Reinterpretation of the Early Cretaceous maniraptoran (Dinosauria: Theropoda) *Zhongornis haoae* as a scansoriopterygid-like non-avian, and morphological resemblances between scansoriopterygids and basal oviraptorosaurs

Jingmai K. O'CONNOR   Corwin SULLIVAN

(*Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology*, *Chinese Academy of Sciences* Beijing 100044   jingmai@ivpp.ac.cn)

Abstract   The recently described maniraptoran theropod *Zhongornis haoae*, known from a single juvenile specimen, was originally identified as a bird. However, morphological re-evaluation reveals striking resemblances to both Oviraptorosauria and Scansoriopterygidae. The reduced, but still long, boney tail is reinterpreted as having approximately twenty vertebrae and is reminiscent of the tails of *Caudipteryx* and *Epidexipteryx* in its proportions and morphology. Other morphological similarities with basal oviraptorosaurs include a short and deep skull, and a reduced minor digit. *Zhongornis* also differs strikingly from other Mesozoic birds, and resembles scansoriopterygids, in the size of the alular metacarpal, the proportions of the manual digits, and the lack of processes on the ischium. These similarities, together with resemblances between basal oviraptorosaurs and previously described scansoriopterygids, may point to a close relationship between these two clades. Cladistic analysis confirms a close relationship between *Zhongornis* and Scansoriopterygidae, which share forelimbs and pedal unguals that are elongate compared to those of oviraptorosaurs, but does not support oviraptorosaur affinities for this clade. Additional specimens will be required in order to determine both the taxonomic placement of this species and the affinities of Scansoriopterygidae, highlighting the drawbacks of basing new species on juvenile material.

Key words   Cretaceous, Theropoda, Scansoriopterygidae, Oviraptorosauria, Aves, *Zhongornis*, tail

1   Introduction

The emergence of birds from among non-avian dinosaurs continues to be a dynamic and controversial subject (Xu et al., 2011). Scientific understanding of maniraptoran dinosaurs, the clade inferred to include Aves (traditionally defined by the common ancestor of *Archaeopteryx* + living birds), has grown rapidly during the past few decades, primarily because of a wealth of new specimens from Upper Jurassic and Lower Cretaceous sediments in China (Xu, 2006; Xu

et al., 2010a). Discoveries of basal troodontids, oviraptorosaurs, and dromaeosaurids, and the new paravian clade Scansoriopterygidae, have reduced the morphological gap between basal birds and non-avian dinosaurs (Xu et al., 2002a,b). However, the increase in specimen data has complicated rather than clarified the problem of identifying the avian sister-group, revealing a mosaic of "avian" morphologies inconsistently distributed among purportedly closely related clades of non-avian dinosaurs. For example, ossified sternal plates (present and fused in all living birds) are known in basal dromaeosaurids, oviraptorosaurs, and scansoriopterygids (forming a fully fused sternum in some individuals of the first two clades), but are absent in troodontids and in the basal birds *Archaeopteryx* and *Sapeornis* (Clark et al., 1999; Norell and Makovicky, 1999; Wellnhofer and Tischlinger, 2004; Xu and Norell, 2004; Zhou and Zhang, 2003). The distribution of "avian" characters strongly suggests evolution in the maniraptoran clade was highly homoplastic.

Basal birds themselves possess disparate morphologies and do not provide a clear picture of the plesiomorphic avian taxon: *Archaeopteryx* strongly resembles troodontids such as *Anchiornis* and *Xiaotingia* (Turner et al., 2012; Xu et al., 2011), while the robust skull of sapeornithiforms most strongly resembles those of recently discovered basal oviraptorosaurs such as *Caudipteryx* (Ji et al., 1998) and of the scansoriopterygid *Epidexipteryx* (Zhang et al., 2008). Even *Caudipteryx* has been interpreted as a flightless bird (Jones et al., 2000). This proposal has since been convincingly refuted (Dyke and Norell, 2005), but nevertheless represents an example of the difficulty in distinguishing between basal birds and derived non-avian dinosaurs in some cases. The 'avian' status of several other taxa (e.g. *Rahonavis*, *Jinfengopteryx*, *Yandangornis*) is or has been similarly controversial, and even *Archaeopteryx* has been suggested to be a non-avian dinosaur (Xu et al., 2011). Some cases of this kind have been decisively resolved: *Jinfengopteryx*, for example, was readily reinterpreted as a troodontid on the basis of a nearly complete specimen with well preserved integumentary features (Turner et al., 2007). In other cases, however, it may be impossible to determine unequivocally the phylogenetic position of a particular taxon because of limits on current understanding of paravian diversity (e.g. *Archaeopteryx*) or incomplete preservation of available specimens (e.g. *Rahonavis*, *Yandangornis*).

The holotype and only known specimen of *Zhongornis haoae* is a poorly preserved, nearly complete, and articulated early juvenile individual, split between a slab (DNHM D2456; Fig. 1) and counterslab (DNHM D2455; Fig. 2A)(Gao et al., 2008). Most skeletal elements appear to have been poorly ossified at the time of death. Many of the bones are preserved primarily as rusty stains on the slab as in the juvenile *Similicaudipteryx* specimen STM4-1 (Fig. 2C; Xu et al., 2010b), severely limiting the amount of unambiguous morphological information that can be discerned. Because the only known specimen is inferred to be a juvenile on the basis of the incomplete ossification of the carpal and tarsal bones and the periosteal surface of most elements (Gao et al., 2008), interpretations of its morphology are complicated by the strong possibility that the specimen might display some ontogenetic
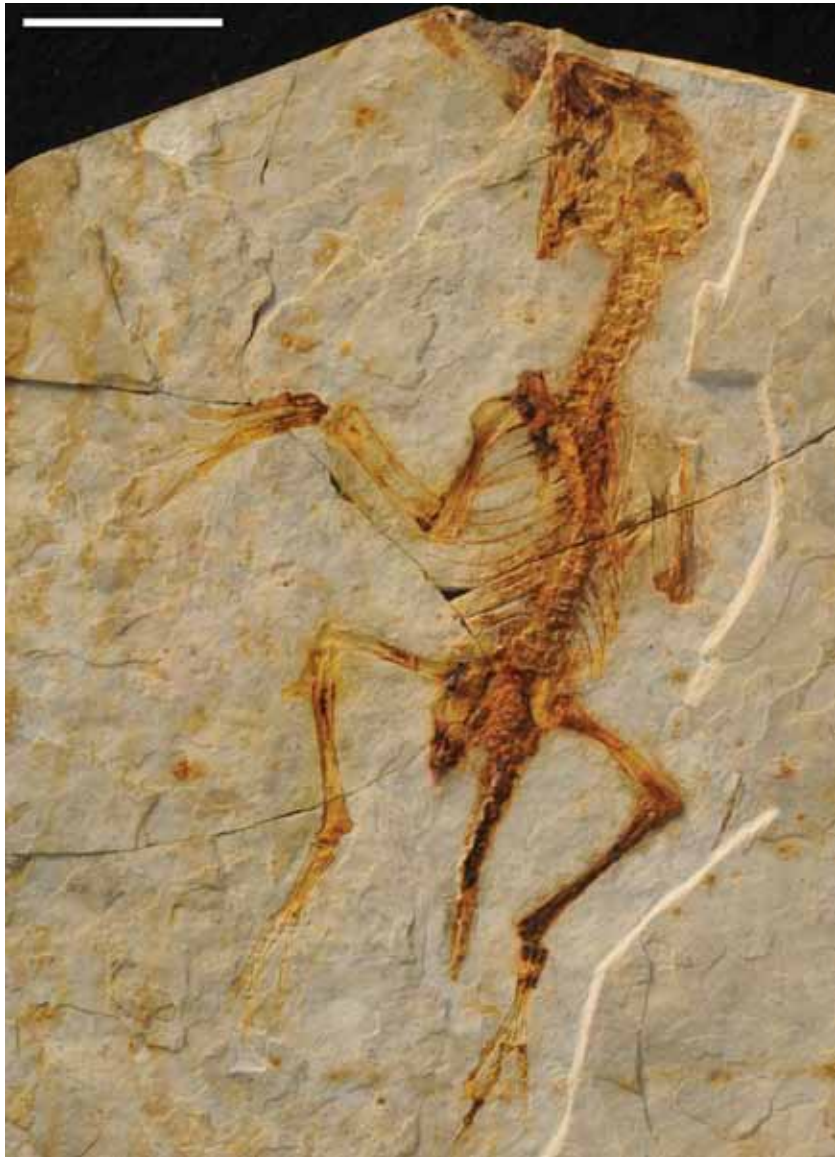
Fig. 1　Photograph of the holotype of *Zhongornis haoae* DNHM D2456
Scale bar equals 2 cm

differences from the adult condition. *Zhongornis* was originally described as the only known bird with a caudal morphology that could be considered transitional between the long boney tail of the most basal birds (e.g. *Archaeopteryx*, *Jeholornis*) and the abbreviated pygostyle-bearing tail of more derived forms (Gao et al., 2008). Furthermore, the manual phalangeal formula of 2-3-3 seen in *Zhongornis* is unique within Aves, and again appears transitional (Gao et al., 2008); this latter feature, which was assumed to be ontogenetically invariant, allowed the specimen to be differentiated from all previously known taxa and assigned to a new species
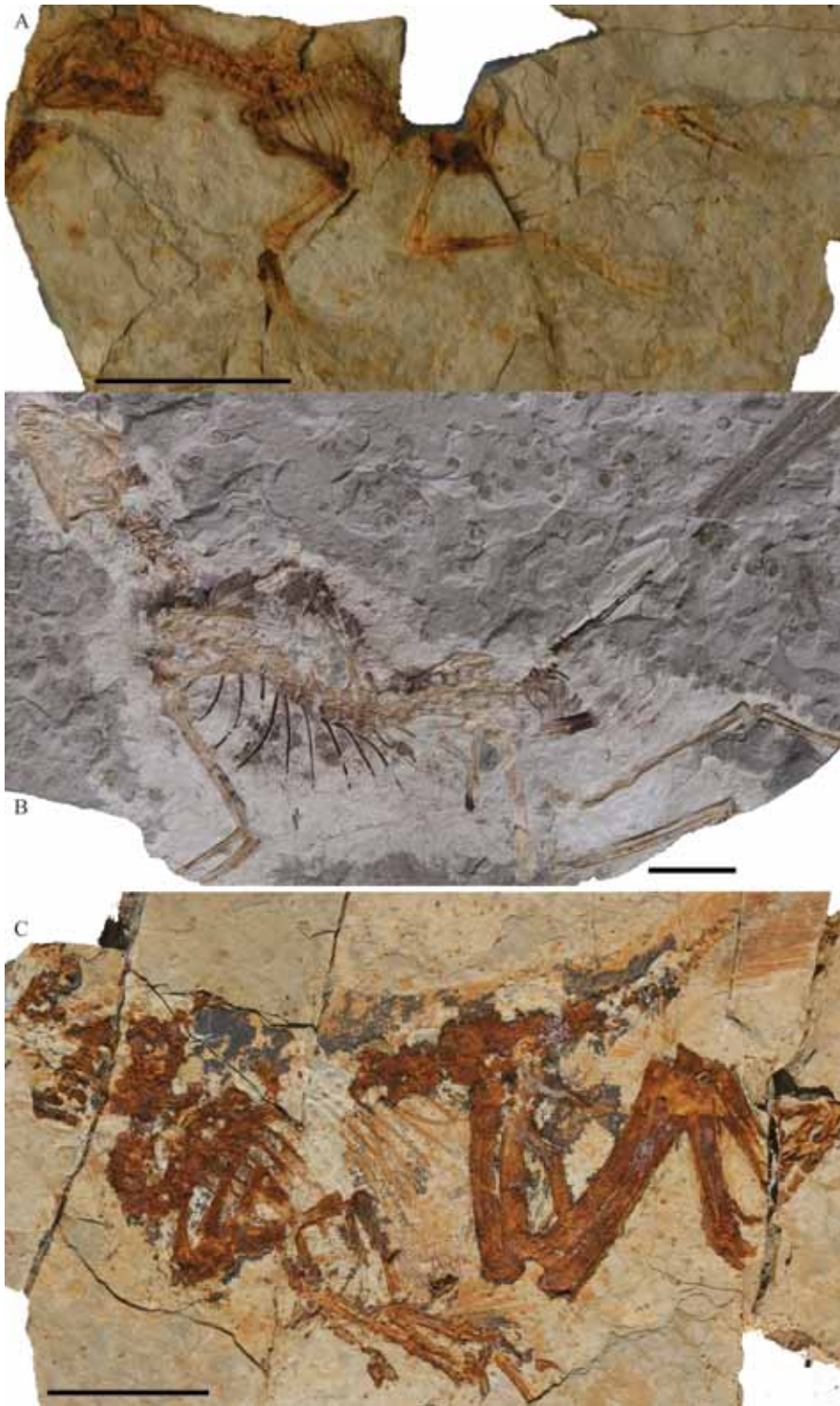
Fig. 2   Photograph of the counterslab of *Zhongornis haoae* DNHM D2455 (A), reversed for comparative
purposes, the holotype of *Epidexipteryx hui* IVPP V 15471 (B) and juvenile *Similicaudipteryx* STM4-1 (C)
All scale bars equal 3 cm

(Gao et al., 2008). Typical basal birds (e.g. *Archaeopteryx*, *Jeholornis*, *Confuciusornis*) have a formula of 2-3-4 but resemble *Zhongornis* and non-avian dinosaurs in retaining claws on all three digits, whereas *Sapeornis* and more derived Mesozoic birds (e.g. enantiornithines, and ornithuromorphs) characteristically have a phalangeal formula of 2-3-2 and lack a claw on the minor digit. A cladistic analysis of Mesozoic birds confirmed that *Zhongornis* occupied a transitional position within Aves, as sister taxon to all birds whose boney tail ends in a pygostyle (Gao et al., 2008).

