第 50 卷 第 1 期
2012 年 1 月

古 脊 椎 动 物 学 报
VERTEBRATA PALASIATICA

pp.25 – 37
figs.1 – 4

对长趾辽宁鸟的重新认识[1)]

邹晶梅
（中国科学院古脊椎动物与古人类研究所，脊椎动物进化系统学重点实验室 北京 100044）

摘要：早期发现于中国东北热河群的今鸟类化石多呈高度零散保存，本文对于惟一已知的长趾辽宁鸟（*Liaoningornis longidigitrus*）标本的研究表明，该分类单元实际上是反鸟类的成员。虽然材料保存较差且破碎，但缺失发达的胸骨、胫骨脊和退化的脚爪，显示其应该被排除于更为进步的鸟胸类（ornithothoracines）之外。辽宁鸟与所有已知的反鸟均有显著不同，但显示了与西班牙发现的 *Eoalulavis hoyasi* 的相似性：它们相似的胸骨特征表明二者可能存在较密切的关系，尽管与其他反鸟类的不同表明，这可能是个体发育造成的假相。由于辽宁鸟标本过于零碎，因此目前难以确定其在反鸟类系统发育中的位置。

关键词：义县组，反鸟类，今鸟类，今鸟形类，辽宁鸟

中图法分类号：Q915.865 **文献标识码：**A **文章编号：**1000 – 3118（2012）01 – 0025 – 13

A REVISED LOOK AT *LIAONINGORNIS LONGIDIGITRUS* (AVES)

Jingmai K. O'CONNOR
(*Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences* Beijing 100044 jingmai@ usc. edu)

Abstract Many of the earliest discovered ornithurine birds from the Jehol Group in northeastern China are highly fragmentary; this current study on the only known specimen of *Liaoningornis longidigitrus*, first described by Hou in 1997, indicates the taxon is in fact a member of Enantiornithes. Although based on fragmentary and poorly preserved material, the absence of a well-developed sternum, lack of developed cnemial crests on the tibiotarsi and reduced pedal unguals suggests *Liaoningornis* should be excluded from the more advanced ornithothoracine clade. The taxon remains distinct from all known enantiornithines, although it shows similarity to the Spanish taxon *Eoalulavis hoyasi*; shared features of the sternum suggest a close relationship between these two, although disparity from other enantiornithines suggests this may be an artifact of ontogeny. The only *Liaoningornis* specimen is too fragmentary to be able to make strong inferences about its placement within the diverse enantiornithine clade.

Key words Yixian Formation, Enantiornithes, Ornithurae, Ornithuromorpha, *Liaoningornis*

1 Introduction

The Jehol Group of northeastern China continues to be the world's richest source of knowledge on Mesozoic avifaunas (Zhang et al., 2003; Zhou and Zhang, 2006a; Chiappe, 2007). Multiple lineages of birds are recognized, each with their own intraclade diversity, ranging from

---

1）国家自然科学基金（批准号：41050110438）资助。

收稿日期：2010 – 11 – 22

primitive long-tailed birds to the close relatives of modern birds, the earliest known members of the clade Ornithurae (Ornithuromorpha). Although the fossil record suggests enantiornithines dominated this Early Cretaceous ecosystem (Zhou and Zhang, 2006a; O'Connor, 2009), the discovery of more advanced ornithurine taxa has continued, steadily revealing a diversity of species (e. g. *Hongshanornis*, *Yanornis*, *Yixianornis*, *Archaeorhynchus*, *Jianchangornis*; Zhou and Zhang, 2001, 2005, 2006b; Zhou et al., 2009). Early discoveries assigned to Ornithurae were very fragmentary (e. g. *Chaoyangia*, *Liaoningornis*, *Songlingornis*; Hou and Zhang, 1993; Hou, 1997a, b), but more recent finds have been largely complete (e. g. *Hongshanornis*, *Yanornis*, *Yixianornis*, *Archaeorhynchus*; Zhou and Zhang, 2001, 2005, 2006b). The absence of available comparative material at the time of the earlier discoveries made it difficult to make taxonomic assignments and, for this reason, restudying fragmentary specimens in light of current information can lead to new insights on fossil taxa (O'Connor et al., 2011).

One of the first of the fragmentary ornithurine discoveries was the bizarre *Liaoningornis longidigitrus* IVPP V 11303 (Hou, 1997a) (Figs. 1, 2). This taxon, first described as a 'carinate' bird, is now widely considered to be an ornithurine (Zhou and Hou, 2002; Clarke et al., 2006; Zhou and Zhang, 2006a). The holotype and only known specimen is fairly incomplete, however it does preserve several autapomorphies, primarily bizarre and unique morphologies of its sternum. At the time the *Liaoningornis* specimen was published only a few Chinese ornithurine specimens were known (a foot from *Gansus*, and the incomplete and poorly preserved *Chaoyangia*; Hou and Liu, 1984; Hou and Zhang, 1993), none of which preserved sternal material for comparison. *Liaoningornis* was nevertheless assigned to Ornithurae (Hou et al., 1996; Hou 1997a), although this taxonomic assignment was never rigorously supported by morphological characters (the proposed characters in support of this assignment do not define Ornithurae [Haeckel, 1866; *sensu* Gauthier and de Queiroz, 2001], e. g. sternum with carina; Hou, 1997a). The possible exception is one character presented by Hou (1997a), a broad sternal margin of the coracoid, which does differentiate most ornithurines from enantiornithines [Walker, 1981]. The original diagnosis was subsequently revised in light of more recent discoveries (Zhou and Hou, 2002) and *Liaoningornis* is currently defined as follows: smaller than *Cathayornis*; elongate sternum with a keel extending along its full length; craniolateral processes of sternum long; sternum broad cranially, caudally narrowing progressively defining a large deep lateral notch on each side; sternum with laterally expanded xiphoid process; tarsometatarsus short and about half as long as tibiotarsus; tarsometatarsus fused at both ends but not along a majority of the shaft; and claws curved. This diagnosis, while able to distinguish *Liaoningornis* from other Mesozoic birds based on sternal characters, fails to provide definitive evidence for its inclusion within Ornithurae. For example, an elongate keeled sternum is plesiomorphic to Ornithothoraces [Chiappe and Calvo, 1994], and a proximally and distally fused tarsometatarsus that is unfused medially does not characterize any group of birds, with ornithurines typically possessing fully fused tarsometatarsi (in the absence of a complete growth series, degree of fusion is more likely to reflect ontogeny than taxonomy and thus a poor diagnostic character). In addition, all known Jehol ornithurines are larger than *Cathayornis*, with *Liaoningornis* representing a distinct outlier in body size (Zhou and Zhang, 2006a).

