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SHORT COMMUNICATION

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A juvenile coelurosaurian theropod from China indicates arboreal habits

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Abstract Here we report an unequivocal arboreal coelurosaur, *Epidendrosaurus ningchengensis* gen. et sp. nov. This juvenile coelurosaur's third manual digit is extremely elongated, distinctively different from that of other known dinosaurs and birds. It represents certainly a type of adaptation previously unreported from the Mesozoic although the exact function of the third manual digit is unclear. The relatively long forelimb, penultimate phalanx of manual digit II, and pedal penultimate phalanges, are interpreted as evidence for the arboreal habit of *Epidendrosaurus*. Because *Epidendrosaurus* is more similar to advanced birds in some arboreal features than to *Archaeopteryx*, we suggest that the initial appearance of tree-adaptation in theropods was probably not directly related to flight but to other functions, such as seeking food or escaping from predators. Electronic Supplementary Material is available if you access this article at http://dx.doi.org/10.1007/s00114-002-0353-8. On that page (frame on the left side), a link takes you directly to the supplementary material.

Introduction

The material described in this paper was collected from a new locality, Daohugou, in east Nei Mongol, northeast China, which is west of Liaoning Province. Many salamanders (Wang 2000), plants and insects (Zhang 2002) have recently been discovered from this new locality. It is notable that an anurognathid rhamphorhynchoid pterosaur with beautiful hair covering the whole body has also been reported from this locality (Wang et al. 2002). The estimated age of the deposit at this locality is very controversial and ranges from the Middle Jurassic or the Early Cretaceous according to various authors (Wang et al. 2000; Zhang 2002); however, most workers currently regard it as being Late Jurassic.

Description of specimen

The specimen is about the size of a house sparrow (*Passer domesticus*) and obviously a juvenile individual as evidenced by many distinctive juvenile features, such as the incomplete ossifications of articular surface, presence of grooves on some limb bones (Sanz et al. 1997) and less well-defined extremities of postcranial long bones (Gauthier 1986) (see Fig. 1).

Taxonomy

Theropod Marsh, 1881

- Coelurosauria Huene, 1914
- Maniraptora Gauthier, 1986
- *Epidendrosaurus ningchengensis* gen. et sp. nov.

Etymology

The generic name is derived from the obvious arboreal adaptation of this animal, the specific name from the locality Ningcheng County of Nei Mongol.

Holotype

IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China) collection number V12653.

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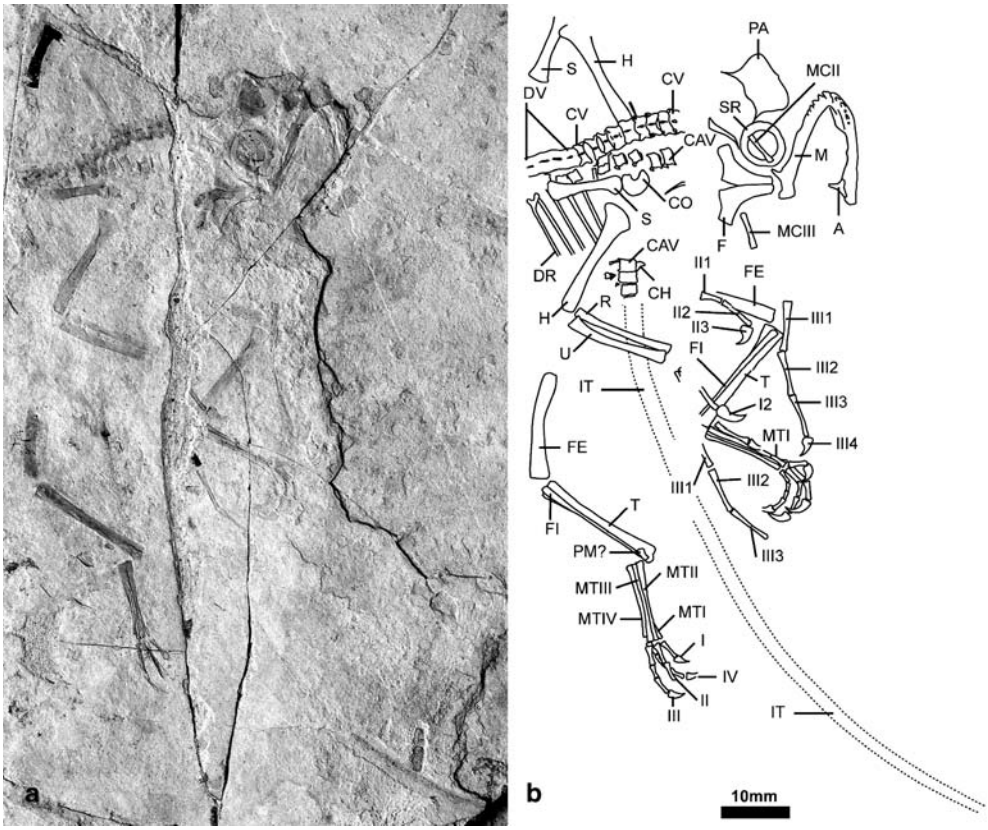