Although the small size, presence of remiges, lack of teeth, pointed rostrum, relatively long forelimb, and seemingly transitional hand and tail morphology are consistent with the interpretation that *Zhongornis* is a basal bird, the holotype also bears important resemblances to another theropod group, the Scansoriopterygidae. This clade is poorly understood and includes only two valid genera, *Epidexipteryx* (Fig. 2B) and *Epidendrosaurus*, both of which are known entirely from immature specimens and are from Mid-Upper Jurassic strata exposed at the Daohugou Locality in eastern Nei Mongol (Inner Mongolia)(Zhang et al., 2002, 2008). Although scansoriopterygids are widely considered to represent the sister taxon to Aves (the two clades combined forming Avialae)(Turner et al., 2012), some recent studies have also suggested a relationship between Scansoriopterygidae and Oviraptorosauria (Agnolin and Novas, 2013; Xu et al., 2010a; Zhang et al., 2008). Morphological descriptions of basal oviraptorosaurs have only begun to appear in recent years (He et al., 2008; Ji et al., 1998; Xu et al., 2002a; Zhou and Wang, 2000; Zhou et al., 2000), and both the partially shortened tail and the reduced third manual digit seen in *Zhongornis* also occur in basal members of Oviraptorosauria. Here we provide a revised anatomical description of *Zhongornis*, based on a new study of the holotype. We compare the specimen with scansoriopterygids and basal oviraptorosaurs, as well as basal birds. This study reveals new morphological information that strongly suggests the holotype of *Zhongornis* is a juvenile scansoriopterygid or close scansoriopterygid relative. *Zhongornis* also shows some important similarities to basal oviraptorosaurs, hinting at the possibility of a close evolutionary relationship between oviraptorosaurs and scansoriopterygids (Fig. 3).

Fig. 3 Hypothetical cladogram illustrating the inferred phylogenetic position of *Zhongornis haoae* based on morphological observations

Institutional abbreviations   BPM, Beipiao Paleontological Museum, Liaoning, China; CAGS, Chinese Academy of Geological Sciences, Beijing, China; DNHM, Dalian Natural History Museum, Dalian, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; STM, Shandong Tianyu Museum of Nature, Pingyi, China.
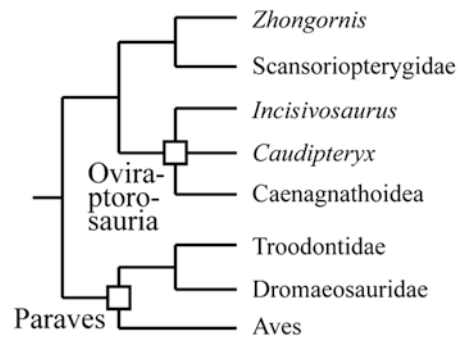
2　Comparative description

Terminology primarily follows Baumel and Witmer (1993); we use avian conventions for designating anatomical surfaces.

Skull　The skull of *Zhongornis* is short and deep, similar to those of oviraptorosaurs (e.g. *Caudipteryx*), scansoriopterygids (e.g. *Epidexipteryx*), and the basal birds *Jeholornis* and *Sapeornis*. The poorly ossified skull is partially articulated but the bones of the braincase (exposed in dorsocaudal view) have been pushed forward over the rostrum (exposed in lateral view), revealing very little clear morphological detail (Fig. 4). The premaxillae appear to be toothless and unfused, with fairly short nasal processes; large teeth are present in the premaxilla of *Epidexipteryx*, similar to those seen in the basal oviraptorosaur *Incisivosaurus* (Xu et al., 2002a). The nasal and maxillary processes of the premaxilla define a wide and deep concavity, as in *Epidexipteryx* and *Caudipteryx*. The maxillary process is appressed against the dorsal margin of the right dentary, but the facial margin of the upper jaw is not preserved; the frontals have been pushed over the rostrum so that the rostral margin of the left frontal is in the left external naris, obscuring the maxilla and most details of the rostrum. The nasal appears to be fairly long, as in *Epidexipteryx* and *Caudipteryx* (Zhou et al., 2000). A triangular postorbital process is present on the jugal, but this structure does not lie at the caudalmost end of the jugal and form a distal fork as in *Archaeopteryx*. In *Zhongornis*, *Epidexipteryx*, basal oviraptorosaurs (e.g. *Caudipteryx* and *Incisivosaurus*), and some basal birds (e.g. *Confuciusornis*, *Sapeornis*), the postorbital process is located rostral to the caudal end of the jugal (Chiappe et al., 1999; Xu et al., 2002a; Zhang et al., 2008; Zhou and Zhang, 2003; Zhou and Wang, 2000). The jugal appears proportionately longer and more delicate than in *Epidexipteryx* and basal oviraptorosaurs, and some basal birds (e.g. *Sapeornis*), although how the jugal changes with ontogeny is unknown. The postorbital process is dorsally directed, rather than caudodorsally as in *Archaeopteryx* (Elzanowski, 2002) and *Epidexipteryx*, and is longer than the quadratojugal process. Both processes are sharply tapered, and between them they define a concave margin as in *Epidexipteryx* (absent in *Sapeornis* and *Confuciusornis*).

The rostral halves of the long frontals are narrow, but caudally these bones expand to five times their rostral width. Although more derived oviraptorosaurs are characterized by short frontals that are approximately equal in length to the parietals (Osmólska et al., 2004), basal taxa such as *Caudipteryx* share the plesiomorphic condition of long, rostrally narrow and caudally expanded frontals (also present in troodontids and basal birds, and to a lesser extent in *Epidexipteryx*). The right quadrate is preserved; Gao et al. (2008) described the orbital ramus in *Zhongornis* as broad, but this feature cannot be confirmed here.

Although the shape of the rostrum is uncertain owing to disarticulation of the bones, the proportions of the mandible suggest the intact rostrum was short. The contacts between the dentary and postdentary bones are also unclear. The mandible appears short, deep, and

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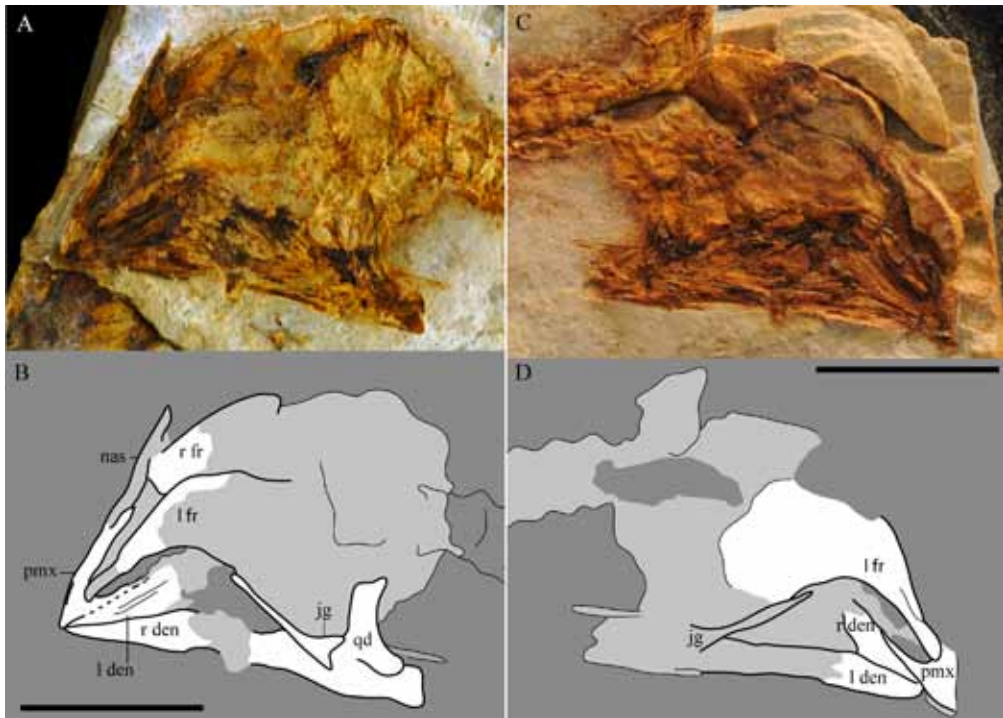
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Fig. 4   Photographs (A, C) and interpretative drawing (B, D) of the skull preserved in *Zhongornis haoae*
A-B. DNHM D2455; C-D. DNHM D2456; scale bars equal 1 cm
Anatomical abbreviations: den. dentary; fr. frontal; jg. jugal; l. left; nas. nasal; pmx. premaxilla;
qd. quadrate; r. right

robust, as in oviraptorosaurs and scansoriopterygids. The mandibular symphysis is clearly preserved in dorsal view in the counterslab (Fig. 4), and is V-shaped with a long midline suture between the rostral ends of the unfused dentaries. In *Epidendrosaurus* and oviraptorosaurs, by contrast, the symphysis is U-shaped (Zhang et al., 2002). The symphysis is similarly long in confuciusornithiforms, but is marked by a rostral notch that does not appear to be present in *Zhongornis*. Both the upper and lower jaws appear to be edentulous in *Zhongornis*, although the presence of very small teeth in the upper jaw cannot be ruled out due to poor preservation. Tooth reduction is common in oviraptorosaurs (derived members are edentulous)(Osmólska et al., 2004), as well as in scansoriopterygids (teeth rostrally restricted)(Zhang et al., 2008) and basal birds; the basal pygostylian *Confuciusornis* is edentulous, whereas the basal pygostylian *Sapeornis* and the long-tailed bird *Jeholornis* show reduced dentition (O'Connor et al., 2011). The basal oviraptorosaurs *Similicaudipteryx*, *Caudipteryx*, and *Protarchaeopteryx* all retain small teeth (He et al., 2008; Ji et al., 1998), whereas the premaxillary teeth of *Incisivosaurus* and the rostralmost dentary teeth of *Epidexipteryx* are hypertrophied (Xu et al., 2002a; Zhang et al., 2008).

