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New toothed Early Cretaceous ornithuromorph bird reveals intraclade diversity in pattern of tooth loss

Min Wang^{a,b*} , Jingmai K. O'Connor^{a,b}, Shuang Zhou^{a,b} and Zhonghe Zhou^{a,b}

^aKey Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, 100044 Beijing, China; ^bCAS Center for Excellence in Life and Palaeoenvironment, 100044 Beijing, China

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The earliest record of the Ornithuomorpha, which includes crown birds, is currently known from the Early Cretaceous Jehol Biota in north-eastern China. Here we describe a new ornithuromorph bird, *Mengciusornis dentatus* gen. et sp. nov., from the Jiufotang Formation of this biota. *Mengciusornis* preserves a suite of morphological features exclusively observed among ornithuromorphs in the sympatric taxon *Schizooura*, including a robust and ‘V’-shaped furcula with a short hypocleidium, and a humerus with a large, rectangular deltopectoral crest in which the distodorsal corner is distinctively developed into a sharp, angular point. The results of our phylogenetic analysis recover these two species together in a clade, positioned stemward within the Ornithuomorpha. *Mengciusornis* has toothed premaxillae, in stark contrast with the edentulous jaws of *Schizooura*, demonstrating that dentition varied considerably between some closely related species. Furthermore, all previously known Jehol ornithuromorphs with toothed premaxillae have an edentulous rostral portion of the element, suggesting that tooth loss in this clade proceeded from the rostral end caudally, whereas in *Mengciusornis* the premaxilla lacks this edentulous rostral tip although the maxilla and dentary are toothless, indicating that the pattern of tooth loss, not unexpectedly, varied between lineages of ornithuromorphs. This observation suggests a strong degree of plasticity in the developmental mechanisms regulating tooth and beak formation, which is supported by earlier evidence that indicates teeth have been lost multiple times within Aves and Dinosauria. *Mengciusornis* preserves a ventrally hooked scapular acromion that is convergently evolved in parallel with some enantiornithines and neornithines, providing further evidence of the homoplasy that characterizes avian evolution.

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Keywords: Cretaceous bird; dentition; tooth loss; homoplasy; Jehol Biota; Ornithuomorpha; phylogeny; *Schizooura*

Introduction

Birds constitute the most diverse clade of extant terrestrial vertebrates, consisting of over 10,000 species that occupy a huge morphospace and ecological diversity. The current success of Aves has long remained a major topic in evolutionary biology (Gill 2007; Lovette & Fitzpatrick 2016). All living birds, members of the crown clade Neornithes, are phylogenetically nested within the stem clade Ornithuomorpha (O'Connor *et al.* 2011; M. Wang & Zhonghe 2017), the earliest fossil representatives of which appeared more than 130 million years ago (M. Wang *et al.* 2015). The discovery of the hongshanornithid *Archaeornithura* in the 130.7 Ma Huajiyang Formation demonstrated that many of the morphological and biological features that characterize modern birds had deep evolutionary origins far outside the appearance of the crown clade (Brusatte *et al.* 2015; O'Connor & Zhou 2015; Chiappe & Meng

2016; X. Wang *et al.* 2018). Compared to contemporaneous enantiornithines, specimens of stem ornithuromorphs are relatively rare. Thus, new discoveries have the potential to advance our understanding of the evolution of key avian features that, over time, shaped the avian body plan. Here we describe a new basal ornithuromorph bird, *Mengciusornis dentatus* gen. et sp. nov., based on a nearly complete skeleton from the Early Cretaceous Jiufotang Formation in north-eastern China, the youngest stage in the Jehol Biota. The new taxon shares features with the previously described *Schizooura lii* and a close relationship is corroborated through phylogenetic analysis, resolving the two taxa in a clade – for which we erect the name Schizoouridae fam. nov. We compare schizoourids with other stem ornithuromorphs and discuss morphological disparity and patterns of tooth loss during the earliest evolutionary phase of this important avian clade.

*Corresponding author. Email: wangmin@ivpp.ac.cn

Table 1. Selected measurements of *Mengciusornis* (IVPP V26275) and *Schizoooura* (IVPP V16861) (in millimetres; * denotes estimation; - denotes missing/incomplete).

Element	IVPP V26275	IVPP V16861
Skull length	59.52	50.01
Scapula length	61.91*	
Coracoid length	30.34	27.47
Humerus length	65.90	56.40
Ulna length	64.85	65.90
Radius length	61.00	57.32
Carpometacarpus length	32.19	31.14
Alular metacarpal length	7.27	6.67
Alular digit 1, 2	13.47, 3.81	11.77, 3.83
Major digit 1, 2, 3	14.55, 14.85	14.41, 14.70, 2.16
Minor digit 1	6.70	5.52
Synsacrum length	27.31	–
Pubis length	51.31*	40.94*
Femur length	47.57	49.00
Tibiotarsus length	60.74	61.17
Tarsometatarsus length	34.25	35.60
Digit I-1, 2	4.9, 3.65	4.63, 3.25
Digit II-1, 2, 3	8.93, 6.81, 5.41	9.65, 7.64, 5.20
Digit III-1, 2, 3, 4	8.83, 6.94, 6.34, 5.99	9.36, 7.72, 6.50, 6.25
Digit IV-1, 2, 3, 4, 5	5.98, 5.70, 4.19, 3.63, 4.46	5.92, 4.99, 4.34, 4.31

Material and methods

Anatomical terminology in this study follows Baumel & Witmer (1993), using the English equivalents of their Latin terms. For structures not described in that study, this paper follows Howard (1929). The lengths of the skeletal elements were measured using a digital calliper (± 0.01 mm) directly from Institute of Vertebrate Paleontology and Paleoanthropology (IVPP V26275 and the holotype of *Schizoooura lii* (IVPP V16861) (Table 1).

To investigate the systematic position of IVPP V26275, a phylogenetic analysis was conducted using a recently published dataset targeting Mesozoic avian phylogeny (M. Wang *et al.* 2018). This dataset is modified with the addition of IVPP V26275 and two enantiornithines: *Shangyang graciles* (Wang & Zhou 2019) and IVPP V18692. The modified dataset consists of 280 morphological characters and 72 taxa, and 69 of them are Mesozoic birds (Supplemental material). The matrix was analysed using the TNT software package v. 1.5 (Goloboff & Catalano 2016), with the following settings: as in the previous study, all the characters were weighted equally, with 35 characters ordered; the ‘New Technology Search’ method was performed with sectorial search, ratchet, tree drift and tree fusion with default settings in TNT; the minimum length trees were found in 10 replicates to recover as many tree islands as possible; the recovered trees were subjected to a traditional tree-bisection-reconnection (TBR) branch swapping search; and branches were collapsed if the minimal length was zero to produce the most parsimonious trees. Bremer support values were calculated using the

Bremer script embedded in TNT. The absolute bootstrap frequency was obtained by performing 1000 replicates in TNT using the same settings as in the primary search.

The holotype of *Schizoooura* (IVPP V16861) was considered edentulous in the original study based on direct observation (S. Zhou *et al.* 2012). However, the presence of dentition could have been obscured by overlap of the upper and lower jaws or possible disarticulation and loss of very small teeth (as is the case in *Hongshanornis*). Therefore, we scanned both the skulls of IVPP V26275 and IVPP V16861 using the 225 kV high-resolution computed tomography (CT) apparatus at the Key Laboratory of Vertebrate Evolution and Human Origins of the Chinese Academy of Sciences with a beam energy of 80 kV and a flux of 60 μ A at a resolution of 24.16 μ m, and 21.61 μ m per pixel, respectively. The CT scanning clearly shows that the upper and lower jaws of *Schizoooura* are toothless.