Fig. 1a, b *Epidendrosaurus ningchengensis* gen. et sp. nov. (IVPP V12653). Bone imprints were preserved in the main slab and its counterpart. The skeletal elements are partially disarticulated. Some skull elements, partial axial bones and the pelvic girdle are missing. **a** Main slab. **b** Composite line drawing, based on the mainslab and counterslab. *A* articular, *CAV* caudal vertebra, *CH* chevron, *CO* coracoid, *CV* cervical vertebra, *DR* dorsal rib, *DV* dorsal vertebra, *F* frontal, *FE* femur, *FI* fibula, *H* humerus, *I2* second phalanx of manual digit I, *I–IV* pedal digits I–IV, *II1–3* first to third phalanges of manual digit II. *III1–4* first to fourth phalanges of manual digit III, *IT* tail imprint, *M* mandible, *MCII–III* Metacarpals II–III, *MTI–IV* metatarsals I–IV, *PA* parietal, *PM?* proximal tarsal?, *R* radius, *S* scapula, *SR* sclerotic ring, *T* tibia, *U* ulna

Locality and horizon

Daohugou, Ningcheng County, East of Nei Mongol. Daohugou Formation, (?) Late Jurassic (Zhang 2002).

Diagnosis

Manual digit III elongated, nearly twice as long as digit II. Metacarpals II and III short, about 30% of the length of humerus. Second phalanx of manual digit II long, nearly 170% the length of the first phalanx (see electronic supplementary material S1).

Description

The frontal and parietal are similar to those of dromaeosaurs, such as *Sinornithosaurus* (Xu et al. 1999), and the basal bird *Archaeopteryx* (Elzanowski and Wellnhofer 1996; Martin and Zhou 1997). The frontals are probably only slightly fused near the caudal region (Fig. 2a). However, the two parietals appear to be completely fused as in *Sinornithosaurus* (Fig. 2b). There are at least 12 teeth in the mandible. The teeth progressively decrease in size caudally and are sparsely distributed as in most early birds including *Archaeopteryx*. The jaws are wide. The two mandibles are tightly contacted at the anterior end, yet it is difficult to determine whether they are fused (Fig. 1). Among non-avian theropods, only oviraptorids have fused mandibular symphysis.

There are at least nine cervical vertebrae preserved in articulation, with the anterior ones longer than the posterior. The total length of the tail is estimated to be 6–7 times as long as the femur (Fig. 1). Near the distal end of the tail, integumentary imprints are faintly preserved, resembling those of *Microraptor* (Xu et al. 2000).

The scapula has a primitive expanded distal end (Currie and Padian 1997). The coracoid is generally similar to that of some advanced non-avian coelurosaurs (Currie and Padian 1997) and *Archaeopteryx* (Ostrom 1976; Wellnhofer 1992). The ulna is posteriorly bowed and slightly wider than the radius. The manus is considerably longer than the humerus. Metacarpals II and III are comparatively short and only about one-third the length of the humerus. The first phalanx of digit II is shorter than the second, as in some other coelurosaurian dinosaurs (Currie and Padian 1997) and the basal birds *Archaeopteryx* (Feduccia 1999; Wellnhofer 1992), *Confuciusornis* (Hou et al. 1999; Chiappe et al. 1999) and *Protopteryx* (Zhang and Zhou 2000); the reverse is true in more advanced birds such as *Sinornis* (Sereno and Rao 1992) and *Cathayornis* (Zhou 1995). One of the most distinctive features of the hand of *Epidendrosaurus* is the extremely elongated digit III; it is nearly twice the length of digit II, differing from all other known dinosaurs and birds (Currie and Padian 1997; Feduccia 1999; Sereno 1999; Norell et al. 2000; Xu et al. 1999; Zhang