Since *Liaoningornis* was described, it has not been extensively restudied (Zhou and Hou, 2002; Zhou and Zhang, 2006a). It has, however, appeared in several cladistic analyses, which typically resolve it within Ornithurae (Zhou and Zhang, 2005, 2006b). However, one previous analysis considered this taxon as a basal pygostylian, diverging earlier than *Confuciusornis* (You et al., 2006), and others have placed it within Enantiornithes (O'Connor, 2009; You et al., 2010), highlighting the need for a reassessment of this taxon. The continued discovery of new, well-preserved specimens of ornithurine birds has, in the meantime, lead to a fairly extensive understanding of basal ornithurine morphologies; in particular the sternum is

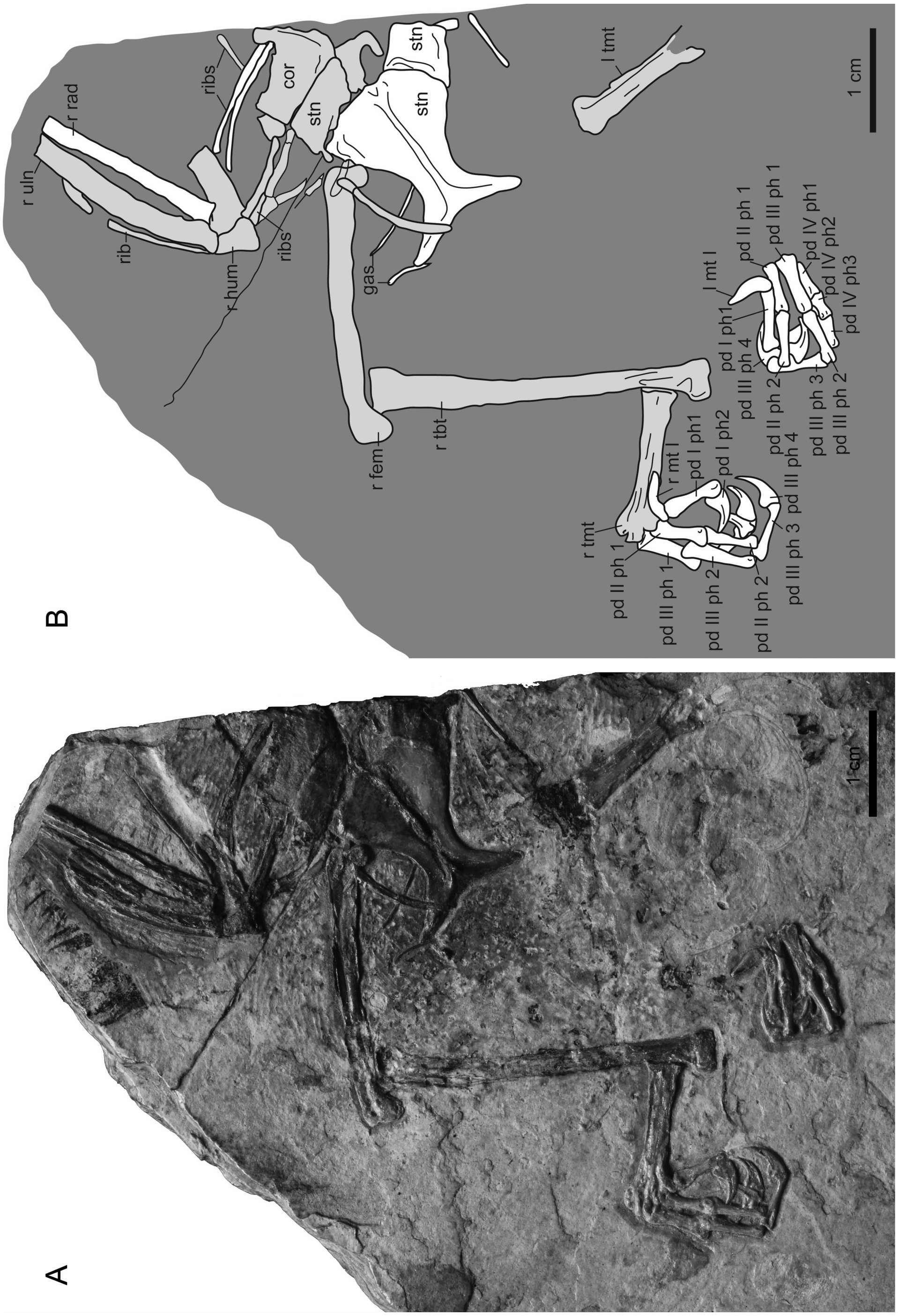

Fig. 1 Photograph (A) and camera lucida drawing (B) of the main slab of IVPP V 11303

Anatomical abbreviations: cor. coracoid; fem. femur; gas. gastralia; hum. humerus; mt I-IV. metatarsals I-IV; pd I-IV ph 1-4. pedal digits I-IV first-fourth phalanx; rad. radius; stn. sternum; tbt. tibiotarsus; tmt. tarsometatarsus; uln. ulna; r. right; l. left

Dark grey indicates matrix, white represents bone and lightgrey indicatespoor preservation

now well-known, as most recent discoveries preserve this element (e. g. the holotypes of *Yixianornis*, *Yanornis*, *Hongshanornis*, *Longicrusavis* and *Archaeorhynchus*, and new specimens of *Gansus*) (Hou and Liu, 1984; Zhou and Zhang, 2001, 2005, 2006b; O'Connor et al., 2010). Here the bizarre morphology of *Liaoningornis longidigitrus* is re-evaluated in light of recent discoveries and a re-examination of the holotype.