Systematic palaeontology

Class *Aves* Linnaeus, 1758
 Ornithothoraces Chiappe, 1995
 Ornithuromorpha Chiappe, 2002
 Schizooridae fam. nov.

Type genus. *Schizoooura* S. Zhou, Zhou & O’Connor, 2012.

Included genera. *Mengciusornis* gen. nov.

Stratigraphical range. Aptian Jiufotang Formation (S. Zhou *et al.* 2012).

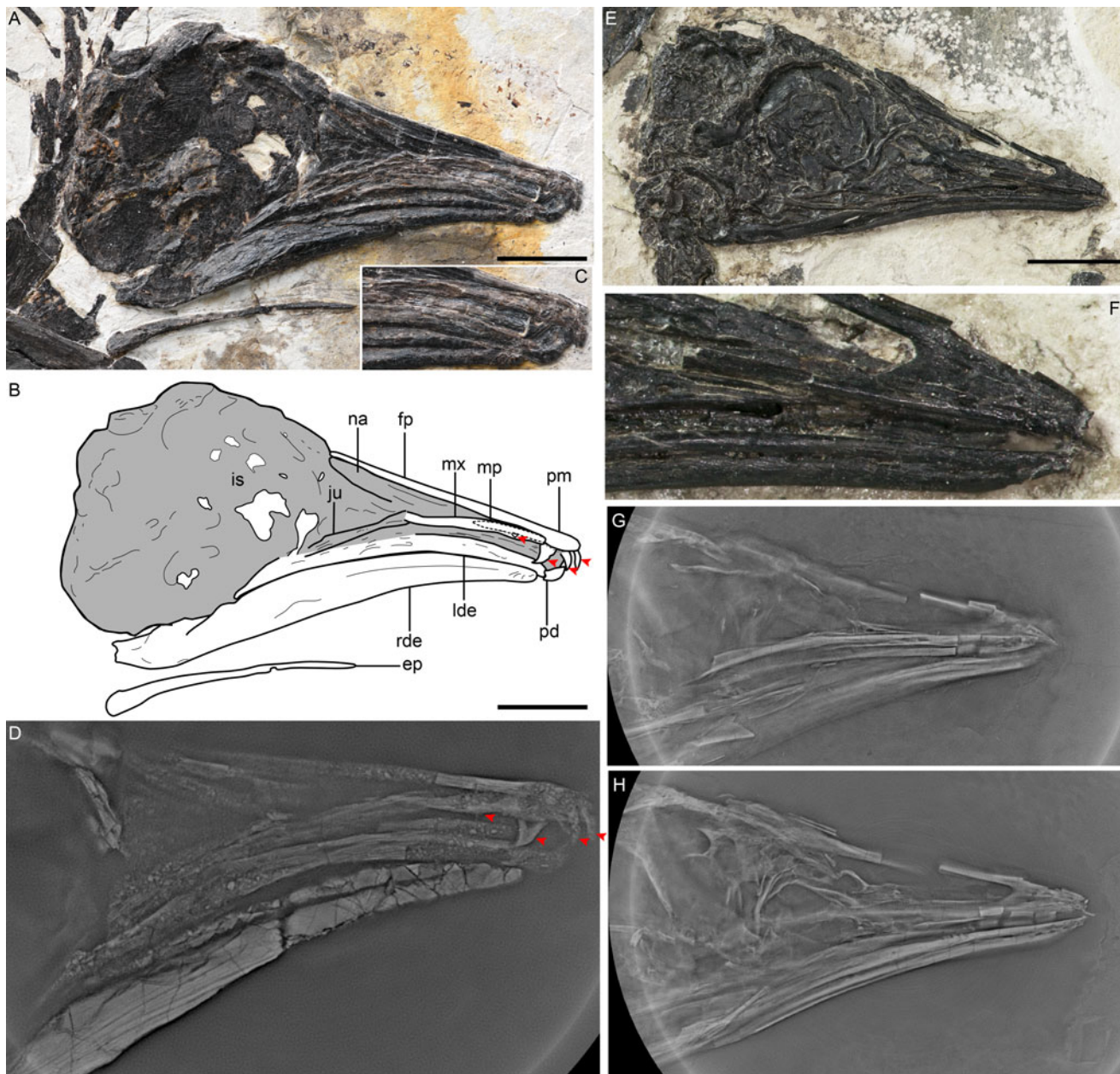


Figure 2. Comparisons of cranial anatomy between *Mengciusornis* and *Schizoooura*. **A**, photograph and **B**, line drawing of *Mengciusornis* (IVPP V26275), with the rostrum under higher magnification (**C**); **D**, computed tomography (CT) scanning of the rostrum of *Mengciusornis*; **E**, skull of *Schizoooura* (holotype, IVPP V16861) with the rostrum under higher magnification (**F**); **G**, **H**, CT scanning of *Schizoooura*. **Abbreviations:** ep, epibranchial of the hyoid; fp, frontal process of premaxilla; is, interorbital septum; ju, jugal; lde, left dentary; mp, maxillary process of premaxilla; mx, maxilla; na, nasal; pd, prementary; pm, premaxilla; rde, right dentary. *Mengciusornis* preserves four premaxillary teeth (red arrowheads in B and D). Scale bars (A, B, E) = 10 mm.

specimen can be differentiated from the morphologically similar taxon *Schizoooura* by the following features: premaxillae toothed (edentulous in *Schizoooura*); hypocleidium relatively more elongate; supracoracoidal nerve foramen absent (present in *Schizoooura*); lateral and medial margins of coracoid subequal in length so that the sternal margin is not strongly angled distodorsally as in *Schizoooura*; hooked

acromion (absent in *Schizoooura*); bicipital crest without a pit-shaped fossa on its craniodistal margin (present in *Schizoooura*); ulna shorter than humerus (opposite condition in *Schizoooura*); forelimb proportionately longer (intermembral index of 1.21 versus 1.06 in *Schizoooura*); and hallux placed relatively higher on the tarsometatarsus.