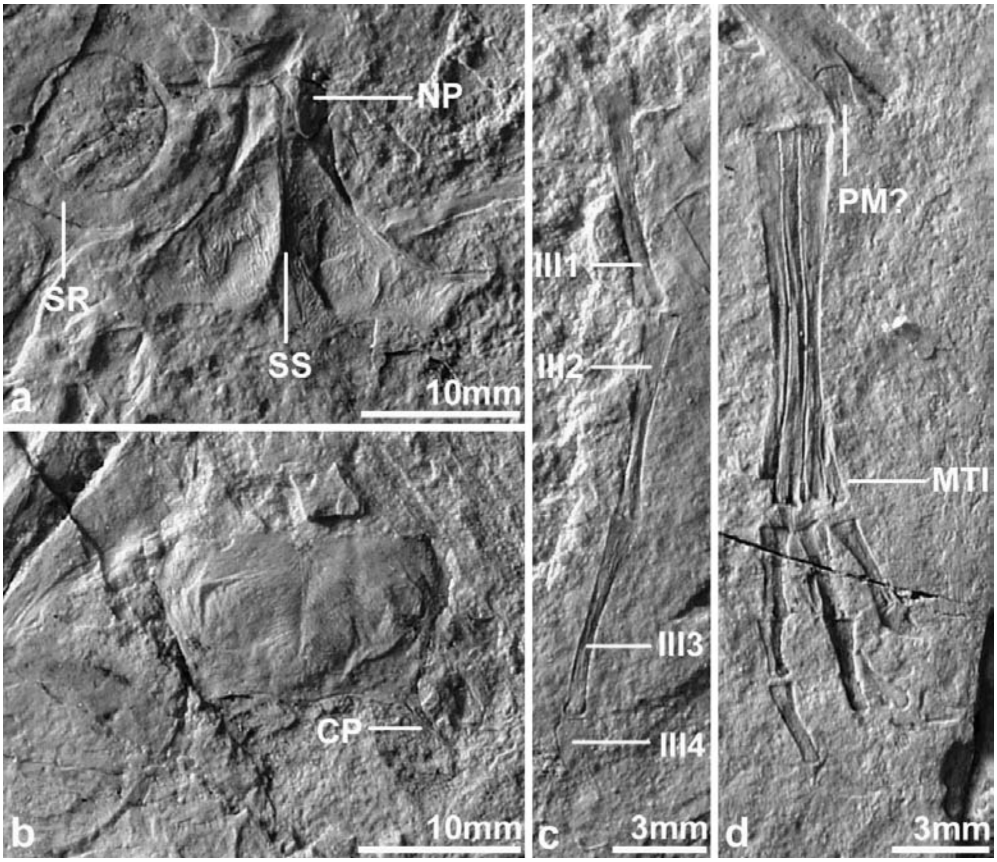

Fig. 2a–d *Epidendrosaurus ningchengensis* gen. et sp. nov. (IVPP V12653). The frontal (**a**) and parietal (**b**) are similar to those *Sinornithosaurus* and *Archaeopteryx*. The third manual digit (**c**) is extremely elongated, different from that of other known dinosaurs and birds. Metatarsal I (**d**) is attached to the distal end of metatarsal II, its trochlea aligns with those of II and III as in advanced perching birds, but not in other known dinosaurs. The pedal digits are shorter than major metatarsals, differing from the situation in birds. *CP* caudolateral process, *SS* sagittal suture, *NP* nasal process. For other abbreviations, refer to Fig. 1