   Axial skeleton   The cervical vertebrae of *Zhongornis* appear short and wide, but morphological details are not preserved (Fig. 5). Gao et al. (2008) reported 13-14 thoracic

vertebrae, although only 11 thoracic ribs are preserved on the left side. Pleurocoels are absent, as in known scansoriopterygid material (Czerkas and Yuan, 2002) and *Caudipteryx* (Zhou and Wang, 2000).
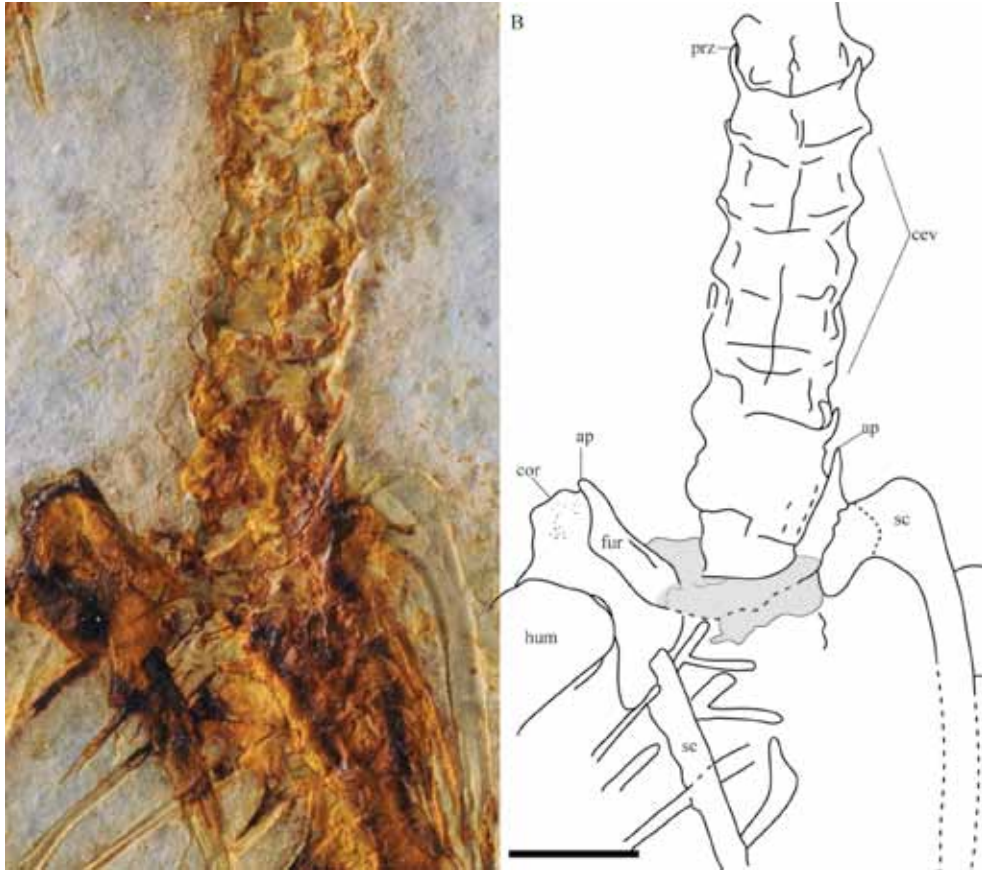

Fig. 5　Photograph (A) and interpretative drawing (B) of the key features preserved in the pectoral girdle of
Zhongornis haoae DNHM D2456
Anatomical abbreviations: ap. acromial process; cev. cervical vertebrae; cor. coracoid; fur. furcula; hum. humerus; prz. prezygapophyses; sc. scapula; scale bar equals 1 cm

Gao et al. (2008) reported six or seven sacrals in *Zhongornis*. Due to poor preservation, the number of sacral vertebrae is difficult to assess (Fig. 6), and we base our identification of the first sacral on the absence of an articulating thoracic rib. Based on our new observations of the counterslab (DNHM D2456), the estimated sacral count is revised to 5-6 vertebrae, which are unfused. The sacral vertebrae are very wide and short, but no further morphological details are preserved (Fig. 6). In oviraptorosaurs the synsacrum is composed of five (e.g. *Caudipteryx*; Ji et al., 1998) to eight (*Nemegtia*)(Lü et al., 2004) vertebrae, and is typically unfused in juveniles (Osmólska et al., 2004). *Epidexipteryx* preserves approximately seven unfused sacral vertebrae (Zhang et al., 2008).

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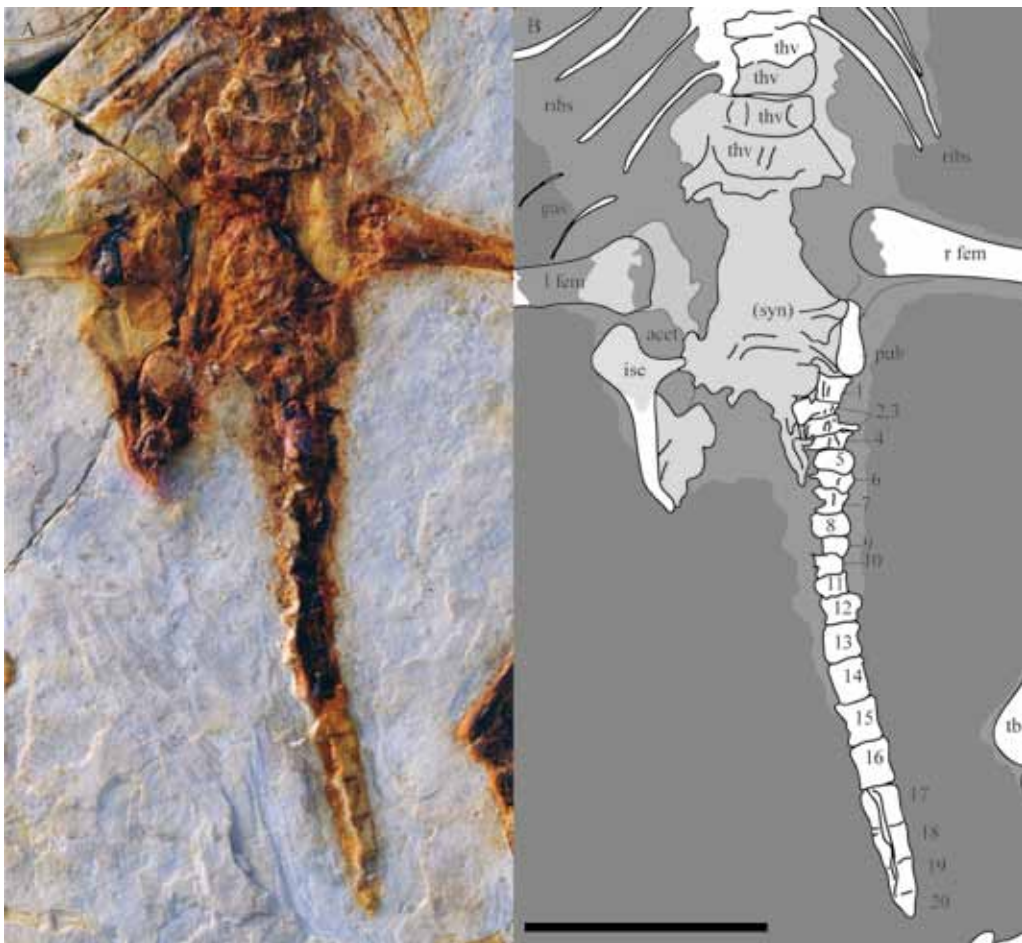
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Fig. 6 Photograph (A) and interpretative drawing (B) of the pelvic girdle and caudal vertebrae of *Zhongornis haoae* DNHM D2456

Anatomical abbreviations not listed in Fig. 4 caption: acet. acetabulum; fem. femur; gas. gastralia; isc. ischium; pub. pubis; syn. sacral vertebrae; tb. tibia; thv. thoracic vertebra; 1–20. caudal vertebrae

Scale bar equals 1 cm

The tail of *Zhongornis* superficially resembles that of basal oviraptorosaurs in its robust construction and in the proportions of the individual caudal vertebrae, which are proximally short and wide but distally less elongated than the vertebrae in deinonychosaurs, *Archaeopteryx*, and the long-tailed jeholornithiform birds (Gao et al., 2008; O'Connor et al., 2011; Osmólska et al., 2004; Persons et al., in press). Accordingly, the tail is similar to those of scansoriopterygids and oviraptorosaurs in lacking a distinct transition point (Figs. 6,7; Persons et al., in press). The distalmost four vertebrae appear to be partially fused, forming an incipient pygostyle. A similar structure is present in *Epidexipteryx*, *Similicaudipteryx*, and several Late Cretaceous oviraptorosaurids (Barsbold et al., 2000). In *Epidexipteryx* the ten caudalmost vertebrae form a pygostyle-like structure but remain unfused (Zhang et al., 2008), a condition

strongly resembling that of the tail in very young juvenile enantiornithines (Chiappe et al., 2007).

Zhongornis was originally described as having fourteen caudal vertebrae (Gao et al., 2008), considerably fewer than in any currently known oviraptorosaur but comparable to the sixteen caudals reported for *Epidexipteryx* (Zhang et al., 2008). However, new observations suggest the tail in *Zhongornis* is actually longer than originally described. In the poorly preserved region distal to the last sacral and proximal to the well-preserved caudalmost 14 vertebrae, previously unrecognized but well-preserved elongate transverse processes are identified (Fig. 6). Poor preservation makes it very difficult to determine the exact number of vertebrae: there are anywhere from four to 11 proximal short vertebrae followed by ten to 13 box-like vertebrae with transverse processes absent (or unossified). Although the total number of caudal vertebrae remains uncertain, we estimate the tail to have been composed of approximately 20 free vertebrae (Figs. 6,7). *Zhongornis* would then have more caudal vertebrae than *Epidexipteryx* but fewer than *Epidendrosaurus*, one specimen of which includes an incomplete tail consisting of 22 free caudals (Czerkas and Yuan, 2002). Among oviraptorosaurs, the number of caudal vertebrae is known to range from 22 (e.g. *Protarchaeopteryx*, *Caudipteryx*) to more than 30 (e.g. *Conchoraptor*, *Citipati*), with Early Cretaceous taxa typically having fewer caudals than Late Cretaceous forms (Osmólska et al., 2004). In all Mesozoic birds and in such maniraptoran dinosaurs as *Zhongornis*, *Caudipteryx*, and *Epidexipteryx*, the proximal free caudal vertebrae are short, being much wider and taller than long, and have long transverse processes. In birds with elongate boney tails, a transition point occurs near the fifth-sixth vertebra, after which the caudals are elongate. In *Jeholornis* and *Archaeopteryx* the distal caudal vertebrae are more than four times as long as they are wide. A similar pattern is observed in deinonychosaurs, but in non-avian dinosaurs the transition point is typically more distally located (ninth-tenth vertebrae). The transition point is especially distally displaced in oviraptorosaurids, in which the proximal and distal caudal morphologies grade into each other distally without a distinct transition and transverse processes persist nearly the entire length of the tail; a weak transition occurs at the 18th caudal in *Nomingia* and at the 25th caudal in *Khaan* (Persons et al., in press). In dromaeosaurids and troodontids, as in long boney-tailed birds, the distal vertebrae are very elongate — more than four times as long as they are wide. However, in oviraptorosaurs (*Caudipteryx*) and *Zhongornis* the distal vertebrae are more robust, being only twice as long as they are wide. In *Epidexipteryx* the vertebrae begin to elongate after the sixth caudal. The middle vertebrae are box-like, but the caudalmost vertebrae are more than twice as long as they are wide. The abrupt transition seen in deinonychosaurs and long tailed birds is absent in *Epidexipteryx*. A similar morphology is preserved in *Epidendrosaurus*; the vertebrae begin to elongate beyond the eighth caudal but never become more than twice as long as they are wide, and decrease in size after the 12th-13th caudal.
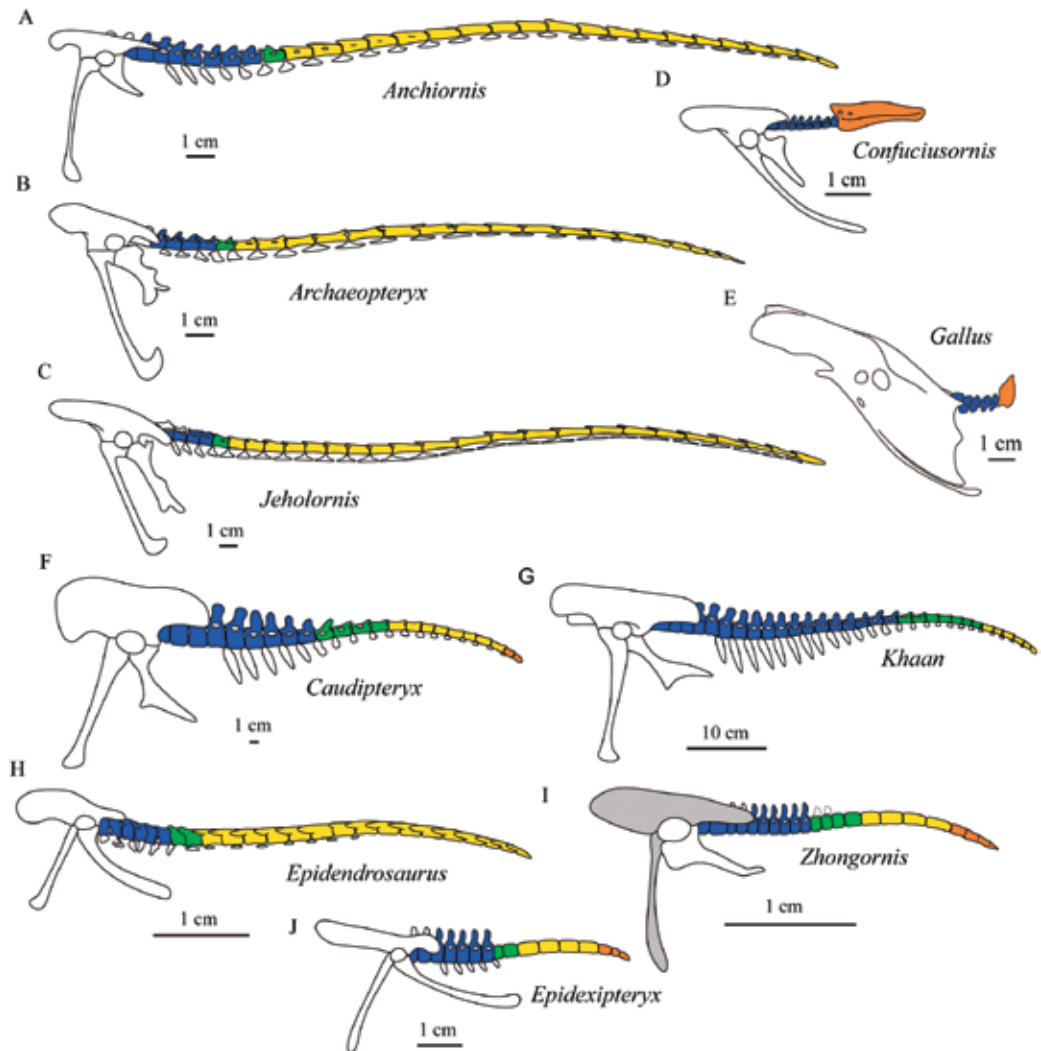
Fig. 7 Tails and pelves of derived maniraptoran theropods (modified from Persons et al., in press)
A. *Anchiornis* (Deinonychosauria: Troodontidae?); B. *Archaeopteryx* (Aves); C. *Jeholornis* (Aves); D. *Confuciusornis* (Aves); E. *Gallus* (Aves); F. *Caudipteryx* (Oviraptorosauria); G. *Khaan* (Oviraptorosauria); H. *Epidendrosaurus* (Scansoriopterygidae); I. *Zhongornis* (incertae sedis); J. *Epidexipteryx* (Scansoriopterygidae)
Color key: blue — short proximal caudal vertebrae; green — transitional caudals; yellow — elongate distal caudals; orange — partially or fully fused terminal caudals (pygostyle)

