that its distal end projects beyond that of the major metacarpal, a synapomorphy of enantiornithines (Chiappe and Walker, 2002). The proximal and distal ends of the minor metacarpal firmly abut the major metacarpal but the minor metacarpal is slightly bowed, creating a sliver of intermetacarpal space. The first phalanx of the minor digit is small, less than half the length and width of the first phalanx of the major digit. It is unclear whether there is a second phalanx; if present, it would have been greatly reduced. The minor digit does not possess a claw.

3.5 Pelvic girdle

The pelvic girdle is incomplete and entirely disarticulated indicating the elements remained unfused, as in *Cathayornis* (Fig. 3i). The preacetabular wing of the ilium is missing on both sides; the postacetabular wing appears to be broad proximally and tapered distally but the distal half is covered by the ischium (D2951). Both ischia are well-preserved and in medial view (Fig. 3i). The ischium is approximately half the length of the pubis. Proximally, the ventral process for articulation with the

pubis is much larger than the corresponding dorsal process for the ilium. The ischium bears a large proximodorsal process but no obturator process. The ischiadic wing is strap-like and blunt, as opposed to curved and tapered as in *Sinornis* (Sereno et al., 2002).

The pubis is disarticulated indicating that the distal ends were not fused; however, the presence of an articular facet on the distal medial surface indicates the two bones were in contact. The pubes are approximately the same length as the femur and nearly twice the length of the ischia; they are slightly bowed in lateral view and laterally compressed with an oval cross-section (Fig. 3i). The proximal ends are broad preserving the articulations for the ischium (convex) and the ilium. Distally, the pubis possesses a boot-like expansion as in many other basal birds, for example, *Archaeopteryx*, *Eoenantiornis*, *Pengornis*, and *Yanornis* (Zhou and Zhang, 2001).

3.6 Pelvic limb

Only the right femur is preserved; the bone is straight but very incomplete and obscured by the tibia (Fig. 3i). The rounded head of the femur is visible at the edge of the slab. A single incomplete tibia, associated with the right side, is preserved overlapping the femur revealing no anatomical information. No fibula is preserved.

The proximal tarsals (astragalus and calcaneum) are fused to each other but not the tibia (Fig. 1–3i). The astragalus possesses a large sheet-like ascending process that tapers proximally. A single triangular distal tarsal is preserved free near the proximal end of the right metatarsals.

Both tarsometatarsi are poorly preserved, one below the pelvic girdle and limb and the other under the skull (Figs. 1, 2). A displaced and disarticulated metatarsal I along with two claws and a phalanx are preserved in D2950. The metatarsal I is J-shaped with a flat laterally directed facet for articulation with metatarsal II and a caudally directed articular facet for the first phalanx so that the hallux is fully reversed. A similar condition is observed in avisaurids, but in these taxa the metatarsal is mediolaterally compressed with a longer caudodistal projection. Metatarsal III appears to be the longest, followed by metatarsal IV, which is slightly longer than metatarsal II, but preservation of the distal end of the tarsometatarsus makes all interpretations equivocal.

The first phalanx of digit I is longer than that of digit II. The second phalanx of digit II is incomplete but longer than the first. The first phalanx of digit III is the longest phalanx preserved. The proximal phalanx of digit IV is short, half the length of the proximal phalanx of digit III. The isolated phalanx is exposed plantarly and deeply excavated. The two isolated claws clearly do not belong to the manus, as

they are larger than and not as recurved as the claws of the wing. The claws differ in size, one being approximately 150% the size of the other, indicating that the pedal claws were not uniform in size. The larger of the preserved claws bears a pronounced laterally projecting longitudinal ridge that extends from the proximal third of the ungual and tapers caudally; this feature, seen in some ornithomimids, is also present in DNHM D2522 and *Shanweiniao* but is much more pronounced in the D2950/1 (Mackovicky et al., 2004; Morschhauser et al., 2006; O'Connor et al., 2009). In the two longipterygids, the ridge only extends the middle third of the claw and does not project laterally as strongly as in D2950/1. The pedal claws preserve long, recurved horny sheaths.

3.7 Integument

Feathers are primarily preserved in D2950 (Fig. 1a); there are two incomplete remiges associated with the right wing and traces of body coverts preserved throughout, especially around the pectoral girdle and skull.