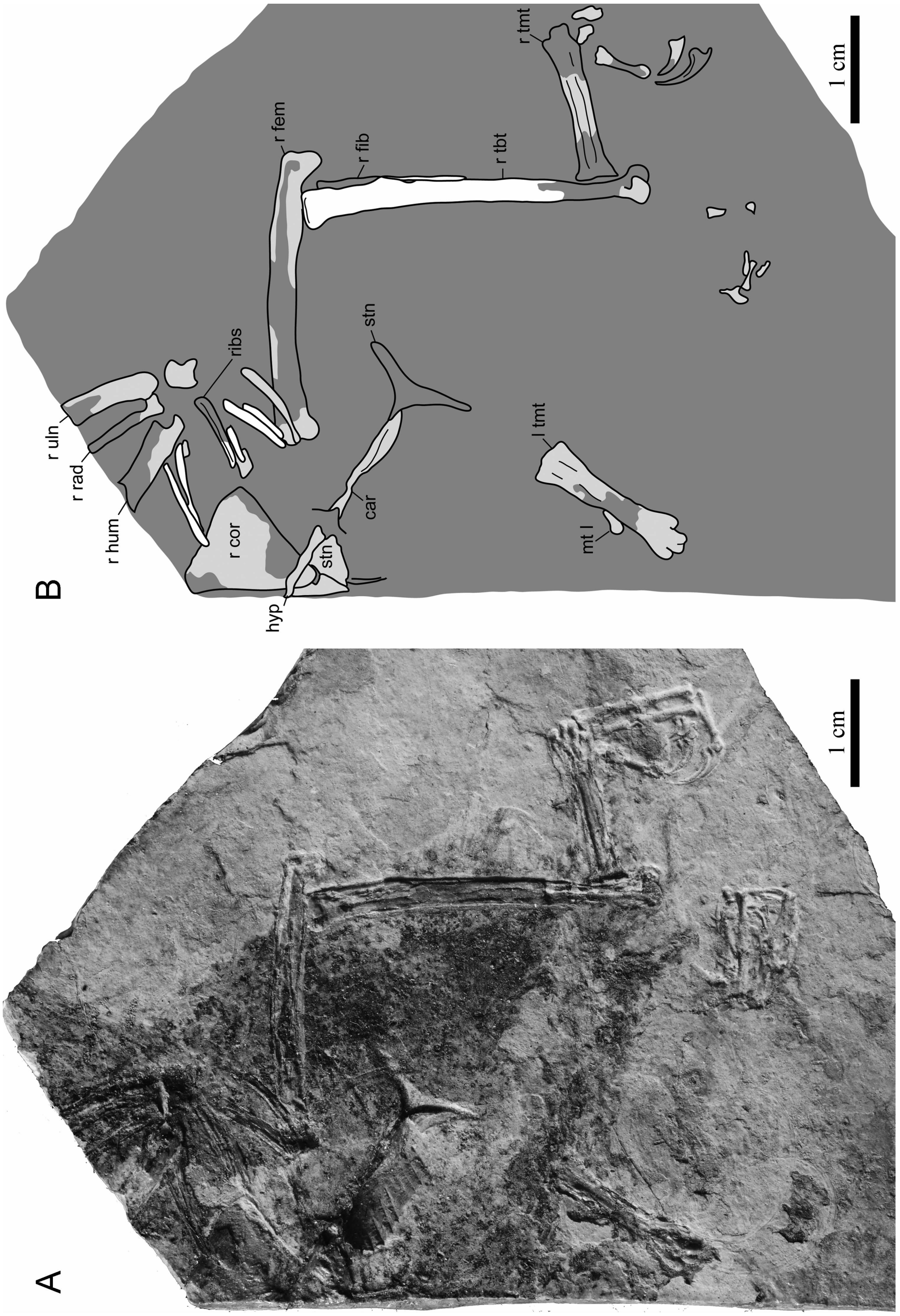

Fig. 2 Photograph (A) and camera lucida drawing (B) of the counterslab of IVPP V 11303
Anatomical abbreviations not listed in fig. 1: car. carina; fib. fibula; hyp. hypocleidium

Institutional abbreviations FRDC, Fossil Research and Development Center, Third Institute of Geology and Mineral Resources, Gansu Provincial Bureau of Geology and Mineral Resources, Lanzhou, China; GMV, Geological Museum of China, Beijing, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthroplogy, Beijing, China; LH, Las Hoyas Collection, Museo de Cuenca, Cuenca, Spain.

2 Morphology

The only known specimen of *Liaoningornis longidigitrus* (IVPP V 11303) is a small individual in a slab and counterslab preserving a partial skeleton of recrystallized bone in ventral view (Hou, 1997a)(Figs. 1, 2). The specimen preserves only the distal part of the right coracoid, the sternum, a partial right wing, the complete left hindlimb, and the right foot (Fig. 1). Some feather impressions are preserved in the counterslab near to the right tibiotarsus (Fig. 2A). The bones are not well-preserved; most elements are either largely abraded (partial wing), broken (tibiotarsus), or split between the two slabs (coracoid). The poor preservation of the specimen is exacerbated by a shiny coat of glue that obscures contacts between individual elements and the degree of fusion in the tarsometatarsus.

The coracoid is missing its proximal half and is poorly preserved, split between the two slabs (Figs. 1, 2). The sternal margin of the coracoid appears fairly wide, however, because the bone is incomplete no ratio can be calculated for comparison and thus this character is ambiguous. The lateral margin is slightly concave proximally and slightly convex distally; the sternal margin is straight. A sternolateral process is absent. The coracoid has been flattened so the presence of a dorsal fossa cannot be determined. A curved element extending from the right coracoid to the humerus has been interpreted previously as the scapula (Hou, 1997a); closer examination of this bone reveals that it is in fact two ribs, proximally in contact, but distally, where they are more poorly preserved, diverging so that they do not contact along their distal third (Fig. 3).

The sternum is nearly complete and defines the specimen apart from other known taxa. It is shaped like a spade (goblet) and caudal trabeculae are absent (Fig. 1). The rostral margin is parabolic but very low so that its midline is not markedly rostral to the craniolateral corners of the sternum (Figs. 1-4). From the left craniolateral margin projects a thin strap-like piece of bone; this has been interpreted as a sternolateral process (Fig. 3)(Zhou and Hou, 2002). This region of the specimen is very difficult to interpret because it is unusual and poorly preserved. A faint margin can be determined between the process and the sternum suggesting that this process is an L-shaped bone fragment, preserved closely pressed against and overlapping the proximal lateral margin of the sternum, and is not a true process of the sternum (Fig. 3C). A similar craniolateral process is absent on the right side of the sternum, where instead a rib is preserved articulating laterally, supporting this current interpretation. In the counterslab there are impressions of two rib fragments that are contiguous with the preserved margin of the right sternum (Fig. 2). Given this evidence, the presence of a diagnostic long craniolateral process is equivocal and here considered absent (*contra* Hou, 1997a; Zhou and Hou, 2002).

The sternum is broad proximally but sharply tapers into a thin waist; distally the xiphoid process is expanded laterally so that the xiphial region has the shape of an inverted T and the lateral margins of the sternum are deeply concave (Zhou and Hou, 2002)(Figs. 1-3). The expanded caudal margin is nearly perpendicular to the long axis of the sternum; the two laterally oriented rami of the xiphoid process are directed slightly distally so that the caudal margin is gently concave (Figs. 1-3). The ventral surface bears a well-developed keel that diverges distally onto the xiphoid process and forms a distinct ventrally projecting labum on the caudal margin (Figs. 1-3). Most of the height of the keel is broken off and preserved in the counterslab (Fig. 2). Approximately a quarter of its length from the cranial margin, the rostral end of the keel diverges into a narrow fork and does not continue further proximally (*contra* Zhou and Hou, 2002). In the counterslab, a rod-like bone is preserved descending almost to the level of the forked keel; in agreement with Hou (1997a), this bone is interpreted as the hypocleidium of the furcula (Fig. 3B).