As is most clearly preserved in the short third free caudal vertebra, the length of a single transverse process of each anterior caudal in *Zhongornis* is approximately equal to the transverse width of the corresponding vertebral body, as in *Caudipteryx*, *Epidexipteryx*, and basal birds (e.g. *Archaeopteryx*, *Confuciusornis*, and the enantiornithines *Concornis* and *Rapaxavis*). We estimate that eight to 10 caudal vertebrae display this morphology, although poor preservation makes this uncertain. From the first clearly preserved centrum, the caudal vertebrae increase in length distally and become more robust; the last fully free

caudal vertebra is the largest, and its length only slightly exceeds its width. As in *Caudipteryx* and *Epidexipteryx*, the last few caudals of *Zhongornis* decrease progressively in size, and the distalmost caudal has a rounded distal margin (Figs. 6,7). Elongate prezygapophyses are present in *Caudipteryx* but are not evident in *Zhongornis*, nor is there any indication in *Zhongornis* of the long, rod-like haemal arches that characterize the cranial part of the tail in *Caudipteryx*. The proximal caudal vertebrae are very poorly preserved in the holotype of *Zhongornis*, and haemal arches might be buried in the sediment if the tail is preserved in a partial dorsal view. Alternatively, the arches may have been unossified at the time of death due to the early ontogenetic status of the holotype of *Zhongornis*. Wide haemal arches are nevertheless preserved in a juvenile individual of *Similicaudipteryx* (STM4-1; Fig. 2C), although this specimen may be more mature. Long transverse processes are present on the caudal vertebrae of the subadult specimen of *Similicaudipteryx* (STM22-6), but are unossified in the juvenile specimen except in the proximalmost part of the tail (Xu et al., 2010b), a situation consistent with observations of *Zhongornis*. In the holotype of *Epidexipteryx* the proximal vertebrae have long, caudally deflected transverse processes; the caudalmost ten vertebrae bear no processes.

Ontogenetic change in the number of free caudal vertebrae has been documented in more derived Mesozoic birds whose tail ends in a pygostyle. The basal ornithuromorph *Archaeorhynchus spathula* is known entirely from subadult specimens, two of which preserve different numbers of free caudal vertebrae and presumably record different stages in the consolidation of the pygostyle (Zhou et al., 2013). Despite differences in the number of free vertebrae and the size of the pygostyle between the two specimens, the overall length of the caudal series appears similar in both. If the tail of *Zhongornis* developed in a similar way, any ontogenetic changes would be more likely to involve the degree of caudal fusion rather than the overall length of the tail relative to the body.

Thoracic girdle The scapula is distally expanded in oviraptorosaurs (*Caudipteryx*, *Similicaudipteryx*) as well as in *Epidexipteryx* and the juvenile *Epidendrosaurus*. This feature does not appear to be present in *Zhongornis*, although the distal half of the scapula is poorly preserved and only visible on the left side (DNHM D2456). The juvenile *Similicaudipteryx* (STM4-1) also appears to lack any distal expansion of the scapula. Oviraptorosaurs also typically have a laterally expanded acromion (hypertrophied in *Avimimus*)(Vickers-Rich et al., 2002), but this is absent in *Caudipteryx* (Zhou and Wang, 2000; Zhou et al., 2000) and its presence is uncertain in scansoriopterygids and *Zhongornis*.

The coracoid is not well-preserved and is largely overlapped by other elements, making it difficult to confirm the original description (Gao et al., 2008) of this bone as strut-like; in DNHM D2456 it appears short, robust, and trapezoidal, a primitive morphology that characterizes oviraptorosaurs and scansoriopterygids, as well as dromaeosaurids, troodontids, *Archaeopteryx* and sapeornithiforms. The proximal end appears relatively robust and only slightly narrower than the distal end, whereas the proximal end is usually very narrow in birds

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with 'strut-like' coracoids. The preserved impression of the bone surface is pitted, indicating that the periosteal surface was incompletely ossified when the individual died and providing further evidence for its juvenile status (Gao et al., 2008). No coracoidal foramen is visible.

The furcula of *Zhongornis* is fairly robust, as in derived oviraptorosaurs and some basal birds (e.g. *Jeholornis*, *Sapeornis*), and has an interclavicular angle of approximately 80° as opposed to the 90° that is typical in derived oviraptorosaurs (Nesbitt et al., 2009)(Fig. 5). The furcula is poorly preserved, especially at the clavicular symphysis, and no hypocleidium is apparent (although this structure is present in derived oviraptorosaurs, *Sapeornis*, and most enantiornithines). The proximal portions of the furcular rami narrow abruptly and the omal tips taper sharply, forming elongate acromial (epicleidial) processes as in some oviraptorosaurs (e.g. *Citipati*, *Oviraptor*; Nesbitt et al., 2009). In basal birds the omal ends of the furcula typically taper weakly to blunt points (e.g. *Jeholornis*, *Sapeornis*, *Confuciusornis*). The tapering acromial processes in *Zhongornis* are proportionately longer than the delicate processes preserved in the ornithuromorph bird *Yixianornis*, but shorter than those of *Citipati*. Unfortunately, the furcula is unknown in scansoriopterygids and poorly known in basal oviraptorosaurs; the furcula is only preserved in a single described specimen of *Caudipteryx* (BPM 0001), and in this case is exposed in lateral view and does not reveal any important morphological data (Zhou et al., 2000).

No sternal plates are preserved in *Zhongornis*, although this is unsurprising given that the specimen is considered an early juvenile. Sternal plates are also absent in the juvenile basal oviraptorosaur *Similicaudipteryx* and the juvenile scansoriopterygid *Epidendrosaurus* (Zhang et al., 2002; Xu et al., 2010b). The sternal plates in *Epidexipteryx* and the basal oviraptorosaur *Caudipteryx* are a pair of free oval elements (Zhou and Wang, 2000; Zhang et al., 2008). Late Cretaceous oviraptorosaurs possess enlarged, medially articulating sternal bones (fused in at least one taxon, '*Ingenia*')(Barsbold, 1981) with advanced features that are also present in some birds, such as craniolateral and lateral processes (Balanoff and Norell, 2012; Clark et al., 1999). A sternum is not preserved in any specimen of *Archaeopteryx* or *Sapeornis*; where present in basal birds (Confuciusornithiformes, Ornithothoraces), the sternum begins to ossify early, small ossifications being present in nearly every juvenile enantiornithine (Zheng et al., 2012).

Thoracic limb   Little more than the general shape of the humerus can be determined in *Zhongornis*, but the morphology of this element is consistent with the oviraptorosaurian condition in that the deltopectoral crest is prominent and the distal end is expanded. The humerus is poorly preserved in all known scansoriopterygids. However, the holotype of *Epidexipteryx* has a fairly prominent deltopectoral crest and this specimen and the referred specimen of *Epidendrosaurus* both preserve a midshaft constriction and expanded distal end, as in *Zhongornis* (Czerkas and Yuan, 2002). The proximal margin of the humerus slopes dorsodistally from the proximoventral corner as in basal birds (e.g. *Confuciusornis*) and derived nonavian maniraptoran theropods (whereas the most proximally prominent area is centered on

the proximal margin in more derived birds). The deltopectoral crest is proportionately more prominent than in *Caudipteryx*, but is comparable in prominence to those of some derived oviraptorosaurs (e.g. *Heyuannia*, *Khaan*)(Osmólska et al., 2004). In *Zhongornis* the ulna seems only slightly more robust than the radius, as in scansoriopterygids; in oviraptorosaurs the two bones show a greater discrepancy in width, although not as great as in basal birds. In *Zhongornis*, both bones are strongly constricted near their mid-length, whereas the degree of constriction is typically less in birds, scansoriopterygids, and oviraptorosaurs. This may also be an ontogenetic feature (potentially the result of incomplete ossification), although it is not evident in the poorly preserved forelimbs of the holotype of *Epidendrosaurus* (Zhang et al., 2002) or the juvenile *Similicaudipteryx* specimen STM4-1 (Xu et al., 2010b).

Zhongornis preserves one or possibly two free small carpal bones, although their size and potential lack of mutual fusion are probably juvenile features (Gao et al., 2008). The more definitively identifiable carpal overlaps the proximal margin of the major metacarpal, but the carpals are interpreted as largely unossified and the true extent of their articulation with the metacarpus is unknown. A single carpal element inferred to be the semilunate is preserved in the referred specimen of *Epidendrosaurus* (CAGS-02-IG-gausa-l/DM 607), but this bone is larger than either carpal of *Zhongornis* and overlaps the proximal margin of the alular metacarpal (Czerkas and Yuan, 2002). One specimen of *Caudipteryx* (IVPP V 12430) preserves three small carpal ossifications (Zhou et al., 2000); the largest of the three is interpreted as the semilunate, and overlaps the proximal margin of the alular metacarpal as in *Epidendrosaurus*.