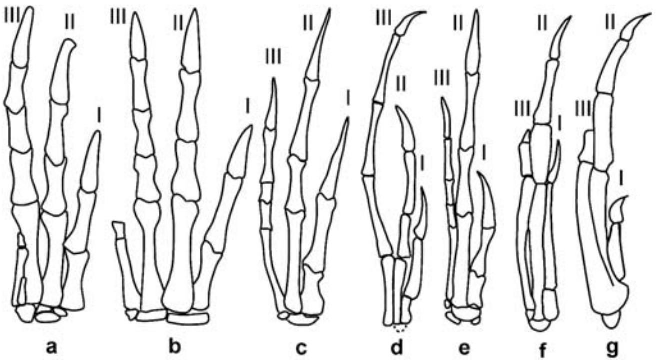

Fig. 3a–g Comparison of the manual elements of some dinosaurs and birds. **a** *Herrerasaurus ischigualastensis* (from Sereno 1993); **b** *Coelophysis* (from Currie and Padian 1997); **c** *Deinonychus antirrhopus* (from Currie and Padian 1997); **d** *Epidendrosaurus ningchengensis*; **e** *Archaeopteryx* (modified from Currie and Padian 1997; Wellnhofer 1992); **f** *Protopteryx fengningensis* (modified from Zhang and Zhou 2000); **g** *Cathayornis yandica* (modified from Zhou 1995)

and Zhou 2000; Sereno and Rao 1992; Zhou 1995; Zhang and Zhou 2001; Chatterjee 1997; Zhou and Zhang 2001) (see Figs. 1, 2c, 3).

The hindlimb is slightly shorter than the forelimb mainly because of the extremely elongated manual digit III. The femur is shorter than the humerus. Metatarsal IV is slightly shorter than both II and III. Metatarsal I is attached to the distal end of metatarsal II. Distally the trochlea of metatarsal I aligns with those of II and III as in advanced perching birds, but not in other known dinosaurs. The pedal digits are relatively short. Among the four pedal digits, IV is longer than II and closer to III in length. The penultimate phalanges of digits III and IV are markedly longer than the neighboring proximal phalanges, whereas in digit II the second phalanx is only slightly longer than the first. Digit I is relatively long, and distally it reaches the middle of the second phalanx of digit III (see Figs. 1, 2d).

Discussion

Many of the features of *Epidendrosaurus* such as the structures of the foot, the hand and the frontal with a deep cerebral fossa clearly show that it is a coelurosaur. *Epidendrosaurus* has also preserved several characters such as the long forelimb compared to the hindlimb, ulna bowed posteriorly, and pedal digit IV longer than II and closer to III in length, indicating that it probably belongs to the Maniraptora. Phylogenetic analysis has shown that *Epidendrosaurus* is very close to the transition to birds (see electronic supplementary material: S2, S3). Due to the incomplete preservation of a juvenile individual, many of the diagnostic features are less certain than in an adult specimen. Therefore, its phylogenetic position as suggested in this paper is at best tentative.

Epidendrosaurus is distinguishable from all other coelurosaurs in having an extremely elongated third manual digit (Fig. 3). Manual digit III is nearly twice the length of manual digit II. In both juvenile and adult non-avian theropods such as *Sinornithosaurus*, *Deinonychus*, and the basal bird *Archaeopteryx* manual digit III is shorter than II. In the basal dinosaur *Herrerasaurus* manual digit III is only slightly longer than II (Fig. 3). The extremely elongated manual digit III does not appear to be well adapted for grasping; however, it probably cannot be completely excluded from playing a minor role in the grasping activity of the hand. One possible explanation for the elongated third manual digit is that it is adapted to a specific niche as in the Malagasy primate Aye-Aye (*Daubentonia madagascariensis*), which uses its long middle finger as a tool for finding insects in trees.

The phalangeal proportions of the manus are also noteworthy. In digit II, the second phalanx is significantly elongated and about 170% as long as the first, more than those of other theropod dinosaurs and basal birds (Fig. 3). The forelimb is slightly longer than the hindlimb. In other non-avian theropods, such as dromaeosaurids, oviraptorids, troodontids and *Protarchaeopteryx*, the forelimb is shorter than the hindlimb (Currie and Padian 1997; Ji et al. 1998). In the specialized cursorial *Caudipteryx*, the forelimb is even shorter (Ji et al. 1998; Zhou et al. 2000). In *Archaeopteryx*, the forelimb is slightly shorter than the hindlimb (Wellnhofer 1992), but in more advanced birds such as *Confuciusornis* (Hou et al. 1999; Chiappe et al. 1999), the forelimb becomes longer than the hindlimb. Another distinctive feature is that the humerus is longer than the femur. These features, especially the long second phalanx of manual digit II and the forelimb, probably indicate grasping (Benton 1997) or grabbing capability.