4 Discussion and Conclusion

Shenqiornis is clearly distinct from *Protopteryx, Paraprotopteryx, Vescornis* and *Jibeinia,* other taxa from Fengning, Hebei Province, China, as well as from all other described enantiornithines (Hou, 1997; Zheng et al., 2007). The taxon differs from the other Hebei enantiornithines in its overall larger size, more robust skull with large teeth, and proportionately short tarsometatarsus. *Shenqiornis* further departs from *Paraprotopteryx, Jibeinia* and *Vescornis* on the presence of a much longer alular digit, and differs from *Protopteryx* in the absence of a procoracoid process on the coracoid, the strong convexity of the lateral margin of the coracoid (restricted distally in *Protopteryx*), and the presence of a xiphoid process on the sternum (xiphial region forms a wide V in *Protopteryx*). *Shenqiornis* is different from all known enantiornithines in its tooth morphology and the presence of a robust postorbital with an elongate jugal process (a complete diagnosis is provided in the Systematic Paleontology section), the most distinct features of the new taxon.

The elongate postorbital differs from that of other closely related taxa. In enantiornithines (*Pengornis* and LP 4450), the postorbital is delicate and reduced – this condition is also shared by the Late Jurassic *Archaeopteryx*. It is unlikely that the rather short jugal process of the postorbital of these taxa contacted the jugal. Whether the postorbital in *Shenqiornis* contacted the jugal ventrally cannot be determined equivocally due to the disarticulated nature of this element; however, its extreme length, comparable to the postorbital in some non-avian taxa (oviraptorosaurs)

suggests the presence of a complete or near complete separation between the orbit and the infratemporal fenestra. An elongate postorbital is known in several lineages of basal birds (Sapeornithidae, Confuciusornithidae); *Confuciusornis* is known to have possessed a fully diapsid skull, the infratemporal fenestra closed rostrally by an overlapping articulation of the jugal and postorbital (Chiappe et al., 1999). An elongate postorbital process is present on the jugal of *Jeholornis* (Zhou and Zhang, 2002) suggesting this taxon may also have possessed the diapsid condition. Because the postorbital in *Archaeopteryx* is somewhat reduced, the condition in *Confuciusornis* is considered secondarily derived (Chiappe et al., 1999). The condition in *Shenqiornis* also suggests a secondary derivation; the jugal appears to have a small caudal fork but no distinct postorbital process, as in *Archaeopteryx* and LP 4450. Based on the position of the postorbital, if it reached the jugal it would have contacted the jugal medially, rostral to the fork; no other Mesozoic bird is known to possess such a postorbital-jugal connection.

The tooth morphology of DNHM D2950/1 represents a departure from that of the more typical enantiornithine, whose teeth resemble those of *Archaeopteryx* (Elzanowski, 2002); teeth are placed throughout the premaxilla, maxilla and dentary, conical with slightly recurved apices (the apex ends just caudal to the midpoint of the base), slightly constricted at the base, and without serrations, as in *Vescornis*, and *Cathayornis* (Zhou, 1995), and the Montsec nestling. Taxa from the Jehol biota, however, have revealed a large diversity of dental morphologies and patterns. *Longipteryx* represents one extreme in the spectrum of caudal curvature, with the apex of the tooth projecting beyond the caudal margin of its corresponding alveolus (Zhang et al., 2001). Other atypical morphologies include the reduced peg-like teeth of *Longirostravis* and *Shanweiniao* and the low-crowned rounded teeth of *Pengornis* (Hou et al., 2003; Zhou et al., 2008; O'Connor et al., 2009). The teeth of DNHM D2950/1 are considerably more robust than the typical enantiornithine, which may be indicative of increased strength and durability, an adaptation for crushing hard materials such as insects. This morphology is most similar to that of the recently described *Pengornis*, although in the latter, the teeth are proportionately much smaller, far more numerous and have much lower crowns (Zhou et al., 2008).

While the exact diet of *Shenqiornis* and the function of its teeth remain speculative, the specimen documents a previously unknown tooth morphology unique among Mesozoic birds. Coupled with the unusually elongate postorbital, *Shenqiornis* represents a considerable departure from the typical enantiornithine skull morphology, indicating that *Shenqiornis* likely occupied a

distinct niche within the clade, utilizing food items unavailable to other taxa.

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