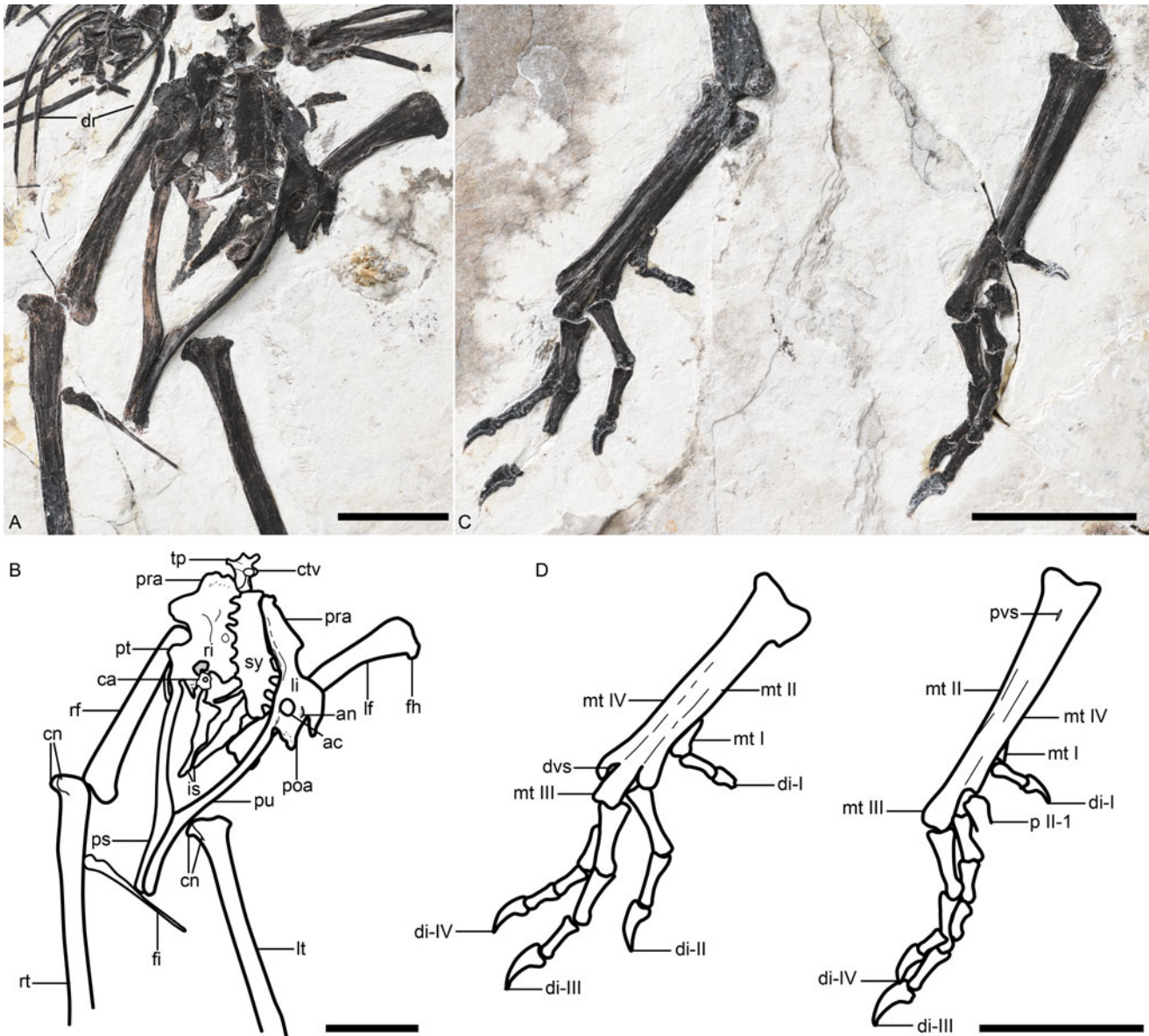


Figure 3. Pelvis and hindlimb anatomy of *Mengciusornis*, IVPP V26275. **A**, photograph and **B**, line drawing of pelvis and partial hindlimb; **C**, photograph and **D**, line drawing of the feet. **Abbreviations:** ac, acetabulum; an, antitrochanter; ca, caudal vertebra; cn, cnemial crests of tibiotarsus; ctv, caudal most thoracic vertebra; di-1 to di-IV, digits I-IV; dr, dorsal rib; dvs, distal vascular foramen; fh, femoral head; fi, fibula; lf, left femur; is, ischium; li, left ilium; lt, left tibiotarsus; mt I-IV, metatarsi I-IV; p II-1, proximal phalanx of digit II; pra, preacetabular process; poa, postacetabular process; pu, pubis; pvs, proximal vascular foramen; ps, pubic symphysis; pt, preacetabular tubercle; rf, right femur; ri, right ilium; rt, right tibiotarsus; tp, transverse process; sy, synsacrum. Scale bars = 20 mm.

Anatomical description and comparison

Skull

The skull is primarily preserved in right lateral view (Fig. 2A). The preorbital region occupies slightly more than half the skull length, as in *Schizoura* (S. Zhou *et al.* 2012) but is proportionately shorter than in *Iteravis* and *Dingavis* (S. Zhou *et al.* 2014a; O'Connor *et al.* 2016). Due to compression and mediolateral

overlap, only a few cranial elements can be identified with certainty. The premaxilla preserves three robust teeth that are readily visible (Fig. 2B-D), and closely packed at the tip of the premaxilla, contrasting with other toothed ornithuromorphs in which the rostral-most portion is edentulous, e.g. *Iteravis*, *Yixianornis*, *Yanornis* and *Ichthyornis* (Clarke *et al.* 2006; Z. Zhou & Martin 2010; Field *et al.* 2018). The teeth are large with sub-conical crowns that are strongly recurved