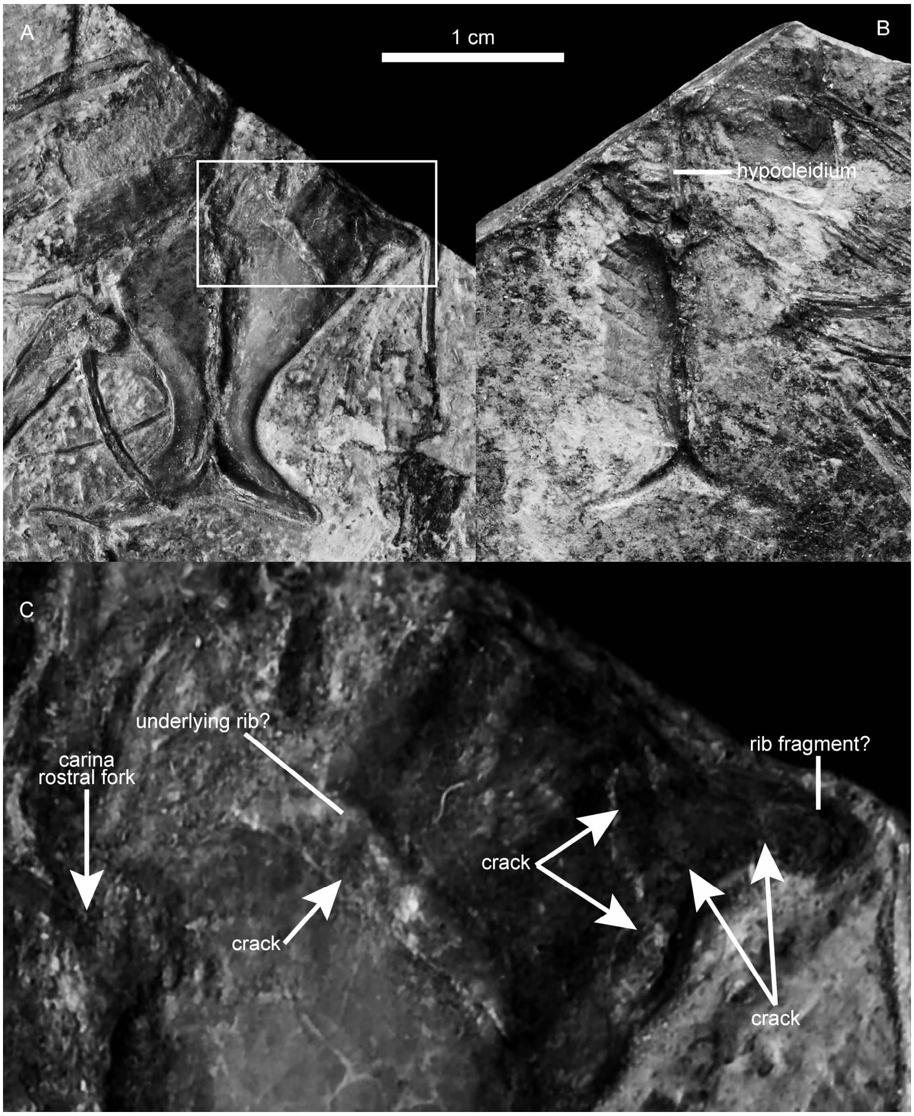

Fig. 3 Close up photographs of the sternal region of the holotype of *Liaoningornis longidigitrus* IVPP V 11303
A. main slab; B. counterslab; C. close up of rectangular region highlighted in A (main slab)
Cracks are indicated with arrows

The rostral fifth of the sternum is separated from the rest, and was described as a possible "presternum" bone by Hou (1997a). On the right, a crack runs across the sternum, separating the rostral margin from the main sternal body (Figs. 1-3). In the corresponding area on the left, a raised line of bone results from an underlying rib fragment; just distal to this rib fragment, the sternum bears a clean, straight crack that parallels the raised part of the sternum, as well as the articular margin for the coracoid (although a groove for the articulation with the sternum is not visible, *contra* Hou, 1997a) (Fig. 3C). This crack is interpreted as the result of compression of the sternum over the underlying rib fragment; the preserved pieces of sternum are reconstructed as having formed a single element in life (Fig. 4). Hou (1997a) also noted these cracks and his statement regarding the presternal bone was equivocal; although either

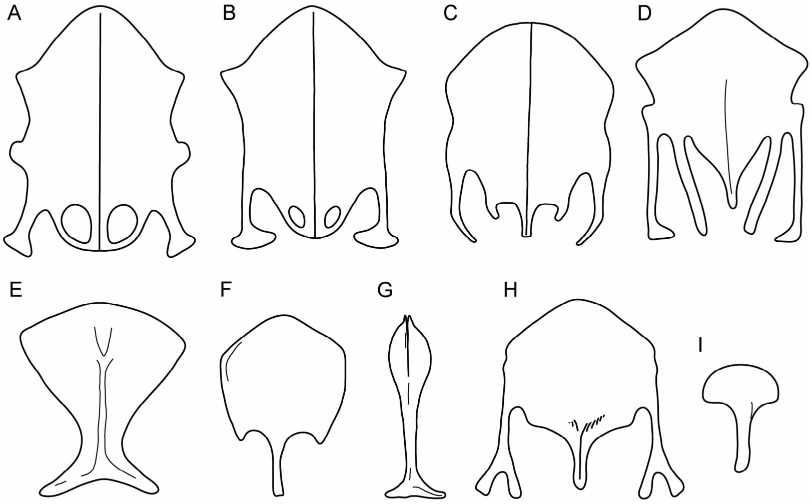

Fig. 4 Reconstructions of Early Cretaceous bird sterna
A. ornithurine *Yixianornis*; B. ornithurine *Yanornis*; C. ornithurine *Hongshanornis*; D. ornithuromorph FRDC-05-CM-021; E. *Liaoningornis*; F. enantiornithine *Eoenantiornis*; G. Spanish enantiornithine *Eoalulavis*; H. enantiornithine *Rapaxavis pani*; I. juvenile enantiornithine GMV 2159. Sterna not figured to scale

interpretation is plausible, to date no presternal bone has been identified in any juvenile enantiornithine or other Mesozoic bird.

A few sternal ribs are preserved, but no uncinate processes can be identified. A few thin rib elements preserved near the distal right half of the sternum are interpreted here as gastralia.

Only the distal-most humerus and proximal halves of the ulna and radius are preserved from the wing. The humerus is badly abraded but it appears its distal margin was angled relative to the long axis of the bone. The ulna is bowed and more robust than the straight radius. The width of the radius is half that of the ulna.

The femur is long, 82% the length of the tibiotarsus. It is preserved in craniomedial view, preventing the identification of a posterior trochanter (one characteristic of enantiornithines birds). The medial surface of the femoral head appears to be deeply concave, although whether this is for ligamental attachment (Hou, 1997a) or abrasion cannot be determined.