A relatively long manus is better adapted to grasping or grabbing than to flapping flight; therefore in the early evolution of birds, the manus became progressively reduced and shortened (Zhou 1995) (Fig. 3). It has been suggested that during the early evolution of the tree-adaptation of birds the forelimb had played a significant role, i.e., the long forelimbs and the long and curved claws were important tools in assisting the arboreal life of early birds (Feduccia 1999; Zhou and Hou 1998; Clark et al. 1998). Only in later advanced birds did the role of the forelimb in arboreal adaptation became gradually reduced. The discovery of the new arboreal coelurosaur with long forelimbs and penultimate phalanges appears to confirm this hypothesis. The forelimb of *Epidendrosaurus* provides further evidence that the climbing/grasping ability is not limited to the hindlimb (Xu et al. 2000; Chatterjee 1997). The elongation of the forelimb is related to arboreal adaptation rather than directly to flight. The discovery also supports the hypothesis that the forelimb played an important role in the arboreal life of coelurosaurs, and lends credence to the arboreal hypothesis of the origin of avian flight (Bock 1986; Ostrom 1986; Pennycuick 1986; Zheng 1996).

The foot of *Epidendrosaurus* is unique among non-avian theropods. Although it does not preserve a reversed hallux, metatarsal I is articulated with metatarsal II at such a low position that the trochleae of metatarsals I–IV are almost on the same level (see Figs. 1, 2d), which is similar to those of perching birds including the Early Cretaceous flying birds *Sinornis* (Sereno 1992) and *Longipteryx* (Zhang and Zhou 2001), as well as many arboreal pterosaurs. This strongly suggests that *Epidendrosaurus* had arboreal capability (see electronic supplementary material S4), which is further evidenced by the toe proportions, i.e., the penultimate phalanges are longer than their neighboring proximal phalanges (Zhou and Hou 1998; Clark et al. 1998; Hopson 2001; Zhou and Farlow 2001). Pedal digit I is also long; distally it reaches the midpoint of the second phalanx of digit II. The pedal unguals are long and curved, and are generally comparable to those of *Microraptor* (Xu et al. 2000) and *Archaeopteryx* (Wellnhofer 1992). The dromaeosaur *Microraptor* (Xu et al. 2000) is the only other known theropod that has possessed arboreal capability, although the presence of arboreal dromaeosaurs has been proposed earlier (Chatterjee 1997). However, the relative position of the articulation of metatarsal I to II is higher than that in *Epidendrosaurus*. The articulation between metatarsals I and II in *Epidendrosaurus* is even lower than that in the basal arboreal birds *Archaeopteryx* and *Confuciusornis*, which possessed perching ability (Feduccia 1999; Bock 1986; Chiappe et al. 1999). It should also be mentioned that since the holotype of *Epidendrosaurus* is a juvenile individual, the proportions of the postcranial skeletal elements will certainly be somewhat different from an adult. Trees could provide relatively safe niches for the defenseless nestlings and juveniles.

It seems that the climbing function in *Epidendrosaurus* was acquired before birds (*Archaeopteryx* and other more advanced birds). Although the arboreal life in the immediate ancestors of birds was critical for the development of the flight of birds, the arboreal habit in *Epidendrosaurus* was most likely for food or for escaping from predators (Bock 1986). Thus the evolution of the arboreal capability in theropods was not necessarily directly related to flight in the beginning.

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References

Benton MJ (1997) Origin and early evolution of dinosaurs. In: Farlow JO, Brett-Surman MK (eds) The complete dinosaur. Indiana University Press, Bloomington, Ind. pp 204–215

Bock WJ (1986) The arboreal origin of avian flight. Mem Calif Acad Sci 8:57–72

Chatterjee S (1997) The rise of birds. John Hopkins University Press, Baltimore, Md.