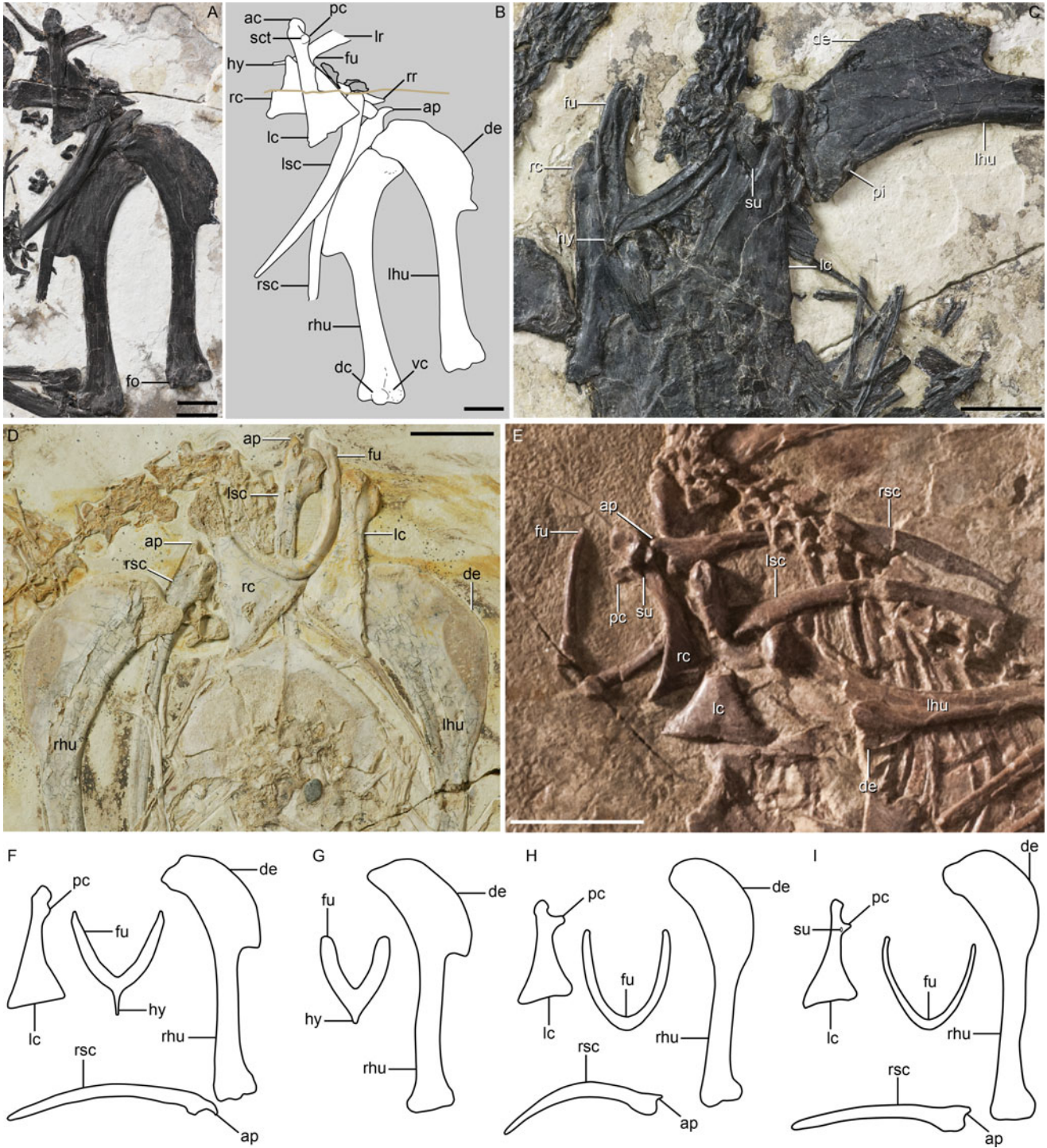


Figure 4. Comparison of pectoral girdle and humerus of *Mengciusornis* and other basal ornithuromorphs. **A**, photograph and **B**, line drawing of *Mengciusornis*, IVPP V26275; **C**, *Schizooura*, IVPP V16861 (primarily in ventral view); **D**, *Archaeorhynchus*, IVPP V14287 (primarily in ventral view); **E**, *Yixianornis*, IVPP V12631; **F–I**, reconstructions of shoulders (furcula and coracoid in dorsal view, scapula in costal view) and humeri (caudal view) of *Mengciusornis* (**F**), *Schizooura* (**G**), *Jianchangornis* (**H**, based on the holotype IVPP V18958), and *Iteravis* (**I**; based on the holotype IVPP V18958, and a referred specimen IVPP V18688). **Abbreviations:** ac, acoracoid process; ap, acromion process; dc, dorsal condyle; de, deltopectoral crest; fo, fossa for attachment of *M. pronator longus*; fu, furcula; hy, hypocleidium; lc, left coracoid; lhu, left humerus; lr, left ramus of furcula; lsc, left scapula; pc, procoracoid process; pi, pit-shaped fossa on bicipital crest; rc, right coracoid; rhu, right humerus; rr, right ramus of furcula; rsc, right scapula; sct, scapular cotyla; su, supracoracoidal nerve foramen; vc, ventral condyle. Scale bars (A–E) = 10mm; F–I not scaled.

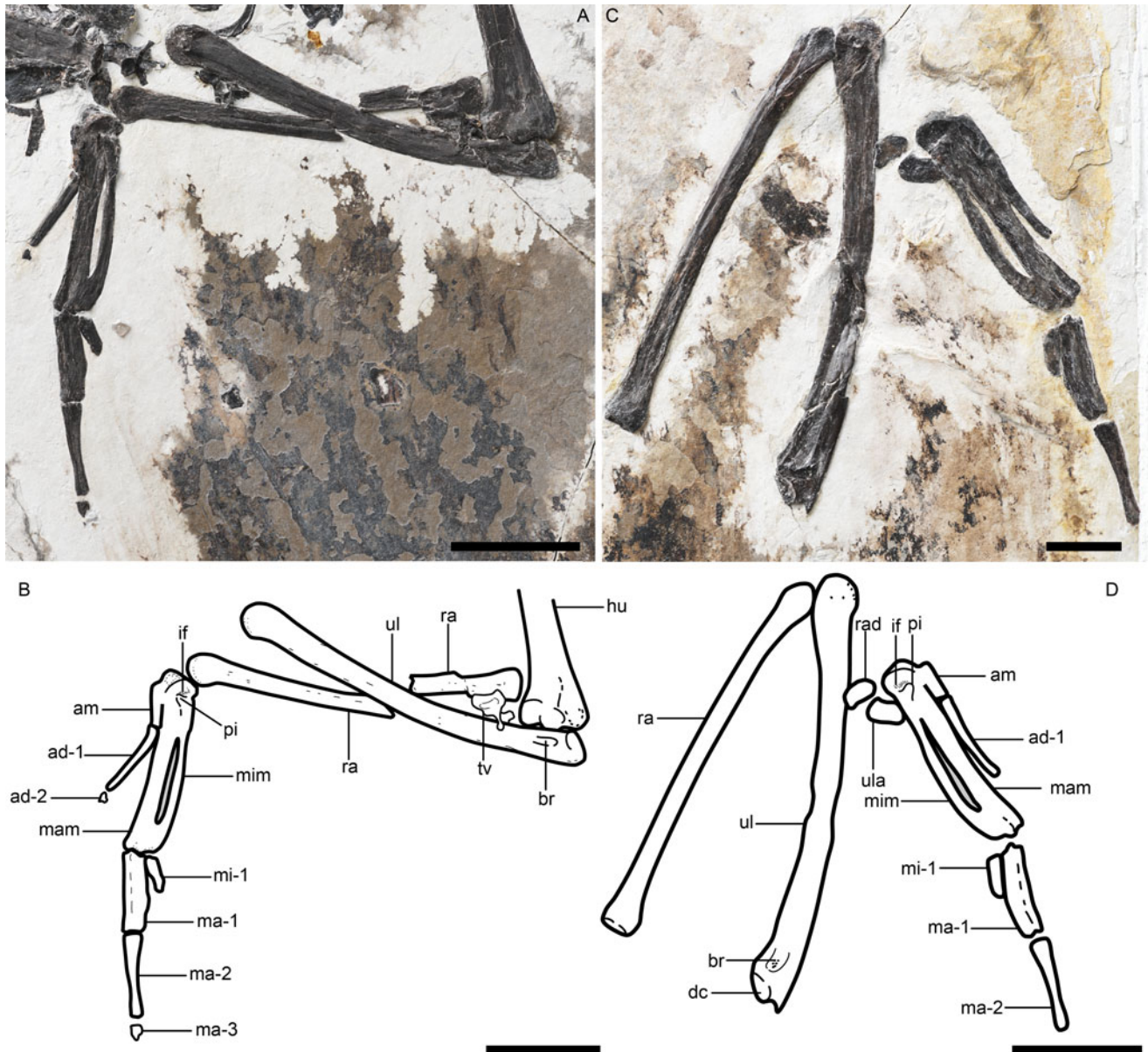


Figure 5. Forearm anatomy of *Mengciusornis*, IVPP V26275. **A**, photograph and **B**, line drawing of the right side; **C**, photograph and **D**, line drawing of the left side. **Abbreviations:** **ad-1**, proximal phalanx of alular digit; **ad-2**, ungula phalanx of alular digit; **am**, alular metacarpal; **br**, brachial impression; **dc**, dorsal cotyla of ulna; **hu**, humerus; **if**, infratrochlear fossa; **mam**, major metacarpal; **ma-1**, **ma-2**, proximal and intermediate phalanges of major digit; **ma-3**, ungula phalanx of major digit; **mim**, minor metacarpal; **mi-1**, proximal phalanx of minor digit; **pi**, pisiform process; **ra**, radius; **rad**, radiale; **tv**, thoracic vertebra; **ul**, ulna; **ula**, ulnare. Scale bars = 20 mm.

caudally, reminiscent of – but less developed than – the condition in the enantiornithine *Longipteryx* (O'Connor & Chiappe 2011). In contrast, the premaxillary teeth are typically small and straight in non-ornithuromorphs such as *Jianchangornis*, *Yanornis* and hongshannornithids (Z. Zhou *et al.* 2009; O'Connor *et al.* 2010). CT scanning reveals that the maxillary process of the premaxilla is caudally tapered and overlaps the medial surface of the maxilla. One additional premaxillary tooth

is recognized by its preserved base that is separated from the third premaxillary tooth by a large diastema that does not contain any visible alveoli. CT scanning shows no other tooth or alveolus is present in the maxillae or the lower jaws (Fig. 2D). In contrast, the upper and lower jaws of *Schizoura* are edentulous (Fig. 2E–H). These premaxillary teeth show a slight heterodonty, particularly in terms of the large size and robustness of the third tooth (Fig. 2B). Similar size variation

is rare among Early Cretaceous ornithuromorphs, but present in a few enantiornithines such as bohaiornithids and longipterygids (O'Connor & Chiappe 2011). As in *Schizooura* (S. Zhou *et al.* 2012), the nasal (frontal) process of the premaxilla is elongate and extends caudally to contact the frontal (Fig. 1C). The interorbital septum appears to be transversely thick and is perforated by irregular foramina, which are probably preservational artefacts. The lower jaws are unfused rostrally and are weakly bowed dorsally along the central portion in lateral view. A small triangular element that remains in articulation with the rostral tip of the left dentary is likely to be the prementary, as reported in other basal ornithuromorphs (Z. Zhou & Martin 2010). Ventral to the caudal half of the lower jaw, there is a straight, anteriorly tapering element. We interpret that bone as the epibranchial of the hyoid apparatus (Fig. 1A, B). If this interpretation is correct, the epibranchial is stouter, especially in the caudal portion, and differs from the ventrally bowed condition reported in other basal birds, including *Confuciusornis*, *Hongshanornis* and an unnamed enantiornithine IVPP V13266 (Li *et al.* 2018).