The large, robust alular metacarpal in *Zhongornis* (DNHM D2455/6) measures one third the length of the major metacarpal, comparable to
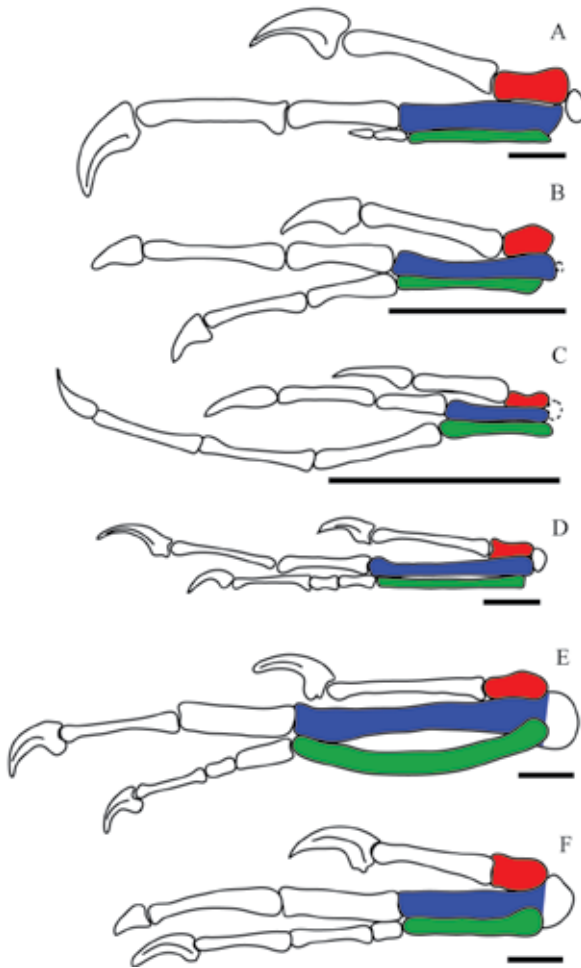

Fig. 8 Hands of derived maniraptoran theropods
A. *Caudipteryx*; B. *Zhongornis*; C. *Epidendrosaurus*;
D. *Archaeopteryx*; E. *Jeholornis*; F. *Confuciusornis*
The alular digit is coded red; the major digit is coded blue;
the minor digit is coded green; scale bars equal 1 cm

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the equivalent ratio in the juvenile *Similicaudipteryx* STM4-1 (35%) and the basal birds *Archaeopteryx* and *Confuciusornis*. The alular metacarpal is proportionately even longer in *Caudipteryx* (~44%), *Protarchaeopteryx* (39%), and *Epidendrosaurus* (38%), but is shorter (19%-25%) in most basal birds, including *Jeholornis*, *Sapeornis*, and *Cathayornis* (Dececchi et al., 2012). Non-avian maniraptorans consistently show higher percentages than birds, with the exception of *Archaeopteryx* and confuciusornithiforms; dromaeosaurids are reported to vary between 25%-35%, with *Microraptor* as a low outlier (25%-26%), while troodontids vary between 37%-42% (Dececchi et al., 2012). In *Zhongornis*, the alular metacarpal is wider than the major metacarpal, which in turn is wider than the minor metacarpal. In *Epidendrosaurus* and *Caudipteryx* the alular and major metacarpals are subequal in width, whereas in *Ingenia* and *Machairasaurus* the alular metacarpal is the widest (Osmólska et al., 2004; Longrich et al., 2010). The condition in *Zhongornis* is distinctly non-avian, given that in all birds the major metacarpal is the widest (Fig. 8)(Chiappe et al. 1999; Zhou and Zhang, 2002, 2003). The alular digit is also much larger than in any known bird; the first phalanx of the alular digit exceeds the major metacarpal in length, as in the scansoriopterygid *Epidendrosaurus* (hand disarticulated and incomplete in *Epidexipteryx*). In *Caudipteryx* and *Similicaudipteryx*, the first alular phalanx is subequal to the major metacarpal in length, but this phalanx is shorter than the major metacarpal in deinonychosaurs, Late Cretaceous oviraptorosaurs (e.g. *Citipati*, *Oviraptor*, *Khaan*), and basal birds (e.g. *Archaeopteryx*, *Confuciusornis*, and *Sapeornis*). In basal birds the first phalanx of the alular digit is both shorter and more slender than the major metacarpal (Fig. 8). The proportions of the digits and the phalanges relative to the metacarpals in *Zhongornis* are more reminiscent of non-avian dinosaurs than birds.

The 2-3-3 phalangeal formula of *Zhongornis* is otherwise unknown among oviraptorosaurs and birds, though it is potentially present in the parvicursorine *Shuvuuia* (Suzuki et al., 2002). Among scansoriopterygids, the hand is well known only in *Epidendrosaurus*, in which it is highly specialized with a phalangeal formula of 2-3-4 and a hyper-elongated minor digit (Zhang et al., 2002). Within Oviraptorosauria the manus typically has a 2-3-4 phalangeal formula (e.g. *Protarchaeopteryx*, *Citipati*, *Oviraptor*, *Ingenia*), with the minor (third) digit typically being nearly as long as the major (second) digit (Longrich et al., 2010). However there is a strong trend toward reduction of the minor digit among some members of the clade, involving loss and/or fusion of phalanges (Osmólska et al., 2004). *Caudipteryx* has a manual formula of 2-3-2 and no claw on the minor digit (Zhou et al., 2000).

In *Zhongornis* the penultimate phalanx of the major digit is longer than the proximal phalanx, as in most theropods including some basal birds (*Archaeopteryx* and *Confuciusornis*). In most birds (*Jeholornis*, *Sapeornis*, ornithothoracines) the penultimate phalanx is the shorter of the two, as the result of a trend towards reduction in the length of the manus. The manual claws of *Zhongornis* are reminiscent of those of scansoriopterygids and basal oviraptorosaurs (e.g. *Caudipteryx*, *Similicaudipteryx*) in being weakly recurved, whereas basal birds have highly recurved manual claws (*Archaeopteryx*, *Jeholornis*, *Sapeornis*, *Confuciusornis*,

Enantiornithes)(Fig. 8). Unlike in *Caudipteryx*, the major digit ungual of *Zhongornis* is poorly developed with a small flexor tubercle, a synapomorphy of scansoriopterygids (Zhang et al., 2002). The claws vary in curvature and development of the flexor tubercles among Late Cretaceous oviraptorosaurs (weakly curved with poorly developed flexor tubercles in *Machairasaurus*)(Longrich et al., 2010).

Pelvic girdle   The pelvic girdle is poorly preserved, with only the ischium providing any real morphological information. However, even this element is so poorly preserved that it is highly subject to interpretation. The ischium of *Zhongornis* was originally described as having a distinct dorsal process, similar to that present in *Sapeornis* and enantiornithines (Gao et al., 2008). We suggest that the "dorsal process" of the ischium may in fact be the iliac peduncle (Fig. 6). Under that interpretation, the proximal end of the ischium is forked, forming iliac and pubic peduncles that collectively define the caudal half of the large, round acetabulum. The pubic peduncle is twice the width of the iliac peduncle; the two peduncles appear subequal in width in *Caudipteryx*, although this is somewhat unclear in available specimens. The ischium of *Zhongornis* is short (ischium:femur ratio 0.53), as in *Caudipteryx* (ischium:femur ratio 0.48)(Zhou and Wang, 2000) and basal birds (*Archaeopteryx* 0.45, *Sapeornis* 0.49, *Confuciusornis* 0.44) but in contrast to scansoriopterygids (ischium:femur ratio 0.71 in *Epidexipteryx*). The corpus of the ischium is strap-like and tapers to a blunt distal end, whereas in oviraptorosaurs the middle of the ischial shaft is ventrally expanded into a triangular process (e.g. *Protarchaeopteryx*, *Nomingia*, *Luoyangia*, *Heyuannia*, *Caudipteryx*, *Similicaudipteryx*). This ventral process appears to be present even in the juvenile *Similicaudipteryx* STM4-1. In scansoriopterygids the ischium is simple, strap-like, and slightly expanded at the distal end (Czerkas and Yuan, 2002; Zhang et al., 2008). In *Zhongornis* the dorsal margin of the ischium is slightly concave so that the distal end of the bone is deflected dorsally, as in scansoriopterygids (Zhang et al., 2008) and some oviraptorosaurs (e.g. *Caudipteryx*, *Nomingia*) (Zhou and Wang, 2000).

Pelvic limb   The hindlimbs are preserved complete in the holotype of *Zhongornis* (Fig. 1) although the femur and fibula are too poorly preserved to yield useful morphological information. The proximal and distal tarsals are not preserved or perhaps were unossified at the time of death, with the exception of a poorly preserved bone associated with the distal end of the left tibia that is likely the astragalus.

In *Zhongornis*, metatarsal III is the longest, followed by IV and then II; metatarsals II and IV are subequal in width, while metatarsal III appears to have a mediolaterally compressed midshaft. These features are all shared by *Epidendrosaurus* (Czerkas and Yuan, 2002) and *Caudipteryx* (Zhou and Wang, 2000). The trochlea of metatarsal III is wider than those of the other metatarsals in *Zhongornis* and *Epidendrosaurus*. The scansorial *Epidendrosaurus* also shows similar pedal proportions to *Zhongornis*, with distally elongated phalanges (Zhang et al., 2002). The pedal phalangeal proportions of *Zhongornis* differ greatly from those of *Caudipteryx*, but this may reflect ecological differences between the two taxa; in *Zhongornis*,

the individual phalanges increase slightly in length from proximal to distal within each digit, indicating a more arboreal habitat (Hopson, 2001; Zhou and Farlow, 2001). By contrast, the foot of *Caudipteryx* is clearly adapted for locomotion on the ground, having short distal phalanges (Zhou and Wang, 2000). The pedal unguals of *Zhongornis* are weakly curved and sharply tapered, like those of *Epidendrosaurus* (Zhang et al., 2002).

The intermembral index (the ratio of the combined length of the humerus and ulna to that of the femur and tibia; distal limb elements are often incompletely preserved and thus were omitted to allow comparisons across a wider range of taxa) in *Zhongornis* is 0.85, which falls in the range of the arboreal scansoriopterygids (0.81 in *Epidexipteryx*, 0.91-0.94 in *Epidendrosaurus*). Perhaps for ecological reasons, these limb proportions are very different from those of basal oviraptorosaurs, which are cursorial animals with elongate hindlimbs and low intermembral indices (0.40 in *Caudipteryx*, 0.53 in the juvenile *Similicaudipteryx* STM4-1). Birds have elongated forelimbs for flight; basal birds have indices close to 1.0 (0.97 in *Archaeopteryx*, 0.98-1.0 in *Confuciusornis*) or even greater (1.3 in *Jeholornis*; 1.6 in *Sapeornis*). The forelimb of *Zhongornis* is proportionately short compared to those of basal birds.

3　Discussion

Based on new morphological data and comparisons with other avian and non-avian taxa, we suggest that the Early Cretaceous 'bird' *Zhongornis haoae* may in fact be either a member or a close relative of the Scansoriopterygidae, an enigmatic maniraptoran clade otherwise known entirely from the Middle-Upper Jurassic Daohugou beds (Sullivan et al., in press). Although poor preservation obscures many morphological details in the holotype and only known specimen of *Zhongornis* (DNHM D2455/6), and some of the visible features probably reflect the fact that the specimen is a young juvenile, sufficient evidence is available to call the previous assignment of *Zhongornis* to Aves into question (Gao et al., 2008). Details of the skull, cervical vertebrae, and pelvic girdle are highly subject to interpretation, but the hand is clearly preserved on both sides in DNHM D2455/6. Comparisons with Mesozoic birds reveal major differences in the proportions of the metacarpals and digits, and in the shape of the claws, whereas *Zhongornis* resembles scansoriopterygids with regard to these same features. *Zhongornis* also shares many notable similarities with basal members of the clade Oviraptorosauria. The morphological similarities between *Zhongornis* and both these clades are explored below.