The tibiotarsus is preserved in craniomedial view; this element is poorly preserved as a partial impression with some bone remaining. The proximal end is crushed and most of the bone is missing, however no cnemial crests are visible in the voids. Due to preservation it cannot be said definitively that these crests were absent, however, if they were present, they would not have been extensive, lacking significant cranial or proximal projection. Whether, or not, the proximal tarsals were fully fused to the tibia also remains uncertain; however, the faint outline of the triangular ascending process of the astragalus can be discerned (Fig. 1B) which indicates fusion was incomplete. Distally, the condyles have been completely abraded away although their preserved outlines suggest they were large and bulbous (Fig. 2B), consistent with other enantiornithines (e.g. *Rapaxavis*, *Soroavisaurus*, *Qiliania*) (Chiappe, 1993; Morschhauser et al., 2009; Ji et al., 2011).

The tarsometatarsus is approximately half the length of the tibiotarsus. The distal tarsals appear fully fused to the metatarsals but the degree of intermetatarsal fusion is unclear. Hou (1997a) reported the distal tarsometatarsus as "unfused" while Zhou and Hou (2002) described this bone as "fused proximally and distally and unfused medially." The poor preservation and glue make this region difficult to interpret. However, while contacts are obscured in some areas, the metatarsals can easily be identified for most of their length, especially on the left tarsometatarsus and in the counterslab (which does not appear to have been coated in glue) (Fig. 2). The tarsometatarsus is reinterpreted as fused proximally and poorly fused along the lengths of the metatarsals, a morphology consistent with other enantiornithines (Chiappe, 1993; O'Connor, 2009). Proximally, a well-developed intercotylar eminence is absent. Metatarsals II, III and IV are coplanar and metatarsal III is not plantarly displaced. The mediolateral width of metatarsal III exceeds that of II and IV, which appear subequal. The third metatarsal is also the longest, followed by IV and then II. The medial surface of the right metatarsal II swells craniomedially, interpreted as the attachment site of the M. *tibialis cranialis*. The first metatarsal is P-shaped, and articulates on the caudomedial surface of metatarsal II. The articular surface of metatarsal I for metatarsal II is strongly concave. The distal end of the metatarsal is caudally deflected. The two articular surfaces of the first metatarsal are nearly parallel so that the hallux would have been caudomedially oriented. The first metatarsal is more than one quarter the length of the tarsometatarsus; on the right it appears slightly disarticulated, as it is preserved overlapping the cranial surface of metatarsal II. The distal articular surface ends proximal to that of the other metatarsals.

The pedal digits are robust and bear relatively large and recurved unguals (Fig. 1). The pedal phalangeal formula is 2-3-4-5-x as in other Mesozoic birds. The first phalanx of the hallux is the most robust and the longest in the foot. The first phalanx of the second digit is more robust but shorter than the penultimate phalanx of the same digit. The third digit is the longest, formed by three robust long phalanges followed by a claw; the first of these appears the most robust, while the middle phalanx is the shortest and the penultimate phalanx is the longest ("subequal" to the first) but the most slender. The fourth digit is covered by the others; however, it appears not to be longer than the third digit and to bear a claw smaller than the other toes. The proximal three phalanges are visible on the left; the first phalanx is longer than the following two, which are subequal.

3 Discussion

Comparison with other Mesozoic birds The morphology of the sternum is the most distinctive feature of *Liaoningornis* and thus comparisons begin with this element. When this specimen was uncovered, no other Early Cretaceous ornithurine sterna were known (Hou, 1997a). Now a majority of specimens preserve this element, revealing a fairly conservative morphology with, unlike their sister clade the enantiornithines, limited variation between the known Early Cretaceous ornithuromorphs. Nearly every taxon possesses a craniocaudally elongate, rectangular, largely imperforate sternum with a pronounced ventrally projecting carina (Fig. 4A-C). Lateral trabeculae are typically short, while intermediate trabeculae are long, although often no longer free, curving in medially to demarcate a pair of caudal sternal fenestrae (Fig. 4; e. g. *Yanornis*, *Yixianornis*, *Songlingornis* and *Gansus*). A second morphology has been more recently recognized (Zhou and Zhang, 2006b; You et al., 2010); in these specimens the sternum bears deep caudal notches, as in some enantiornithines, and thus the imperforate body of the sternum is proportionately much shorter (Fig. 4D). These taxa differ from enantiornithines in that the intermediate trabeculae of the sternum are still very long, reaching or surpassing the distal end of the xiphoid process (Zhou and Zhang, 2006b; You et al., 2010). Enantiornithines, in contrast with most ornithurines, have less massive sterna formed by a short rectangular imperforate region proximally with elongate lateral trabeculae and rudimentary intermediate trabeculae extending caudally, and a small caudally restricted carina (Fig. 4H) (a well-developed, cranially projecting carina is known in a single Late Cretaceous taxon, *Neuquenornis*; Chiappe and Calvo, 1994; O'Connor, 2009).

Enantiornithines, on the other hand, possess a wide range of sternal morphologies including several significant departures from the typical morphology, such as the spear-shaped sternum of *Eoalulavis* (Fig. 4G), the moose-antler distal expansions of the lateral trabeculae in *Longirostravis*, *and the very long and laterally splayed trabeculae in the sternum of Elsornis* (Chiappe et al., 2007). Craniolateral processes of the sternum, when present in ornithothoracines, typically are triangular craniolateral projections; this feature is more common among ornithurines, although the shape of this purported process in *Liaoningornis* is not consistent with any previously recognized morphology (Fig. 4).

The sternal morphology of *Liaoningornis* represents a significant departure from other recognized ornithurines and bears a strong resemblance to the bizarre sternum of the Spanish Early Cretaceous enantiornithine *Eoalulavis hoyasi* (Sanz et al., 1996), which is itself quite different from other known enantiornithines. The completeness of the holotype (and only known specimen), however, allows the specimen to be easily referred to Enantiornithes (Sanz et al., 1996). The sternum of *Eoalulavis* differs from *Liaoningornis* in that it is overall much more narrow; proximally, it lacks ossified coracoidal sulci on the rostral margin as well as a craniolateral process, and its widest point is the caudal margin (whereas it is the rostral margin in *Liaoningornis*). The sternum of *Eoalulavis* also possesses a deep and narrow mid-line notch that extends its proximal third, contiguous with a low, caudally restricted keel. Because the rostral midline is poorly preserved, it is unclear whether, or not, the sternal body possessed a deep notch in IVPP V 11303, however the keel at least, forms a narrow rostral notch (Figs. 3C, 4E). The keel is forked rostrally in a number of enantiornithines (e. g. *Concornis*, *Elsornis*), however in these taxa the diverging keel demarcates an angle of approximately 40°-60° (53° in *Elsornis*); the notch in *Eoalulavis* and in the keel of *Liaoningornis* form a much narrower angle of approximately 8° in the former and 25° in the latter. As in *Liaoningornis*, the keel in *Eoalulavis* extends for nearly the entire length of the sternum and is continuous with the T-shaped xiphoid process, the caudal margin of which is slightly concave. The sternum of *Liaoningornis* and *Eoalulavis* both lack caudal trabeculae; within Ornithothoraces, the absence of this feature is only recognized in enantiornithine taxa (e. g. *Eoenantiornis*, *Eoalulavis*, and clear juveniles GMV 2158, GMV 2159, and "*Liaoxiornis*")(Fig. 4F, G, I).