Axial skeleton

The vertebral column is disarticulated and incomplete. The cervicals are either crushed or overlain by the pectoral girdle, providing no information other than the concave cranial articular facet of the centrum. Four thoracics are closely preserved together and exhibit amphicoelous articular facets (Fig. 1A). The craniocaudal length of the centra exceeds their dorsoventral height and the lateral surfaces are excavated by broad fossae as in some other ornithuromorphs, e.g. *Iteravis*, *Piscivoravis* (S. Zhou *et al.* 2014a, b), but absent in *Bellulornis* (M. Wang *et al.* 2016b). The rectangular spinal processes are located caudally on the centrum and are nearly as tall as their associated centra. The vertebral foramen is less than half the height of the cranial articular surface. The postzygapophyses project caudally beyond the caudal articular surface of the centra, whereas the cranial margins of the prezygapophyses are level with the cranial articular surfaces. A ventral process, reportedly present in the second to fourth preserved vertebrae of *Piscivoravis* (S. Zhou *et al.* 2014b), is not present in any of the preserved thoracic vertebrae of IVPP V26275. The last presacral vertebra is slightly disarticulated from the synsacrum and exposed cranioventrally (Fig. 3A, B). The centrum is spool-like with a convex ventral surface. Similar to the cranial thoracic vertebrae, the lateral surfaces of the centrum are excavated by deep fossae. The concave cranial articular surface is mediolaterally wider than dorsoventrally high. The transverse processes project dorsolaterally and are

shorter than the width of the centrum. The synsacrum, exposed in ventral view, is composed of nine completely ankylosed vertebrae (Fig. 3A), which is also the number estimated to be present in *Schizooura*. The cranial articular facet is concave. The ventral surface of the synsacrum is flat, without the furrow present in *Patagopteryx* or the groove in *Schizooura* and some enantiornithines (Chiappe 2002; S. Zhou *et al.* 2012). The fused vertebral centra together form a spindle shape in ventral view that rapidly narrows cranially and caudally and is widest at the fifth vertebra. The transverse processes of the cranial seven sacra are short and laterally directed, but those of the eighth sacral become prominently elongate and caudolaterally orientated. The last sacral has no transverse processes, a rare condition among ornithuromorphs, although whether this absence is genuine or a preservational artefact is uncertain. A small isolated vertebra, preserved near the caudal end of the right ilium, probably represents a free caudal that is exposed either in cranial or caudal view (Fig. 3B). The vertebral foramen of this caudal approaches the dorsoventral height of the articular facet of the centrum. A pygostyle is not preserved. Most of the preserved dorsal ribs are disarticulated from their corresponding vertebrae (Fig. 1). The proximal half of the dorsal ribs are excavated by longitudinal furrows medially, most pronounced near the connection between the capitulum and tuberculum (Fig. 3A), as in some neornithines (e.g. *Pucrasia macrolopha*). The disarticulated gastralia are delicate and short.

Pectoral girdle

The furcula is largely covered by the coracoids, with only the incomplete symphyseal half of the left ramus, the omal end of the complete right ramus, and the delicate distal end of the hypocleidium exposed. As in *Schizooura* (S. Zhou *et al.* 2012), the furcula is 'V'-shaped and robust, distinct from the delicate 'U'-shaped form typical of other Cretaceous ornithuromorphs, e.g. *Archaeorhynchus*, *Yixianornis* and *Yanornis* (Z. Zhou & Zhang 2001, 2006; Fig. 4). A hypocleidium is present as in *Schizooura* and *Bellulornis* (Fig. 4F), whereas this structure is typically absent in most Cretaceous ornithuromorphs (O'Connor *et al.* 2010; S. Zhou *et al.* 2012; M. Wang *et al.* 2016b). As preserved, the hypocleidium in IVPP V26275 is more elongate than in *Schizooura*, but it may be incomplete in the latter taxon. The exposed left furcular ramus is craniocaudally compressed and its dorsal surface is weakly concave. The omal end is tapered (Fig. 4A, B).

Both coracoids are caudally exposed, with the right element preserved overlain by the left. The coracoid is strut-like with straight medial and lateral margins (Fig.

4A). The scapular cotyla is shallower than in *Yixianornis* and *Iteravis*. The small procoracoid process is knob-like (Fig. 4F), unlike the large rectangular condition in most other ornithuromorphs, including *Jianchangornis* and *Yixianornis* (Fig. 4D–I), and the large tapering morphology in *Schizooura* (Clarke *et al.* 2006; Z. Zhou *et al.* 2009; S. Zhou *et al.* 2012; Fig. 4C). A supracoracoid nerve foramen, which commonly lies near the base of the procoracoid process in other ornithuromorphs including *Schizooura* (Clarke & Norell 2002; You *et al.* 2006; S. Zhou *et al.* 2012; Fig. 4), is absent. As in *Schizooura* and *Archaeorhynchus*, a lateral process is absent; this appears to be a derived feature as it is typically present in more crownward ornithuromorphs such as *Yixianornis* and *Gansus* (Clarke *et al.* 2006; You *et al.* 2006). The sternal margin is straight and the lateral and medial margins are subequal in length so that the sternal margin is not strongly angled distolaterally, as it is in *Schizooura* (S. Zhou *et al.* 2012). The lateral margin of the coracoid is dorsoventrally thicker than the medial margin. The sternal half of the coracoid bears a shallow sternocoracoid impression, whereas this impression is more strongly defined in *Yixianornis* (Fig. 4E).

The scapula measures approximately 93% of the humeral length, proportionately longer than in most other non-ornithurine ornithuromorphs (this ratio is 0.83 in *Schizooura*, 0.71 in *Jianchangornis* and 0.67 in *Iteravis*). Notably, the acromion process of the scapula is large and ventrally hooked (Fig. 4B), similar to the condition in the Late Cretaceous *Apsaravis* among non-ornithurine ornithuromorphs (Clarke & Norell 2002). In contrast, the acromion is typically short and straight in other non-ornithurine ornithuromorphs (Z. Zhou & Zhang 2001; S. Zhou *et al.* 2013, 2014a; Fig. 4D, E, H, I). Among Mesozoic birds, similarly hooked acromion processes are also present in the enantiornithine clade, the Pengornithidae (Z. Zhou *et al.* 2008; Hu *et al.* 2015), and also in some extant neornithines (e.g. *Numida*). The scapular blade is narrow and curved and tapers distally, as is typical of the Cretaceous ornithuromorphs.