3.1　Scansoriopterygid similarities

The skull of *Zhongornis* shows an overall similarity to the scansoriopterygid condition in its short and deep proportions, although detailed comparisons are impossible due to the poor preservation of all the relevant known specimens. The limb proportions of *Zhongornis*

are strikingly similar to those of scansoriopterygids, the intermembral index being 0.85 in *Zhongornis*, 0.81 in *Epidexipteryx* and 0.91-0.94 in *Epidendrosaurus*. In contrast, basal birds have relatively longer forelimbs (~1.0 in *Archaeopteryx*, *Confuciusornis*; 1.3 in *Jeholornis*), although the hindlimbs become secondarily elongated in some derived ornithuromorphs (e.g. the Hongshanornithidae, with intermembral indices of 0.71-0.75). The tail of *Zhongornis* shares several features with that of *Epidexipteryx*: the number of caudal vertebrae is reduced, there is no distinct transition point or extreme elongation of the distal caudal centra, and the robust tail ends in an incipient pygostyle. *Epidendrosaurus* has a more elongate tail (more than 22 caudal vertebrae), so known scansoriopterygids are not uniform in this regard; however, the distal caudal vertebrae of *Epidendrosaurus* still lack the extreme elongation observed in deinonychosaurs and basal birds. *Zhongornis* lacks a hyper-elongated minor manual digit, but bears a close resemblance to *Epidendrosaurus* in other features of the manus. The first alular phalanx is longer than the major metacarpal in both *Zhongornis* and *Epidendrosaurus*, an extreme condition that is not evident in either oviraptorosaurs or basal birds. The manual claws are also similar in being only weakly curved and having poorly developed flexor tubercles. In *Epidexipteryx* the hand is too incompletely preserved for its proportions to be clear. Despite differences in the relative length of the ischium between *Zhongornis* and *Epidexipteryx*, these taxa are similar in that this element is fairly slender and lacks dorsal or ventral processes. The foot is unknown in *Epidexipteryx* but in *Epidendrosaurus* the penultimate phalanx is the longest in each pedal digit, and the hallux is elongate. The penultimate pedal phalanges are also elongate in *Zhongornis*, although the hallux is much shorter. Pedal phalanges that become longer from proximal to distal within each digit are associated with arboreality in living birds (Hopson, 2001; Zhou and Farlow, 2001). Partly for this reason, arboreality has also been inferred for scansoriopterygids (Czerkas and Yuan, 2002; Sullivan et al., in press; Xu et al., 2010a; Zhang et al., 2002).

3.2　Oviraptorosaurian similarities

Many oviraptorosaurian synapomorphies are cranial features whose presence cannot be either confirmed or refuted in the poorly preserved holotype of *Zhongornis*. However, the preserved morphology of the premaxilla (concave rostral margin of naris defined by premaxilla), nasal (long), and frontal (long, rostrally narrow and caudally expanded) in *Zhongornis* is similar to that of the equivalent bones in *Caudipteryx*. The small number of sacral vertebrae preserved in *Zhongornis* (estimated to be five or six) is also consistent with the condition in basal members of this clade (five in *Caudipteryx* and *Similicaudipteryx*)(Ji et al., 1998). A relatively short and robust tail, like that in *Zhongornis*, is also a characteristic oviraptorosaurian feature (Longrich et al., 2010), whereas the caudal skeleton is characterized by a distinct transition point and extreme elongation of the distal centra in long boney-tailed birds and deinonychosaurs. Although the number of caudal vertebrae can only be loosely estimated in *Zhongornis*, we suggest approximately 20 caudals were present, close to the

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number recorded in the basal oviraptorosaur *Caudipteryx* (22 caudals). Furthermore, the juvenile *Zhongornis* preserves an incipient pygostyle, a feature that is present in several Late Cretaceous oviraptorosaurs as well as *Caudipteryx* (Persons et al., in press). The distalmost five caudals in *Caudipteryx*, although unfused, are reported to form a distinct unit (Persons et al., in press). The robust furcula, with its well developed epicleidia, resembles the condition in Late Cretaceous oviraptorosaurs (Nesbitt et al., 2009); unfortunately, this element is poorly known in Early Cretaceous forms. The hand of *Zhongornis* differs greatly from that of basal birds, but is similar in its proportions to those of some oviraptorosaurs. The alular metacarpal is 33% the length of the major metacarpal, a value smaller than those for most other oviraptorosaurs (39%-50%) but comparable to that for the juvenile *Similicaudipteryx* (35%) and considerably larger than those for most basal birds (<25% in *Jeholornis*, *Sapeornis*, and Ornithothoraces; 33% in *Archaeopteryx* and *Confuciusornis*). The alular metacarpal is wider than the major metacarpal in *Zhongornis* and oviraptorosaurs, whereas among birds the major metacarpal is always the widest. The first phalanx of the alular digit is slightly longer than the major metacarpal in *Zhongornis*; this phalanx is subequal in length to the major metacarpal in some oviraptorosaurs (e.g. *Caudipteryx*, *Similicaudipteryx*, *Citipati*), but in other oviraptorosaurs and all birds it is shorter than the major metacarpal. Although the 2-3-3 manual phalangeal formula of *Zhongornis* is unique among maniraptorans, the basal oviraptorosaur *Caudipteryx* has a reduced hand with a manual phalangeal formula of 2-3-2, the same formula seen in *Sapeornis* and ornithothoracine birds. Basal birds and most oviraptorosaurs have a manual phalangeal formula of 2-3-4. Thus, the manual phalangeal formula of *Zhongornis* is intermediate between the extreme ones observed within both birds and oviraptorosaurs. The low degree of manual claw curvature is also reminiscent of the condition in some oviraptorosaurs (e.g. *Caudipteryx*, *Citipati*, *Machairasaurus*), whereas basal birds tend to have highly recurved claws (e.g. *Archaeopteryx*, *Jeholornis*, *Sapeornis*, *Confuciusornis*).

3.3 *Zhongornis*, Oviraptorosauria and Scansoriopterygidae

Some features of *Zhongornis* are shared by both scansoriopterygids and basal oviraptorosaurs. The most obvious is the tail, which distinguishes scansoriopterygids and *Zhongornis* from other paravian theropods (deinonychosaurs and Aves); a reduced tail, lacking distally elongate vertebrae and having an incipient pygostyle, is present in both *Epidexipteryx* and *Caudipteryx*. Our new estimate of the number of caudal vertebrae in *Zhongornis* (approximately 20) is comparable to observations for both scansoriopterygids (16 in *Epidexipteryx*, 22+ in *Epidendrosaurus*) and basal oviraptorosaurs (22 in *Caudipteryx*). The hand of *Zhongornis*, although unlike that of any avian, is similar to those of oviraptorosaurs and scansoriopterygids in that the alular metacarpal is roughly similar in width to the major metacarpal (slightly wider in *Zhongornis*, subequal in *Caudipteryx* and *Epidendrosaurus*, narrower in birds). In *Zhongornis*, the alular metacarpal is one third the length of the major metacarpal, comparable to the juvenile *Similicaudipteryx* (35%); the alular metacarpal

is proportionately slightly longer in *Caudipteryx* (~44%), *Protarchaeopteryx* (39%), and *Epidendrosaurus* (38%)(shorter in most birds, with the exception of *Confuciusornis*). In addition, the alular digit is proportionately longer in *Zhongornis* than in any bird, but similar proportions are observed in both Scansoriopterygidae and Oviraptorosauria, with the first alular phalanx similar to the major metacarpal in length (always shorter in Aves); the two elements are subequal in *Caudipteryx* and *Similicaudipteryx*, but the first alular phalanx is proportionately even longer than the major metacarpal in *Epidendrosaurus* and *Zhongornis*. Furthermore, the manual claws are only weakly recurved in *Zhongornis*, *Epidendrosaurus*, and basal oviraptorosaurs (e.g. *Caudipteryx*).

3.4   Oviraptorosauria and Scansoriopterygidae

Very little is known about the enigmatic scansoriopterygids; only two taxa have been previously assigned to this clade, and the holotype of *Epidexipteryx* is a subadult while that of *Epidendrosaurus* is a juvenile. This makes it difficult to put forth strong arguments in support of a relationship between this clade and any other. However, basal oviraptorosaurs like *Caudipteryx* and *Incisivosaurus* share several features with scansoriopterygids, including a short and deep skull with robust rostral dentition, unserrated teeth, a distally expanded scapula, and a relatively robust but reduced long boney-tail without a distinct transition point in the caudal vertebrae (Turner et al., 2012). The hand shows similarities in that the length ratio between the alular and major metacarpals is comparable, at 38% in *Epidendrosaurus* and 39% in *Protarchaeopteryx*, and the first phalanx of the alular digit is elongate in both *Caudipteryx* (subequal in length to the major metacarpal) and *Epidendrosaurus* (longer than the major metacarpal). If the two clades are closely related in some way, their resemblances presumably represent synapomorphies. The differences in their overall proportions might then result from adaptation to contrasting ecological niches, in that known scansoriopterygids are inferred to have been arboreal whereas oviraptorosaurs were cursorial. Alternatively, scansoriopterygids and oviraptorosaurs may not be particularly close relatives, in which case any derived, exclusive similarities between the two clades would be the result of some kind of homoplasy (Xu et al., 2011). Some of the resemblances between oviraptorosaurs, scansoriopterygids, and basal birds other than *Archaeopteryx* may be ancestral for all derived maniraptorans but secondarily absent in deinonychosaurs (Xu et al., 2011). Another factor that might have produced homoplastic resemblances is dietary similarity, given that several features that unite the two clades (e.g. unserrated dentition) are considered indicators of herbivory (Zanno and Makovicky, 2011).

Scansoriopterygidae is known exclusively from the Middle-Late Jurassic Daohugou locality in Nei Mongol. However, the fossils from this site are part of a wider Daohugou Biota whose geographic distribution corresponds to that of the Early Cretaceous Jehol Biota, encompassing western Liaoning and northern Hebei provinces in addition to southeasternmost Nei Mongol (Sullivan et al., in press). The oldest and basalmost oviraptorosaurs *Incisivosaurus*,

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Protarchaeopteryx, and *Caudipteryx*, like *Zhongornis*, are from localities in Liaoning of the Early Cretaceous Yixian Formation of the Jehol Group (Osmólska et al., 2004). The holotype of *Zhongornis* is reported to be from the Dawangzhangzi beds (122.5 Ma) of the Yixian Formation near Lingyuan, Chaoyang, Liaoning, northeastern China. However, the county-level city of Lingyuan contains numerous fossil localities, including the Wubaiding locality of the Daohugou Biota (Sullivan et al., in press). Unfortunately, no precise locality information is available because the specimen was obtained from a dealer, but the presence of the fish *Lycoptera* in the slab containing the holotype of *Zhongornis* confirms that this taxon belongs to the Jehol Biota. The apparent scansoriopterygid affinities of *Zhongornis* would suggest the clade persisted from the Mid-Late Jurassic Daohugou times into Early Cretaceous Jehol times.

As a result of the high amount of homoplasy that characterizes derived maniraptoran evolution, the identity of the avian sister taxon remains debated despite the rapid accumulation of morphological data. Recent analyses have consistently resolved a troodontid and dromaeosaurid clade (Deinonychosauria) as the avian sister-taxon (Turner et al., 2012). The discovery of the scansoriopterygid *Epidexipteryx* led to the suggestion that this enigmatic clade may also be closely related to birds (Zhang et al., 2008). Several analyses have indeed resolved this clade as sister taxon to Aves, forming the clade Avialae which in turn is sister taxon to Deinonychosauria (Xu et al., 2011). A close relationship between oviraptorosaurs and birds has also been proposed in the past (Maryanska et al., 2002), and supported by numerous lines of evidence (Kundrát, 2007). However, the 'avian' features typically present in derived oviraptorosaurs (e.g. edentulous rostrum, tricondylar quadrate, pygostyle) are not seen in either basal birds or basal oviraptorosaurs, suggesting that they evolved convergently (de Queiroz, 1985). Shared postcranial features such as the absence of a transition point in the tail, the distally expanded scapula, and the incipient pygostyle also support a close relationship between scansoriopterygids and oviraptorosaurs. 'Avian characteristics' that originally suggested *Zhongornis* was a bird, and that suggest scansoriopterygids are the avian sister group, may be the result of convergently evolved arboreal adaptations.