Coracoidal morphology has been used previously to align *Liaoningornis* with Ornithurae (Hou, 1997a). The sternal margin of the coracoid has been described as wide; generally speaking, comparing ornithurines and enantiornithines, the coracoids of the latter are much narrower, deeply excavated dorsally, and typically have shorter sternal margins. Unfortunately, the presence of a relatively wide sternal margin of the coracoid cannot be confirmed in IVPP V 11303 due to the incomplete preservation of this bone, and thus this character cannot be used in support of an ornithurine assignment for *Liaoningornis*. However, the sternolateral margin of the coracoid is simple, lacking a rudimentary (e. g. *Archaeorhynchus*) or true lateral process (e. g. *Yixianornis*, *Hongshanornis*) like that in most sympatric ornithurines (exception, *Schizooura*; Zhou et al., 2012). In contrast, most enantiornithines do not possess this feature, with the exception of the basal *Protopteryx*, which possesses a small expansion of the sternolateral margin reminiscent of the lateral process in ornithurines (Zhang and Zhou, 2000). Furthermore, the preserved morphology of the lateral margin in IVPP V 11303, slightly concave proximally, and slightly convex distally, is comparable to the morphology in *Eoalulavis* as well as some other enantiornithines (i. e. *Elsornis*, *Concornis*). Furthermore, a fragment of bone has been interpreted as the hypocleidium of the furcula; although there is not enough information to make this identification unequivocal, the presence of an elongate hypocleidium would also suggest an enantiornithine affinity for the specimen (a short hypocleidium is definitively known in only a single Early Cretaceous ornithurine, *Schizooura*; Zhou et al., 2012). A curved scapula is, on the other hand, characteristic of ornithurines but the curved bone previously interpreted as this element (Hou, 1997a) is reinterpreted here as two closely associated ribs; no scapula is preserved.

The angled distal margin of the humerus is consistent with enantiornithines that have an enlarged flexor process (e. g. *Alexornis*, *Vescornis*, *Longirostravis*) (Brodkorb, 1976; Zhang et al., 2004; Hou et al., 2004). This feature is also present in *Eoalulavis*. The tibiotarsus does not appear to possess prominent cnemial crests, although small, low cnemial crests like that of some enantiornithines cannot be ruled out (e. g. *Soroavisaurus*). All known basal ornithurines, even those who lack derived features such as a globe-shaped humerus or a rostrocaudally elongate sternum (e. g. *Archaeorhynchus*), possess prominent cnemial crests (e. g. *Longicrusavis*, *Yixianornis*, *Yanornis*, *Jianchangornis*).

Distally the possibly incomplete fusion of the tibiotarsus and tarsometatarsus suggest an enantiornithine assignment, as these compound bones are fully fused in nearly every ornithurine, with the exception of *Archaeorhynchus* that is known from a juvenile specimen (Zhou and Zhang, 2005). However, given that the ontogenetic age of the holotype of *Liaoningornis* is unknown, this character is not very diagnostic. The morphology of the tarsometatarsus, however, is also consistent with enantiornithines; the metatarsals are aligned in the same plane (metatarsal III proximally not plantarly displaced as in ornithurines, i. e. *Yanornis*, *Longicrusavis*, *Patagopteryx*) (Chiappe and Calvo, 1989), an intercotylar eminence is absent, and the tubercle for the M. *tibialis cranialis* is proximodistally elongate, and located on metatarsal II approximately 20% from the proximal end (e. g. *Rapaxavis*, *Longipteryx*, *Vescornis*). In ornithurines, this attachment site is typically much smaller, more proximally located, and completely on the dorsal surface of metatarsal III (e. g. *Longicrusavis*, *Gansus*, *Ichthyornis*).

The size and proportions of the pedal phalanges and unguals are also more consistent with enantiornithines than with ornithurines; the distal elongation of the phalanges within the digit, and the large size and strong degree of curvature of the claws, are both consistent with Early Cretaceous enantiornithines (e. g. *Concornis*, *Longipteryx*, *Rapaxavis*). Although some extant ornithurines share these morphologies (Hopson, 2001), Early Cretaceous taxa typically have proximally elongated pedal phalanges and small, weakly recurved claws (e. g. *Hongshanornis*, *Yanornis*, *Yixianornis*, *Jianchangornis*).

Phylogenetic placement Recent cladistic analyses have all differed in the phylogenetic placement of *Liaoningornis* (You et al., 2006, 2010; Zhou and Zhang, 2005, 2006b), likely a combined result of the fragmentary nature of the only specimen and the objectiveness of cladistic analyses. Analyses by Zhou and Zhang (2005, 2006b) consistently placed *Liaoningornis* in a clade with other ornithurines. Analyses by You et al. (2006, 2010) have differed; an earlier, smaller analysis resolved *Liaoningornis* as a basal pygostylian. A more recent analysis, which dealt with the discovery of a new ornithurine sternum, resolved *Liaoningornis* with enantiornithines, forming a clade with *Eoalulavis* (You et al., 2010). This node is weakly supported by a single character regarding the caudal morphology of the sternum (expanded into a T-shape), but receives unambiguous support from this one character (You et al., 2010). An enantiornithine analysis that included all valid taxa and a large ornithurine in-group resolved the same sister relationship between *Eoalulavis* and *Liaoningornis* (O'Connor, 2009). Morphological comparison with other Cretaceous birds most strongly aligns *Liaoningornis* with enantiornithines, although the specimen does not definitively preserve any synapomorphies of the clade (e. g. minor metacarpal extending beyond the distal margin of major metacarpal, Y-shaped furcula). Because cladistic matrices reflect morphology, phylogenetic support for such a hypothesis will always be limited until new *Liaoningornis* material is discovered.

This hypothesis has been suggested not only through morphology and cladistics, but through morphometrics; a recent principle component analysis on the morphology of the tarsometatarsus in living birds applied to Mesozoic taxa has also suggested *Liaoningornis* be more closely aligned with enantiornithines than ornithurines (Zhang, 2006). In this analysis, *Liaoningornis* represents a distinct outlier from other known ornithurines but groups well within the enantiornithines. Alternatively, this could simply be an ecological signature, as could be several of the morphologies used to align *Liaoningornis* with this clade (e. g. morphology of the pedal phalanges). Nevertheless, resolution of this debate is important because current hypotheses cite *Liaoningornis* as the only Early Cretaceous evidence that ornithurines shared the arboreal-perching ecological niche with enantiornithines (Zhou and Zhang, 2006a).