Forelimb

The forelimb is long relative to the hind limb, with an intermembral index (humerus + ulna/femur + tibiotarsus) of 1.21, which is much greater than that of *Schizooura* (1.06), *Yixianornis* (0.97) or *Iteravis* (1.04) (M. Wang *et al.* 2016b, table 2). The humerus is robust with a large deltopectoral crest (Fig. 4A, B). The crest projects dorsally and approaches the mediolateral width of the humeral shaft. As in *Schizooura* (S. Zhou *et al.* 2012), the deltopectoral crest is rectangular with the distodorsal

corner forming a sharp angle (Fig. 4A, C), whereas this crest is typically rounded in other Cretaceous ornithuromorphs, e.g. *Archaeorhynchus*, *Bellulornis*, *Yixianornis* (Fig. 4) and hongshanornithids (Z. Zhou *et al.* 2013; M. Wang *et al.* 2015, 2016b). The proximocranial surface is nearly flat as in *Schizooura*, lacking the convex globe-like humeral head which characterizes other ornithuromorphs (Clarke & Norell 2002; O'Connor *et al.* 2010). The proximoventral corner (presumably the bicapital crest) projects strongly ventrally and is separated from the convex proximal margin of the humeral head by a wide and shallow concavity. A pit-shaped fossa, located on the craniodistal surface of the bicapital crest in *Schizooura* (Fig. 4C) is absent from the corresponding area in *Mengciusornis* (Fig. 4A). The distal end of the humerus is expanded relative to the midpoint of the shaft. The dorsal and ventral condyles are prominent; the former appears to be dorsoventrally orientated, whereas the latter is ventrodistally inclined. A brachial impression is present. The medial surface of the ventral epicondyle is recessed by an ovoid fossa (Fig. 4A), presumably for the attachment of *M. pronator longus* based on the similar anatomical position of this attachment in the Neornithes (Owre 1967). The distal margin is perpendicular to the longitudinal axis of the shaft.

The robust ulna is slightly shorter than the humerus, opposite to the condition in other ornithuromorphs including *Schizooura* (Z. Zhou & Zhang 2006; M. Wang *et al.* 2015), and most modern volant birds (Nudds *et al.* 2007). The ulna is weakly bowed and has a poorly developed olecranon process (Fig. 5). Proximally, a brachial impression is clearly visible. A bicapital tubercle is absent. The dorsal condyle is convex such that the distal margin is rounded in dorsal view. The radius is robust and measures approximately 75% of the width of the ulna at its midpoint. The bone is straight with a semilunate distal articular facet for the radiale (Fig. 5A, B). The ulnare is rectangular in ventral view and bears a shallow metacarpal incision (Fig. 5C, D). The trapezoid radiale is as large as the ulnare.

Both manus are exposed ventrally (Fig. 5). The distal carpals and major and minor metacarpals are fully fused proximally, forming a carpometacarpus. Proximally, the minor metacarpal curves onto the ventral surface of the major metacarpal and is continuous with the pisiform process as in *Yixianornis* and *Longicrusavis* (Clarke *et al.* 2006; O'Connor *et al.* 2010). An infratrochlear fossa is well developed (Fig. 5B, D). The minor metacarpal is bowed caudally and fused with the major metacarpal distally just proximal to the distal end of the latter element, defining a moderate intermetacarpal space slightly narrower than the thickness of the minor metacarpal. The alular and major metacarpals are only

fully fused proximally, with a suture still visible distally. As in *Schizooura* (S. Zhou *et al.* 2012), the cranial margin of the alular metacarpal is straight without an extensor process, which is present in more derived ornithuromorphs such as *Iteravis*, *Yixianornis* and *Gansus* (Clarke *et al.* 2006; You *et al.* 2006; S. Zhou *et al.* 2014a). The alular metacarpal is less than one-quarter the length of the major metacarpal, ending slightly proximal to the level of the proximal end of the intermetacarpal space. The first phalanx of the alular digit is slightly bowed caudally and articulates with a small, poorly recurved ungual (Fig. 5A, B). The alular digit terminates proximal to the distal end of the major metacarpal as in *Gansus*, proportionately shorter than in some Jehol ornithuromorphs, e.g. *Yixianornis*, *Jianchangornis* and hongshanornithids, in which the alular digit reaches the distal margin of the major metacarpal (Clarke *et al.* 2006; Z. Zhou *et al.* 2009; M. Wang *et al.* 2015). Like *Schizooura*, the proximal phalanx of the major digit, although robust, lacks the caudal expansion present in most other ornithuromorphs (Z. Zhou & Zhang 2006; O'Connor *et al.* 2010; Fig. 5). The intermediate phalanx is slender but slightly longer than the preceding phalanx, as in *Schizooura*. The ungual phalanx is poorly preserved but appears to be smaller than that of the alular digit. The minor digit preserves only one phalanx, which is less than half the length of the proximal phalanx of the major digit.

Pelvis

The right ilium is exposed ventrally and the left is in lateral view (Fig. 3A, B). The ilia appear to be fused to the synsacrum, but poor preservation makes this interpretation equivocal. The ilium, pubis and ischium are fused at the level of the fully perforated acetabulum. The prominent antitrochanter is placed on the dorsal margin of the acetabulum (Fig. 3B); it is more caudally positioned in *Schizooura* and other ornithuromorphs including *Bellulornis*, *Gansus* and *Iteravis*. The cranio-lateral corner of the ilium projects ventrally such that the ventral margin is concave cranial to the pubic pedicel (Fig. 3A). A triangular process projecting from the cranial margin of the pubic pedicel of the right ilium is identified as the preacetabular tubercle (Fig. 3B), similar to that present in neornithines (Baumel & Witmer 1993). The corresponding area on the left ilium, although broken, is visibly thickened. The pubes are caudally directed and form a distal symphysis that extends for more than one-third the length of the pubis, which is longer than the pubic symphysis observed in *Schizooura*. The distal ends of the pubes are only weakly expanded. The ischia are sharply tapered distally and also contact, forming a symphysis that extends

along the distal half to one-quarter the length of the element.

Hind limb

The femur is slightly shorter than 80% of the length of the tibiotarsus. The proximocranial surface of the tibiotarsus bears two short, low cnemial crests (Fig. 3A, B), which are restricted to the proximal surface without the expansion beyond the proximal articular facet observed in *Iteravis* and *Gansus* (You *et al.* 2006; S. Zhou *et al.* 2014a). The distal tibiotarsi are crushed, revealing no anatomical details. Only one fibula is identifiable (Fig. 5B). The proximal end of the fibula is broad but the bone rapidly tapers distally. Based on the preserved portion and the distal impression of this element, we estimated the ratio of the length of the fibula to the length of the tibiotarsus to be 0.6. In contrast, the fibula extends nearly to the distal tarsals in *Schizooura*, *Archaeorhynchus* and *Patagopteryx* (Chiappe 2002; S. Zhou *et al.* 2012, 2013).

Both feet are nearly complete and largely remain in articulation (Fig. 3C, D). Metatarsals II to IV are fused proximally with the distal tarsals; distally, faintly visible sutures allow the individual metatarsals to be distinguished. As in *Schizooura*, metatarsal III is coplanar with metatarsals II and IV, rather than ventrally displaced as in *Iteravis* and *Yixianornis* (Clarke *et al.* 2006; S. Zhou *et al.* 2014a). Metatarsal III is the longest and most robust, followed by metatarsal IV, which terminates at the level of the proximal margin of the metatarsal III trochlea. Metatarsal II is shorter than metatarsal IV. Approximately 4 mm from the proximal margin of the tarsometatarsus, metatarsals III and IV are perforated by a short, slit-like foramen (Fig. 3D). A similar structure is observed in *Confuciusornis* and was interpreted as the lateral proximal vascular foramen (Chiappe *et al.* 1999). The metatarsal III trochlea is much broader than that of the others. The distal end of metatarsal II is medially deflected and lacks a ginglymous articulation. The trochlea of metatarsal IV is reduced to a single condyle that encloses a distal vascular foramen with the metatarsal III trochlea, similar to the condition in many enantiornithines. Compared with *Schizooura*, metatarsal I is more proximally placed on metatarsal II such that its distal end is far proximal to the level of the metatarsal II trochlea. As in other Jehol ornithuromorphs (O'Connor *et al.* 2010; S. Zhou *et al.* 2013), the phalanges decrease in length distally and the ungual phalanges are short and weakly recurved, suggesting they are adapted for a more terrestrial lifestyle (Hopson 2001). As in *Schizooura*, digit III is the longest, followed by digit IV and then digit II. The hallux is slender and less than half the length of digit II. The

proximal phalanx of digit II is the longest, but that of digit III is the most robust.