Basal oviraptorosaurs have only recently begun to be understood and Scansoriopterygidae, with only two poorly preserved taxa, remains an enigmatic clade. We suggest that accumulating morphological information regarding both scansoriopterygids and basal oviraptorosaurs may eventually demonstrate that the former clade is either on the oviraptorosaurian stem or nested within basal Oviraptorosauria (Fig. 3), and convergently evolved 'avian characteristics' as a result of adaptation to an arboreal lifestyle. This is supported by the temporal distribution of known specimens (scansoriopterygids older than known oviraptorosaurs) and the results of a recent phylogenetic analysis, in which only one additional step was required to unite the scansoriopterygid *Epidexipteryx* with the Oviraptorosauria (Turner et al., 2012). The relatively short forelimbs and short hallux in *Zhongornis* may suggest this taxon is a basal scansoriopterygid, close to the divergence of this clade from basal oviraptorosaurs, although this is inconsistent with its occurrence in the Yixian. Alternatively, 'primitive' features may be

a result of the early ontogenetic stage of the holotype of *Zhongornis*.

3.5 *Zhongornis* and Confuciusornithiformes?

Recent large-scale phylogenetic analysis of Mesozoic birds have resolved *Zhongornis* as the sister taxon to Confuciusornithiformes (O'Connor et al., 2011). Support for the relationship is limited to two character state reversals (144: 1→0, ulna shorter than humerus; 156: 1→0, absence of a pisiform process), but this result nevertheless broaches the possibility that *Zhongornis* may be a juvenile confuciusornithiform. This clade does show a limited degree of overall similarity to *Zhongornis*, in that both have robust, edentulous skulls, with a long mandibular symphysis and a proportionately large alular metacarpal and digit. However, the overall morphology of the hand differs significantly between the two taxa, with different digital proportions and phalangeal formulas. *Confuciusornis* has a characteristically enlarged claw on the minor digit whereas in *Zhongornis* the unguals of the major and minor digits are subequal in size. The alular and minor digit unguals in *Confuciusornis* are large and recurved (smaller and weakly curved in *Zhongornis*), and a well-developed flexor tubercle, like that in *Confuciusornis*, is absent from the minor digit ungual in *Zhongornis*. Although the potential for comparison is limited since no juvenile specimens of *Confuciusornis* have been recognized, *Zhongornis* also lacks a fenestra perforating the deltopectoral crest of the humerus (also absent in the subadult holotype of *Eoconfuciusornis*, the oldest and most basal known confuciusornithiform), has more free caudal vertebrae than are present in *Confuciusornis*, and has well-developed acromial processes on the furcula. These differences suggest that these two taxa are in fact not closely related. Furthermore, the absence of any non-avian taxa in the dataset (apart from the family Dromaeosauridae, which was used as the outgroup) rendered the analysis of O'Connor et al. (2011) unable to explore potential relationships between *Zhongornis* and more basal maniraptorans.

3.6 Phylogenetic analysis

In order to test the strength of the morphological evidence that *Zhongornis* falls phylogenetically outside Aves, we added this taxon to the Xu et al. (2011) dataset (see Supplemental Information). The matrix contains 90 taxa, including *Zhongornis*, and 374 characters. The dataset was analyzed using TNT (Goloboff et al., 2008). We conducted a heuristic search retaining the single shortest tree from every 1000 trees followed by an additional round of tree bisection and reconnection (TBR) branch swapping. The first round of TBR produced 134 most parsimonious trees (MPTs) 1428 steps long; the second round of TBR produced a total of 540 MPTs 1428 steps long. A Nelson strict consensus tree was generated from the MPTs (Fig. 9; CI = 0.318; RI = 0.735).

The results largely concur with those of Xu et al. (2011), although relationships among basal maniraptorans are less fully resolved. Scansoriopterygidae is recovered as the sister taxon to Aves, with the two together forming the clade Avialae. In turn, Avialae

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and Deinonychosauria (which includes Archaeopterygidae) combine to form Paraves. Paraves forms a polytomy with Therizinosauroidea, a *Caudipteryx* + derived oviraptorosaur clade, and the basal oviraptorosaurs *Protarchaeopteryx*, *Incisivosaurus*, and *Similicaudipteryx*. *Zhongornis* is resolved as sister taxon to Avialae (Scansoriopterygidae + Aves) supporting our hypothesis that *Zhongornis* is closely related to scansoriopterygids. The basal position of *Zhongornis* may be exaggerated by the juvenile ontogenetic stage of the holotype. Although an oviraptorosaur + scansoriopterygid clade is not supported here, the addition of *Zhongornis* to the dataset has resulted in
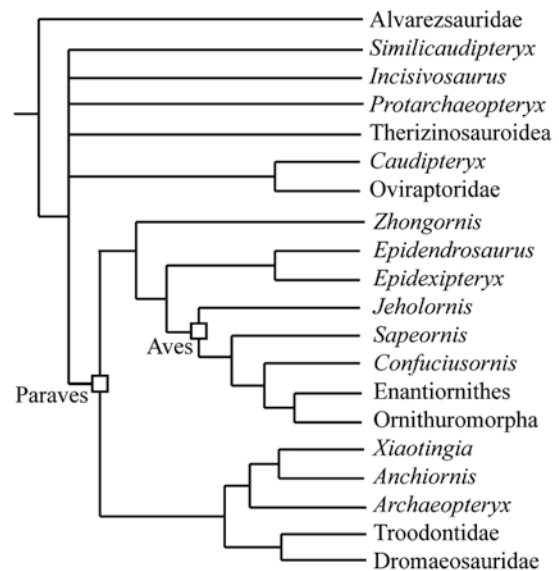

Fig. 9 Simplified strict consensus cladogram produced from the 540 MPTs (L = 1428 steps)

less resolution among basal members of the oviraptorosaur clade. A relationship between *Zhongornis* and Scansoriopterygidae is supported by six characters (101, 103, 166, 273, 317, and 325); however, scorings for most of these characters are ambiguous in *Zhongornis* because of missing data. The only one whose presence can be confirmed in *Zhongornis*, namely the fact that the minor digit is shorter than the major digit, is absent in *Epidendrosaurus*.

The poor preservation and juvenile status of the only known specimen of *Zhongornis* is a major problem that makes the phylogenetic position of this taxon hard to determine. Some 66% of the characters in the analysis could not be scored for *Zhongornis*, and many aspects of its osteology (e.g. degree of skeletal fusion, carpal morphology) might be subject to change over ontogeny. The similar condition of the holotype of *Epidendrosaurus* led some authors to suggest this taxon should not be included in cladistic analyses until new information is available (Turner et al., 2012). Given these limitations, the results of this analysis could be strongly affected by new information, particularly from adult specimens.

3.7 Pygostyle evolution in Aves

Zhongornis was originally described by Gao et al. (2008) as belonging to a new (unnamed) basal lineage of birds — a 'missing link' between birds with three manual claws and those with two, and between birds with a long boney tail and those with a pygostyle. The latter transition is one of the most morphologically obvious in the evolution of Aves, yet *Zhongornis* was the first taxon ever to be identified as a putative intermediate. All modern birds possess a pygostyle, a compound bone that forms the distal end of the reduced boney tail. The formation of this structure in living birds is not well known, and the number of caudal

vertebrae that come to be incorporated likely varies between species; in some taxa, a fairly large number of individual vertebrae apparently begin to chondrify separately before fusing into a single element (Maxwell and Harrison, 2008), while in other taxa the number is quite low (Brusatte et al., 2010). *Zhongornis* preserves a long boney-tail composed of approximately 14 vertebrae, the last four of which form an incipient pygostyle (Gao et al., 2008), and was accordingly interpreted as partially filling the morphological gap between birds with and without a pygostyle. The discovery of this taxon suggested that, in at least one basal avian lineage, reduction of the tail initially involved a decrease in the number of caudal vertebrae, rather than in their size. However, reinterpretation of the tail invalidates this hypothesis and leaves the fossil record devoid of clues to how tail reduction proceeded within Aves. Furthermore, we infer that approximately 20 caudal vertebrae were preserved in the holotype of *Zhongornis*, although the actual number may have been higher. The condition present in *Zhongornis* resembles that seen in scansoriopterygids (*Epidendrosaurus*, *Epidexipteryx*) and basal oviraptorosaurs (*Caudipteryx*), which also have proportionately short tails compared to basal paravians. The dichotomy in tail length lies mainly in the proportionate length of the distal caudal vertebrae, rather than in the number of caudals. Distally elongate caudal vertebrae appear to be absent from other theropod groups, and their presence in *Archaeopteryx* and *Jeholornis* supports a close affinity between Aves and Deinonychosauria. Therefore, both the hand proportions and tail morphology of *Zhongornis*, although strongly indicating this taxon is not a bird, may be plesiomorphic features inherited from more primitive theropods.

4　Conclusions

Revised anatomical interpretation of the tail and more detailed comparisons with non-avian dinosaurs strongly suggest that *Zhongornis haoae* is not a bird but a member or close relative of the enigmatic maniraptoran clade Scansoriopterygidae. Although the poor preservation and immature ontogenetic status of all known specimens of this clade prevent detailed comparisons, proportions of the hand support a close affinity with *Zhongornis*, while at the same time revealing significant differences between this genus and known basal birds. *Zhongornis* also bears some similarity to basal oviraptorosaurs, supporting the hypothesis that the Jurassic scansoriopterygids may be stem-group relatives of the Cretaceous Oviraptorosauria. This suggests that the Aves + Scansoriopterygidae clade, as resolved here including *Zhongornis*, may be an artifact of homoplasy and the currently limited information available for scansoriopterygids. Although we consider *Zhongornis* too poorly preserved and the current information too limited to definitively reassign this taxon to Scansoriopterygidae, we consider that there is ample evidence to strongly question the previous assignment of this taxon to Aves.

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早白垩世手盗龙类郝氏中鸟(恐龙：兽脚类)归入非鸟类似擅攀鸟龙类的再研究及擅攀鸟龙类和基干窃蛋龙类形态相似的讨论

邹晶梅　舒柯文

(中国科学院古脊椎动物与古人类研究所，中国科学院脊椎动物演化与人类起源重点实验室　北京　100044)

摘要：手盗龙类郝氏中鸟(*Zhongornis haoae*)的标本只有一件，并且为幼年个体，其最初被归入鸟类。然而对其解剖学的重新研究显示，郝氏中鸟与窃蛋龙下目(Oviraptorosauria)和擅攀鸟龙科(Scansoriopterygidae)具有很多相似的形态特征。中鸟的尾部虽然有所退化，但仍然很长，本文认为其约有20枚尾椎，其尾部的形态和比例都与尾羽龙(*Caudipteryx*)和耀龙(*Epidexipteryx*)相似。中鸟与基干窃蛋龙类的相似之处还包括：头骨短而高，小手指退化。在小翼掌骨的大小、手指的比例、坐骨不发育背侧和腹侧突起方面，中鸟与擅攀鸟龙类相似，而明显区别于中生代的鸟类。基于上述相似的形态特征以及基干窃蛋龙类和擅攀鸟龙类共有的其他特征，提出了窃蛋龙类和擅攀鸟龙类之间具有较近亲缘关系的假说。分支系统学的研究表明，相比于窃蛋龙类，中鸟与擅攀鸟龙科之间的亲缘关系更近，中鸟和擅攀鸟龙类都具有伸长的前肢和脚爪。有关中鸟的分类位置及其与擅攀鸟龙科之间确切关系的研究，还需要新标本的发现；本文对中鸟分类位置的讨论，也说明了基于幼年个体进行新种命名时所存在的问题。

关键词：白垩纪，兽脚类恐龙，擅攀鸟龙科，窃蛋龙下目，鸟纲，中鸟，尾部

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References

Agnolin F L, Novas F, 2013. Avian Ancestors: A Review of the Phylogenetic Relationships of the Theropods Unenlagiidae, Microraptoria, *Anchiornis* and Scansoriopterygidae. Berlin: Springer-Verlag. 1–96

Balanoff A, Norell M A, 2012. Osteology of *Khaan mckennai* (Oviraptorosauria: Theropoda). Bull Am Mus Nat Hist, 372: 1–77

Barsbold R, 1981. Toothless dinosaurs of Mongolia. Trans Joint Soviet-Mongol Paleont Exped, 15: 28–39