Although there are no characters that allow us to definitively assign *Liaoningornis* to Enantiornithes, the preserved combination of features strongly suggests such a relationship, while clear diagnostic features of ornithurines are entirely lacking from the specimen. Given the absence of any true enantiornithine synapomorphies preserved in IVPP V 11303, it would be most parsimonious to await new material to support this reassignment. Such a discovery, however, may take decades—the only known specimen was collected over 15 years ago and despite continuous collecting in the region, no referred material has surfaced. *Liaoningornis* is thus reassigned to Enantiornithes with the recommendation that researchers use this taxon with caution, especially when forming evolutionary hypotheses that may rely upon it.

Systematic paleontology (revised)

Aves Linnaeus, 1758

Enantiornithes Walker, 1981

Ord. and Fam. Indet.

***Liaoningornis longidigitrus* Hou, 1997a**

Revised diagnosis A small enantiornithine with the following unique combination of characters: small, imperforate sternum lacking trabeculae; T-shaped xiphoid process; proximally forked, ventrally projecting keel that does not extend to the rostral margin; keel low distally and continuous with T-shaped xiphoid process; femur 82% of tibiotarsus; metatarsal I P-shaped with nearly parallel articular surfaces; large curved claws.

Implications The possible reassignment of *Liaoningornis longidigitrus* to Enantiornithes not only increases diversity in the latter clade, but also strongly affects existing hypotheses regarding avian evolution that have incorporated this taxon. For a long time, *Liaoningornis* was considered the oldest and earliest phylogenetic divergence within ornithurine birds (Hou et al., 1996; Zhou and Zhang, 2006a). This widely accepted inference regarding the phylogenetic position of this taxon has been used to suggest that basal ornithurines were small (Zhou and Zhang, 2006a) and arboreal, an ecology retained ancestrally from closely related non-avian dinosaurs (Hou et al., 1996; Zhou and Zhang, 2006a). This also implies that the cursoriality of ornithurines and their large size are derived features, and provides support for an arboreal origin flight. However, the reassignment of this taxon to Enantiornithes would mean that the fossil record no longer supports these hypotheses.

The similarity between the sterna of *Eoalulavis* and *Liaoningornis* (Fig. 4) suggests a relationship between the two taxa, despite the temporal and geographical separation of the two specimens. Unfortunately, the poor preservation of the *Liaoningornis* holotype prevents the identification of additional features to support such a relationship. The morphology of the sterna of these two taxa is not only highly consistent, but also distinct from sympatric taxa (e. g. *Concornis* from Las Hoyas, Spain; *Longirostravis*, *Protopteryx*, and *Vescornis* from the Yixian Formation), all of which possess trabeculae, with the exception of juvenile specimens (Chiappe et al., 2007) and the controversial *Eoenantiornis* (IVPP V 11537; Hou et al., 1999; Zhou et al., 2005; O'Connor, 2009). The sternum of *Eoenantiornis* is interpreted as lacking trabeculae (Hou et al., 1999; *contra* Zhou et al., 2005; O'Connor, 2009); the illustrated trabecula in Zhou et al. (2005) is interpreted here as the distal end of the right humerus (as in Hou et al., 1999). The morphology in IVPP V 11537 (Fig. 4F) is reminiscent of that in early juvenile enantiornithines (Chiappe et al., 2007). In all published juvenile enantiornithines, the sternum is small and incomplete (Fig. 4I); the bone possesses a rounded rostral margin, followed by a very short corpus, ending in a long xiphoid process (e. g. GMV 2158, GMV 2159, '*Liao-*

xiornis')(Hou and Chen, 1999). This is essentially the morphology preserved in the holotype of *Eoenantiornis*, however with more of the corpus ossified in the latter, larger specimen. Although this cannot be verified without histological analysis, it is hypothesized that the sternum in the holotype of *Eoenantiornis* may have ossified trabeculae later during development. Given that there are so few enantiornithine specimens with comparable sternal morphology, the morphology in *Eoalulavis* and *Liaoningornis*, like that in *Eoenantiornis*, may represent an ephemeral ontogenetic stage, and thus departs from the more commonly preserved "adult" morphology. Alternatively, there are no other enantiornithines with an expanded xiphoid process, a feature unlikely to disappear with ontogeny, suggesting that this unique morphology does characterize these taxa. Comparison with *Liaoningornis* and the differences between the two taxa suggests that the morphology in the holotype of *Eoalulavis* may have been subject to further development, and possibly have ossified coracoidal sulci and a well-projected keel if the individual had not died. These two specimens lack other indicators that they are subadults, such as unfused compound bones, and pitted bone surfaces (Sanz et al., 2002; Zhou et al., 2005). This suggests a slow growth strategy in enantiornithines like that of the extant *Apteryx*, in which the animal reaches skeletal maturity fairly quickly but takes several years to reach full size (Bourdon et al., 2009). However, the preserved sternum may or may not represent the adult condition.

Acknowledgements Thanks to Jia Liantao for photographing the specimen, Zhou Shuang for translating the Chinese abstract, Gareth Dyke and Zhou Zhonghe for useful comments during the preparation of this manuscript and two reviewers for their comments which benefited this publication. Funding for this research was provided by the Chinese National Natural Science Foundation (grant #41050110438).

References

Bourdon E, Castanet J, de Ricqles A J et al., 2009. Bone growth marks reveal protracted growth in New Zealand kiwi (Aves, Apterygidae). Biol Lett, **5**(3): 1-4

Brodkorb P, 1976. Discovery of a Cretaceous bird, apparently ancestral to the Orders Coraciiformes and Piciformes (Aves: Carinatae). In: Olson S L ed. Collected Papers in Avian Paleontology Honoring the 90th Birthday of Alexander Wetmore. Washington D. C.: Smithsonian Institution Press. 67-73

Chiappe L M, 1993. Enantiornithine (Aves) tarsometatarsi from the Cretaceous Lecho Formation of northwestern Argentina. Am Mus Novit, (3083): 1-27

Chiappe L M, 2007. Glorified Dinosaurs: the Origin and Early Evolution of Birds. Hoboken: John Wiley & Sons, Inc. 1-263

Chiappe L M, Calvo J O, 1989. Nuevos hallazgos de Aves en el Cretacico de Patagonia. Cienc Invest, **43**(1): 20-24

Chiappe L M, Calvo J O, 1994. *Neuquenornis volans*, a new Late Cretaceous bird (Enantiornithes: Avisauridae) from Patagonia, Argentina. J Vert Paleont, **14**(2): 230-246