Both wings, preserved as carbonized traces, appear to be semi-folded (Fig. 1). Although detailed features are obscured by poor preservation, as preserved the longest remiges are approximately three times as long as the humerus. The relative length of the wings is obscured by poor preservation in the holotype and the only known specimen of *Schizooura*, preventing comparison.

Discussion

Phylogenetic analysis

Our phylogenetic analysis returned 2124 most parsimonious trees with 1271 steps (consistency index = 0.306, retention index = 0.665). The strict consensus tree is relatively well resolved within the Ornithuromorpha (Fig. 6). The new cladogram is consistent with recent studies in the placement of the major clades (S. Zhou *et al.* 2014a; Field *et al.* 2018; M. Wang *et al.* 2018). *Mengciusornis* is recovered in a clade with *Schizooura* basal within the Ornithuromorpha. These two taxa share similar morphologies, particularly in the humerus, furcula and manus, which readily distinguish them from other ornithuromorphs, leading us to erect a new clade, Schizoouridae. Four synapomorphies were optimized in support of Schizoouridae: intermetacarpal space terminates distal to the end of the alular metacarpal (character 165:1); proximal phalanx of the major digit lacks caudal expansion (character 169:0); metatarsals II to IV are incompletely fused along their length with visible sutures (character 222:1); and the deltopectoral crest ends abruptly with the humeral shaft distally (that is, the distal margin of the deltopectoral crest forms a large angle with the shaft) (character 253:0). The interrelationships of the Ornithuromorpha are nearly completely resolved, with the exception of a small polytomy consisting of *Apsaravis*, *Patagopteryx* and *Vorona*. As in previous studies (M. Wang *et al.* 2015, 2018; O'Connor *et al.* 2016), *Archaeorhynchus* emerges as the most basal ornithuromorph, followed by *Jianchangornis*. *Bellulornis* and the Schizoouridae form successive outgroups to the polytomy mentioned above, which all fall outside of the clade consisting of Hongshanornithidae and more derived taxa. As in S. Zhou *et al.* (2014a), *Iteravis* represents the most crownward taxon so far recovered from the Jehol Biota.

Morphological disparity of basal ornithuromorphs

The nearly complete skeleton of *Mengciusornis* and its close affinity with the stemward ornithuromorph

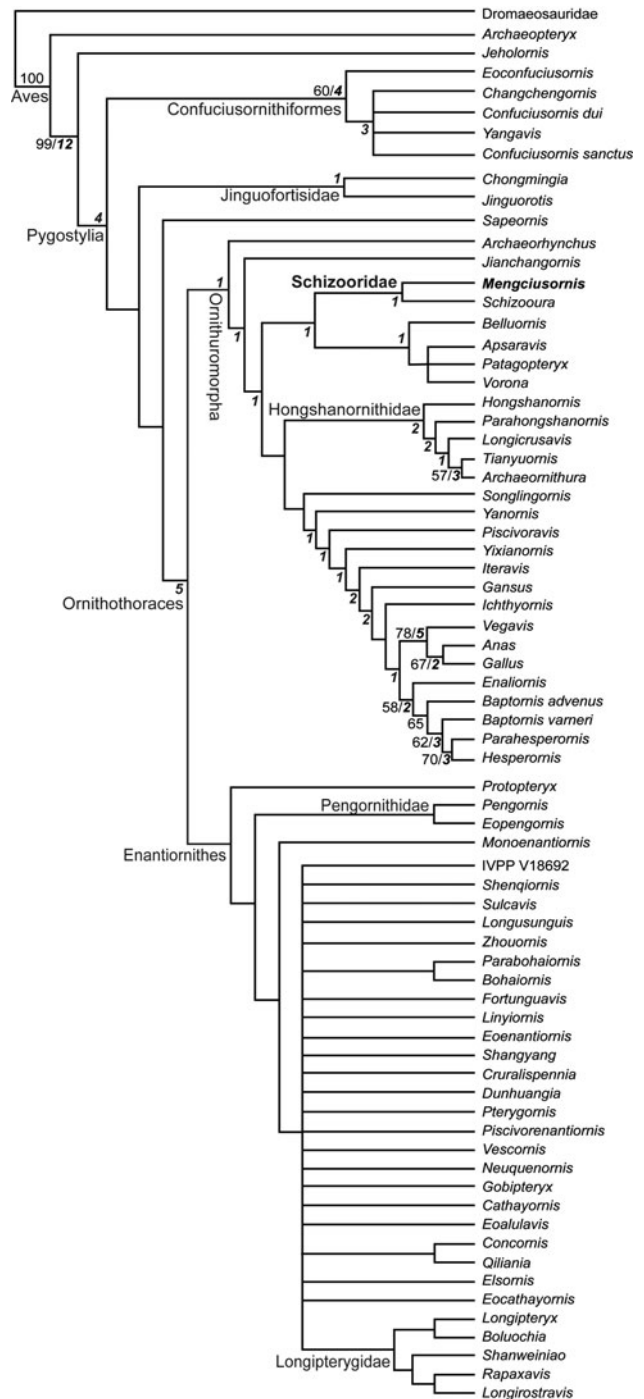


Figure 6. Phylogenetic position of *Mengciusornis* with respect to other Mesozoic birds. The cladogram is the strict consensus tree based on the 2124 most parsimonious trees recovered in present study. Absolute bootstrap and Bremer values are indicated in normal and bold italic fonts near corresponding nodes, respectively.

Schizooura provides important new information regarding the morphological disparity of basal members of the Ornithuromorpha. Despite the fact that nearly all

enantiornithines with the exception of the Late Cretaceous *Gobipteryx* have teeth (O'Connor & Chiappe 2011), tooth reduction and loss, as well as increases in the number of teeth, have evolved independently numerous times within multiple ornithuromorph lineages and more frequently than in the Enantiornithes (Z. Zhou *et al.* 2010; Louchart & Viriot 2011; Y. Zhou *et al.* 2019). Teeth are completely absent in the most basal ornithuromorph *Archaeorhynchus*, as well as in more derived taxa such as *Zhongjianornis*, *Xinghaiornis* and *Eogranivora* (Z. Zhou *et al.* 2010; Chiappe & Meng 2016; Zheng *et al.* 2018), each most likely representing independent losses in light of current phylogenies (M. Wang *et al.* 2018; Fig. 6). In most ornithuromorphs, teeth are absent from the rostral tip of the premaxillae (Z. Zhou & Martin 2010), and in *Iteravis* and the ornithurines *Ichthyornis* and *Hesperornis*, the entire premaxilla is toothless (S. Zhou *et al.* 2014a; Field *et al.* 2018). This led to the hypothesis that tooth loss in the Ornithuromorpha began rostrally and proceeded caudally (Louchart & Viriot 2011; Y. Zhou *et al.* 2019). Despite this rostral edentulous portion, *Yanornis* has the typical four premaxillary teeth and over 20 dentary teeth (Z. Zhou & Zhang 2001), and the number of dentary teeth is even higher in the Late Cretaceous ornithurines *Hesperornis* and *Ichthyornis* (Gingerich 1973). Compared to its edentulous close relative *Schizoura*, *Mengciusornis* has four robust premaxillary teeth (Fig. 2), demonstrating how drastically dentition can vary within the Ornithuromorpha even among closely related taxa. Notably, although teeth are reduced in *Mengciusornis* (the maxilla and dentary are toothless), the rostral-most portion of the premaxilla is toothed, indicating that patterns of tooth loss in the Ornithuromorpha were more diverse than previously recognized and tooth loss did not proceed rostrocaudally in all Cretaceous lineages. On the basis of the rare preservation of the rhamphotheca and the presence of edentulous jaws in numerous Cretaceous birds spanning the entire stem avian phylogeny (Hou *et al.* 1995; Chiappe *et al.* 1999; Z. Zhou & Zhang 2006; Zheng *et al.* 2018), it can be inferred that a horny beak evolved multiple times and is widely distributed within the phylogeny of Cretaceous birds (O'Connor & Chiappe 2011; O'Connor *et al.* 2011; Brusatte *et al.* 2015). The evolution of the beak probably occurred along different developmental pathways in each lineage in which this feature arose and may have been triggered by different evolutionary pressures.