Barsbold R, Currie P J, Myhrvold N P et al., 2000. A pygostyle from a non-avian theropod. Nature, 403: 155–156

Baumel J J, Witmer L M, 1993. Osteologia. In: Baumel J J, King A S, Breazile J E et al. eds. Handbook of Avian Anatomy: Nomina Anatomica Avium. 2nd Ed. Cambridge: Nuttall Ornithological Club. 45–132

Brusatte S L, Nesbitt S J, Irmis R B et al., 2010. The origin and early radiation of dinosaurs. Earth Sci Rev, 101: 68–100

Chiappe L M, Ji S A, Ji Q, 2007. Juvenile birds from the Early Cretaceous of China: implications for enantiornithine ontogeny. Am Mus Novit, 3594: 1–46

Chiappe L M, Ji S A, Ji Q et al., 1999. Anatomy and systematics of the Confuciusornithidae (Theropoda: Aves) from the Late Mesozoic of northeastern China. Bull Am Mus Nat Hist, 242: 1–89

Clark J M, Norell M A, Chiappe L M, 1999. An oviraptorid skeleton from the Late Cretaceous of Ukhaa Tolgod, Mongolia, preserved in an avianlike brooding position over an oviraptorid nest. Am Mus Novit, 3265: 1–36

Czerkas S A, Yuan C, 2002. An arboreal maniraptoran from northeast China. In: Czerkas S J ed. Feathered Dinosaurs and the Origin of Flight. Blanding: The Dinosaur Museum. 63–95

Dececchi T A, Larsson H C E, Hone D W, 2012. *Yixianosaurus longimanus* (Theropoda: Dinosauria) and its bearing on the evolution of Maniraptora and ecology of the Jehol Fauna. Vert PalAsiat, 50(2): 111–139

de Queiroz K, 1985. The ontogenetic method for determining character polarity and its relevance to phylogenetic systematics. Syst Zool, 34(3): 280–299

Dyke G J, Norell M A, 2005. *Caudipteryx* as a non-avialan theropod rather than a flightless bird. Acta Palaeont Pol, **50**(1): 101–116

Elzanowski A, 2002. Archaeopterygidae (Upper Jurassic of Germany). In: Chiappe L M, Witmer L M eds. Mesozoic Birds: Above the Heads of Dinosaurs. Berkeley: University of California Press. 129–159

Gao C L, Chiappe L M, Meng Q J et al., 2008. A new basal lineage of Early Cretaceous birds from China and its implications on the evolution of the avian tail. Palaeontology, 51(4): 775–791

Goloboff P A, Farris J S, Nixon K C, 2008. TNT, a free program for phylogenetic analysis. Cladistics, 24: 774–786

He T, Wang X L, Zhou Z H, 2008. A new genus and species of caudipterid dinosaur from the Lower Cretaceous Jiufotang Formation of western Liaoning, China. Vert PalAsiat, 46(3): 178–189

Hopson J A, 2001. Ecomorphology of avian and nonavian theropod phalangeal proportions: implications for the arboreal versus terrestrial origin of bird flight. In: Gauthier J, Gall L F eds. New Perspectives on the Origin and Early Evolution of Birds. New Haven: Peabody Museum of Natural History. 211–235

Ji Q, Currie P J, Norell M A et al., 1998. Two feathered dinosaurs from northeastern China. Nature, 393: 753–761

Jones T D, Farlow J O, Ruben J A et al., 2000. Cursoriality in bipedal archosaurs. Nature, 406: 716–718

Kundrát M, 2007. Avian-like attributes of a virtual brain model of the oviraptorid theropod *Conchoraptor gracilis*. Naturwissenschaften, 94(6): 499–504

Longrich N R, Currie P J, Dong Z M, 2010. A new oviraptorid (Dinosauria: Theropoda) from the Upper Cretaceous of Bayan Mandahu, Inner Mongolia. Palaeontology, 53(5): 945–960

Lü J C, Tomida Y, Azuma Y et al., 2004. New oviraptorid dinosaur (Dinosauria: Oviraptorosauria) from the Nemegt Formation of southwestern Mongolia. Bull Natl Sci Mus Tokyo, Ser C: Geol Paleont, 30: 95–130

Maryanska T, Osmólska H, Wolsan M, 2002. Avialan status for Oviraptorosauria. Acta Palaeont Pol, 47(1): 97–116

Maxwell E E, Harrison L B, 2008. Ossification sequence of the common tern (*Sterna hirundo*) and its implications for the interrelationships of the Lari (Aves, Charadriiformes). J Morphol, 269(9): 1056–1072

Nesbitt S J, Turner A H, Spaulding M et al., 2009. The theropod furcula. J Morphol, 270(7): 856–879

Norell M A, Makovicky P J, 1999. Important features of the dromaeosaurid skeleton II: information from newly collected specimens of *Velociraptor mongoliensis*. Am Mus Novit, 3282: 1–45

O'Connor J K, Chiappe L M, Bell A, 2011. Pre-modern birds: avian divergences in the Mesozoic. In: Dyke G D, Kaiser G

1期

O'Connor & Sullivan: Reinterpretation of the Early Cretaceous maniraptoran (Dinosauria:
Theropoda) *Zhongornis haoae* as a scansoriopterygid-like non-avian, and morphological
resemblances between scansoriopterygids and basal oviraptorosaurs

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eds. Living Dinosaurs: the Evolutionary History of Birds. New Jersey: J. Wiley & Sons. 39–114

Osmólska H, Currie P J, Barsbold R, 2004. Oviraptorosauria. In: Weishampel D B, Dodson P, Osmólska H eds. The
Dinosauria. 2nd ed. Berkeley: University of California Press. 165–183

Persons W S, Currie P J, Norell M A (in press). Oviraptorosaur tail forms and functions. Acta Palaeont Pol, available online
04 Jan 2013 doi: http://dx.doi.org/10.4202/app.2012.0093

Sullivan C, Hone D W, Wang Y et al. (in press). The vertebrates of the Middle-Upper Jurassic Daohugou Biota of
northeastern China. J Vert Paleont

Suzuki S, Chiappe L M, Dyke G J et al., 2002. A new specimen of *Shuvuuia deserti* Chiappe et al., 1998 from the Mongolian
Late Cretaceous with a discussion of the relationships of alvarezsaurids to other theropod dinosaurs. Contrib Sci, 494:
1–18

Turner A H, Makovicky P J, Norell M A, 2012. A review of dromaeosaurid systematics and paravian phylogeny. Bull Am
Mus Nat Hist, 371: 1–206

Turner A H, Pol D, Clarke J A et al., 2007. A basal dromaeosaurid and size evolution preceding avian flight. Science, 317:
1378–1381

Vickers-Rich P, Chiappe L M, Kurzanov S, 2002. The enigmatic birdlike dinosaur *Avimimus portentosus*. In: Chiappe L M,
Witmer L M eds. Mesozoic Birds: Above the Heads of Dinosaurs. Berkeley: University of California Press. 65–86

Wellnhofer P, Tischlinger H, 2004. Das "Brustbein" von *Archaeopteryx bavarica* Wellnhofer 1993 — eine Revision.
Archaeopteryx, 22: 3–15

Xu X, 2006. Feathered dinosaurs from China and the evolution of major avian characters. Integr Zool, 1(1): 4–11

Xu X, Cheng Y N, Wang X L et al., 2002a. An unusual oviraptorosaurian dinosaur from China. Nature, 419: 291–293

Xu X, Norell M A, Wang X L et al., 2002b. A basal troodontid from the Early Cretaceous of China. Nature, 415: 780–784

Xu X, Norell M A, 2004. A new troodontid dinosaur from China with avian-like sleeping posture. Nature, 431: 838–841

Xu X, Ma Q Y, Hu D Y, 2010a. Pre-*Archaeopteryx* coelurosaurian dinosaurs and their implications for understanding avian
origins. Chin Sci Bull, 55: 3971–3977

Xu X, Zheng X T, You H L, 2010b. Exceptional dinosaur fossils show ontogenetic development of early feathers. Nature,
464: 1339–1341

Xu X, You H L, Du K et al., 2011. An *Archaeopteryx*-like theropod from China and the origin of Avialae. Nature, 475: 465–
470

Zanno L E, Makovicky P J, 2011. Herbivorous ecomorphology and specialization patterns in theropod dinosaur evolution.
Proc Nat Acad Sci USA, 108(1): 232–237

Zhang F C, Zhou Z H, Xu X et al., 2002. A juvenile coelurosaurian theropod from China indicates arboreal habits.
Naturwissenschaften, 89(9): 394–398

Zhang F C, Zhou Z H, Xu X et al., 2008. A bizarre Jurassic maniraptoran from China with elongate ribbon-like feathers.
Nature, 455: 1105–1108

Zheng X T, Wang X L, O'Connor J K et al., 2012. Insight into the early evolution of the avian sternum from juvenile
enantiornithines. Nat Commun, 3: 1116

Zhou S, Zhou Z H, O'Connor J K, 2013. Anatomy of the Early Cretaceous *Archaeorhynchus spathula*. J Vert Paleont, 33(1):
141–152

Zhou Z H, Farlow J O, 2001. Flight capability and habits of *Confuciusornis*. In: Gauthier J, Gall L F eds. New Perspectives

on the Origin and Early Evolution of Birds. New Haven: Peabody Museum of Natural History. 237–254

Zhou Z H, Wang X L, 2000. A new species of *Caudipteryx* from the Yixian Formation of Liaoning, northeast China. Vert PalAsiat, 38(2): 111–127

Zhou Z H, Wang X L, Zhang F C et al., 2000. Important features of *Caudipteryx* — evidence from two nearly complete new specimens. Vert PalAsiat, 38(4): 242–254

Zhou Z H, Zhang F C, 2002. Largest bird from the Early Cretaceous and its implications for the earliest avian ecological diversification. Naturwissenschaften, 89: 34–38

Zhou Z H, Zhang F C, 2003. Anatomy of the primitive bird *Sapeornis chaoyangensis* from the Early Cretaceous of Liaoning, China. Can J Earth Sci, 40(5): 731–747

【消息】

中国古生物学会第11次全国会员代表大会在浙江东阳召开

中国古生物学会第11次全国会员代表大会暨第27届学术年会于2013年11月15~17日在被誉为"中国恐龙之乡"的浙江东阳成功召开。来自全国各地高等院校、科研院所、能源与地质勘探和生产部门、博物馆、地质公园、化石保护以及出版等行业近80个单位450多名专家学者、科技工作者和研究生代表等参加了这次年会。

大会特邀6位知名学者做了大会学术报告，内容涉及蓝田生物群、寒武纪生物群、早期被子植物、古脊椎动物学、侏罗–白垩系海陆相地层对比和白垩纪温室气候研究等主题。会议收到论文摘要近300篇，设立23个分会场并安排主题报告近40个，口头学术报告195个，展版报告25个，有50多位专家担任工作会议和分会场主持人。年会研讨内容反映了我国古生物学近年来取得的新进展和新成果，涉及早期生命和多细胞演化，特异化石库及埋藏学，古生代生物多样性及其演化，二叠—三叠纪之交生态系统演变，热河与燕辽生物群研究进展，重大地史时期生物的绝灭与复苏，白垩纪生物群与K-T界线，中、新生代生物多样性与环境变化(含古人类学)，古生态学，古地理学以及古气候学，综合地层学，旋回地层与高分辨率地层，古植物学与孢粉学，微体古生物学及其应用，古脊椎动物类群的起源与演化，地球生物学与环境，分子古生物学，古生物化石数据库，古生物学教学与人才培养，古生物学博物馆与科普教育以及古生物化石及其保护等。

本次会议选举产生了由65位理事组成的中国古生物学会第11届理事会，以及由21人组成的常务理事会，并选举产生了第11届理事会负责人。

大会向3位科学家颁发了尹赞勋地层古生物学奖，向4位青年学者颁发了青年古生物学奖。另外有15位同学获得研究生优秀口头报告奖，4位同学获得研究生优秀展板报告奖，还表彰了8位学会活动积极分子。

浙江省化石资源丰富，国际标准层型剖面和点位(GSSP, 俗称"金钉子")以及恐龙化石举世闻名。本次大会还组织了浙江省内三条路线的野外地质考察活动。

（编辑部）