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

Clarke J A, Zhou Z H, Zhang F C, 2006. Insight into the evolution of avian flight from a new clade of Early Cretaceous ornithurines from China and the morphology of *Yixianornis grabaui*. J Anat, **208**: 287-308

Gauthier J, de Queiroz K, 2001. Feathered dinosaurs, flying dinosaurs, crown dinosaurs, and the name 'Aves'. In: Gauthier J, Gall L F eds. New Perspectives on the Origin and Early Evolution of Birds. New Haven: Peabody Museum of Natural History. 7-41

Haeckel E, 1866. Generelle Morphologie der Organismen. Berlin: Verlag von Georg Reimer. 1-574

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

Hou L H, 1997a. A carinate bird from the Upper Jurassic of western Liaoning, China. Chin Sci Bull, **42**(5): 413-416

Hou L H, 1997b. Mesozoic Birds of China. Taiwan: Feng-Huang-Ku Bird Park. 1-228

Hou L H, Chen P J, 1999. *Liaoxiornis delicatus* gen. et sp. nov., the smallest Mesozoic bird. Chin Sci Bull, **44**(9): 834-838

Hou L H, Chiappe L M, Zhang F C et al., 2004. New Early Cretaceous fossil from China documents a novel trophic specialization for Mesozoic birds. Naturwissenschaften, **91**: 22–25

Hou L H, Liu Z C, 1984. A new fossil bird from Lower Cretaceous of Gansu and early evolution of birds. Sci Sin, Ser B, **27** (12): 1296–1301

Hou L H, Martin L D, Zhou Z H et al., 1996. Early adaptive radiation of birds: evidence from fossils from northeastern China. Science, **274**: 1164–1167

Hou L H(侯连海), Martin L D, Zhou Z H(周忠和) et al., 1999. *Archaeopteryx* to opposite birds—missing link from the Mesozoic of China. Vert PalAsiat(古脊椎动物学报), **37**(2): 88–95

Hou L H(侯连海), Zhang J Y(张江永), 1993. A new fossil bird from Lower Cretaceous of Liaoning. Vert PalAsiat(古脊椎动物学报), **31**(3): 217–224(in Chinese with English summary)

Ji S A, Atterholt J A, O'Connor J K et al., 2011. A new, three-dimensionally preserved enantiornithian (Aves: Ornithothoraces) from Gansu Province, northwestern China. Zool J Linn Soc, **162**: 201–219

Morschhauser E, Varricchio D J, Gao C H et al., 2009. Anatomy of the Early Cretaceous bird *Rapaxavis pani*, a new species from Liaoning Province, China. J Vert Paleont, **29**(2): 545–554

O'Connor J K, 2009. A systematic review of Enantiornithes (Aves: Ornithothoraces). PhD thesis. Los Angeles: University of Southern California. 1–600

O'Connor J K, Gao K Q, Chiappe L M, 2010. A new ornithuromorph (Aves: Ornithothoraces) bird from the Jehol Group indicative of higher-level diversity. J Vert Paleont, **30**(2): 311–321

O'Connor J K, Zhou Z H, Zhang F C, 2011. A reappraisal of *Boluochia zhengi* (Aves: Enantiornithes) and a discussion of intraclade diversity in the Jehol avifauna, China. J Syst Palaeont, **9**(1): 51–63

Sanz J L, Chiappe L M, Pérez-Moreno B P et al., 1996. An Early Cretaceous bird from Spain and its implications for the evolution of avian flight. Nature, **382**: 442–445

Sanz J L, Pérez-Moreno B P, Chiappe L M et al., 2002. The birds from the Lower Cretaceous of Las Hoyas (province of Cuenca, Spain). In: Chiappe L M, Witmer L M eds. Mesozoic birds: Above the Heads of Dinosaurs. Berkeley: University of California Press. 209–229

Walker C A, 1981. New subclass of birds from the Cretaceous of South America. Nature, **292**: 51–53

You H L, Atterholt J A, O'Connor J K et al., 2010. A second ornithuromorph from the Changma Basin, Gansu Province, northwestern China. Acta Palaeont Pol, **55**(4): 617–625

You H L, Lamanna M C, Harris J D et al., 2006. A nearly modern amphibious bird from the Early Cretaceous of northwestern China. Science, **312**: 1640–1643

Zhang F C, Ericson P G, Zhou Z H, 2004. Description of a new enantiornithine bird from the Early Cretaceous of Hebei, northern China. Can J Earth Sci, **41**(9): 1097–1107

Zhang F C, Zhou Z H, 2000. A primitive enantiornithine bird and the origin of feathers. Science, **290**: 1955–1960

Zhang F C, Zhou Z H, Hou L H, 2003. Birds. In: Chang M M, Chen P J, Wang Y Q et al. eds. The Jehol Biota: the Emergence of Feathered Dinosaurs, Beaked Birds and Flowering Plant. Shanghai: Shanghai Scientific and Technical Publishers. 129–150

Zhang Y G(张玉光), 2006. Morphology of the distal tarsometatarsus and perching habits in birds. Sichuan J Zool(四川动物), **25**(1): 21–27(in Chinese with English abstract)

Zhou S(周爽), Zhou Z H(周忠和), O'Connor J K, 2012. A new basal beaked ornithurine bird from the Lower Cretaceous of western Liaoning, China. Vert PalAsiat(古脊椎动物学报), **50**(1): 9–24

Zhou Z H, Chiappe L M, Zhang F C, 2005. Anatomy of the Early Cretaceous bird *Eoenantiornis buhleri* (Aves: Enantiornithes) from China. Can J Earth Sci, **42**(7): 1331–1338

Zhou Z H, Hou L H, 2002. The discovery and study of Mesozoic birds in China. In: Chiappe L M, Witmer L M eds. Mesozoic Birds: Above the Heads of Dinosaurs. Berkeley: University of California Press. 160–183

Zhou Z H, Zhang F C, 2001. Two new ornithurine birds from the Early Cretaceous of western Liaoning, China. Chin Sci Bull, **46**(15): 1258–1264

Zhou Z H, Zhang F C, 2005. Discovery of an ornithurine bird and its implication for Early Cretaceous avian radiation. Proc Nat Acad Sci, **102**: 18998–19002

Zhou Z H(周忠和), Zhang F C(张福成), 2006a. Mesozoic birds of China—a synoptic review. Vert PalAsiat(古脊椎动物学报), **44**(1): 74–98

Zhou Z H, Zhang F C, 2006b. A beaked basal ornithurine bird (Aves, Ornithurae) from the Lower Cretaceous of China. Zool Scr, **35**(4): 363–373

Zhou Z H(周忠和), Zhang F C(张福成), Li Z H(李志恒), 2009. A new basal orithurine (*Jianchangornis microdonta* gen. et sp. nov.) from the Lower Cretaceous of China. Vert PalAsiat(古脊椎动物学报), **47**(4): 299–310