Different hypotheses have been put forward to explain the cause and pattern of tooth reduction that characterizes avian evolution. Hypotheses for the broad trend towards tooth reduction that characterizes Aves as a

whole include enhanced flight performance by reducing body weight (Z. Zhou *et al.* 2010; Louchart & Viriot 2011), trophic adaptation (Zheng *et al.* 2014; O'Connor 2019), or the evolution of the rhamphotheca, inhibiting tooth formation (S. Wang *et al.* 2017). A recent study demonstrated that teeth have a negligible effect on body weight (Y. Zhou *et al.* 2019), making the weight reduction hypothesis less plausible, especially in light of the fact that dentition, although plastic, persisted for 90 million years of avian evolution. Diet appears to correlate well with dentition and may be a main factor affecting the evolution of various dental patterns, although it probably does not explain evolutionary patterns of tooth loss entirely. *Archaeorhynchus* and *Eogranivora* are fully edentulous and have larger gastral masses than those found in toothed ornithuromorphs (S. Zhou *et al.* 2013; Zheng *et al.* 2018). Both are inferred to be granivorous and this is directly supported by the preservation of seeds in the crop of *Eogranivora* (Zheng *et al.* 2018). The presence of ingested seeds and gastroliths preserved in some specimens of the more primitive non-ornithothoracine birds *Jeholornis* and *Sapeornis* indicates a granivorous diet similar to that of *Eogranivora* (O'Connor & Zhou, in press). Although these taxa exhibit considerably different dentition, they all share the presence of dental reduction in some portion of the rostrum, supporting a correlation between tooth loss and granivory (O'Connor 2019). Differences in the degree of dental reduction may reflect differences in the function of the digestive tract in these stem avian lineages and/or differences in the seeds or grains being consumed by each taxon, and/or differences in the time elapsed since the acquisition of the granivorous diet (if recently acquired then perhaps tooth loss has only just begun in some lineages, as suggested in *Sapeornis* by the presence of two vestigial teeth in the dentary followed by three empty alveoli). The ornithuromorph *Iteravis* has an edentulous premaxilla, at least eight maxillary and over 15 dentary teeth, and preserves a relatively smaller number of large gizzard stones compared to presumably granivorous, edentulous ornithuromorphs such as *Eogranivora* and *Archaeorhynchus* (S. Zhou *et al.* 2013; Zheng *et al.* 2018; O'Connor 2019). Similar gastral masses (consisting of a few large stones) are present in all ornithuromorphs that retain teeth (O'Connor 2019). The holotype of *Iteravis* preserves a pellet containing bone and gastroliths (O'Connor & Zhou, in press). Although the presence of gizzard stones is generally linked to herbivory in non-avian dinosaurs and stem birds (Zanno & Makovicky 2011), modern birds with a wide variety of diets utilize gastroliths (e.g. carnivores feeding on various invertebrates; Gionfriddo & Best 1999; Gill 2007; Lovette & Fitzpatrick 2016). The

existing correlation between gastroliths and herbivory in non-avian dinosaurs may not hold for non-avian dinosaurs and stem birds, based on recent evidence that *Iteravis* and the non-avian scansoriopterygid *Ambopteryx* both preserve indicators that they were at least partially carnivorous despite the presence of gastroliths (M. Wang *et al.* 2019; O'Connor & Zhou, in press). Although tooth loss may be favoured by a granivorous diet, herbivory may not have triggered the evolution of the edentulous rostral portion of the premaxilla in ornithuromorphs, which notably did not involve a loss of teeth, given that this feature is present in *Yanornis*, despite the increase in tooth number in the maxilla and dentary and clear evidence indicating a piscivorous diet (Zheng *et al.* 2014).

Little is known about the diet of the Enantiornithes (O'Connor 2019), because direct trophic-related evidence has only been preserved in three taxa, and two of these identifications are controversial (M. Wang *et al.* 2016a; O'Connor 2019). However, the complete absence of gastroliths in the thousands of known specimens suggests that Early Cretaceous members of this clade were not obligate granivores. Since granivory is linked with dental reduction, this is consistent with the absence of complete tooth loss in Early Cretaceous enantiornithines. Evidence from *Yanornis* indicates that teeth were not used for food processing but likely were used for prey capture (Zheng *et al.* 2014). Extrapolating to all stem birds, the diverse tooth patterns in non-herbivorous stem avians most likely at least partially represent adaptations for the capture of different prey. The dental pattern in *Mengciusornis* is most similar to that of the enantiornithine *Longipteryx*; however, diet is unknown in this taxon, preventing further comparison.

Schizoourids are bizarre among basal ornithuromorphs in sharing some unique features with enantiornithines, including a 'V'-shaped furcula with a hypocleidium (a synapomorphy of the Enantiornithes; Chiappe & Walker 2002), a hooked acromion of the scapula (a diagnostic feature of the Pengornithidae; Hu *et al.* 2015), and a proximal phalanx of the major digit that is unmodified as in enantiornithines and non-ornithothoracine birds, rather than caudally expanded as in other, presumably more derived ornithuromorphs. Despite these similarities, schizoourids do not emerge as the basal-most ornithuromorphs in our cladistic analysis. This suggests some of these characters were evolved independently in schizoourids in parallel to enantiornithines, adding to the tally of numerous instances of homoplasy that characterizes early bird evolution. Notably, despite the shared presence of these unique morphologies, *Mengciusornis* and *Schizooura* are otherwise very different with regards to forelimb proportions and, as

previously discussed, dentition. Differences in forelimb proportions may suggest that *Mengciusornis* had relatively more limited flight abilities or at least a different flight style than that utilized by *Schizooura*, given that the ulna is shorter than the humerus in *Mengciusornis*, which in extant birds is indicative of poor maneuverability or flightlessness (Middleton & Gatesy 2000). However, *Mengciusornis* has a proportionately longer forelimb that is not the result of a shortened hind limb given the subequal size of femora between *Mengciusornis* and *Schizooura*, which may reflect early experimentation within the Ornithuromorpha for dealing with the functional demands of volant behaviour, which favours forelimb elongation. These differences suggest that despite the fact these two taxa form a clade, they are likely still separated by considerable evolutionary changes along the lineage of each individual taxon. Alternatively, these differences may be indicative of rapid evolutionary changes suggesting strong plasticity in forelimb proportions, as already demonstrated in the dentition.

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Supplemental material

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ORCID

Min Wang  <http://orcid.org/0000-0001-8506-1213>

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