Chiappe LM, Ji S, Ji Q, Norell MA (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 JM, Hopson JA, Hernandez R, Fastovsky DE, Montellano M (1998) Foot posture in a primitive pterosaur. Nature 391:886–889

Currie PJ, Padian K (1997) Encyclopedia of dinosaurs. Academic Press, London

Elzanowski A, Wellnhofer P (1996) Cranial morphology of *Archaeopteryx*: evidence from the seventh skeleton. J Vertebr Paleontol 16:81–94

Feduccia A (1999) The origin and evolution of birds, 2nd edn. Yale University Press, New Haven, N.J.

Gauthier J (1986) Saurischian monophyly and the origin of birds. Mem Calif Acad Sci 8:1–55

Hopson J (2001) Ecomorphology of avian and nonavian theropod phalangeal proportions: implications for the arboreal versus terrestrial origin of bird flight. In: Gauthier J, Gall LF (eds) New perspectives on the origin and early evolution of birds. (Special publication of the Peabody Museum of Natural History) Yale University, New Haven, N.J. pp 211–236

Hou L, Martin LD, Zhou Z, Feduccia A, Zhang F (1999) A diapsid skull in a new species of the primitive bird *Confuciusornis*. Nature 399:679–682

Ji Q, Currie PJ, Norell MA, Ji S (1998) Two feathered dinosaurs from northeastern China. Nature 393:753–761

Martin LD, Zhou Z (1997) Archaeopteryx-like skull in enantiornithine bird. Nature 389:556

Norell MA, Makovicky PJ, Clark JM (2000) A new troodontid theropod from Ukhaa Tolgod Mongolia. J Vertebr Paleontol 20:7–11

Ostrom JH (1976) Some hypothetical anatomical stages in the evolution of avian flight. Smithsonian Contrib Paleobiol 27:1–21

Ostrom JH (1986) The cursorial origin of avian flight. Mem Calif Acad Sci 8:73–81

Pennycuick CJ (1986) Mechanical constraints on the evolution of flight. Mem Calif Acad Sci 8:83–98

Sanz JL, Chiappe LM, Pérez-Moreno BP, Moratalla JJ, Hernandéz-Carrasquilla F, Buscalioni AD, Ortega F, Poyato-Ariza F, Rasskin-Gutman D, Martínez-Delclòs X (1997) A nestling bird from the Lower Cretaceous of Spain: implications for avian skull and neck evolution. Science 276:1543–1546

Sereno PC (1993) The pectoral girdle and forelimb of the basal theropod *Herrerasaurus ischigualastensis*. J Vertebr Paleontol 13:425–450

Sereno PC (1999) The evolution of dinosaurs. Science 284:2137–2147

Sereno PC, Rao C (1992) Early evolution of avian flight and perching: new evidence from the Lower Cretaceous of China. Science 255:845–848

Wang X, Zhou Z-H, Jin F, Hu Y-M, Gu G, Zhang H-C (2000) Vertebrate biostratigraphy of the Lower Cretaceous Yixian Formation in Lingyuan, western Liaoning and neighboring southern Nei Mongol (inner Mongolia), China. Vertebr PalAsiat 38(2):95–100

Wang X, Zhou Z, Zhang F, Xu X (2002) A nearly completely articulated rhamphorhynchoid pterosaur with exceptionally well-preserved wing membranes and “hairs” from inner Mongolia, northeast China. Chin Sci Bull 47:226–230

Wang Y (2000) A new salamander (Amphibia: Caudata) from the Early Cretaceous Jehol biota. Vertebr PalAsiat 38(2):100–103

Wellnhofer PA (1992) A new specimen of *Archaeopteryx* from the Solnhofen Limestone. Nat Hist Mus Los Angeles County Sci Ser 36:3–23

Xu X, Wang X, Wu X (1999) A dromaeosaurid dinosaur with a filamentous integument from the Yixian Formation of China. Nature 401:262–266

Xu X, Zhou Z, Wang X (2000) The smallest known non-avian theropod dinosaur. Nature 408:705–708

Zhang F, Zhou Z (2000) A primitive enantiornithine bird and the origin of feathers. Science 290:1955–1959

Zhang F, Zhou Z (2001) Early diversification of birds: evidence from a new opposite bird. Chin Sci Bull 46:945–950

Zhang J (2002) Discovery of Daohugou biota (pre-Jehol biota) with a discussion on its geological age. J Stratigr 26(3):174–178

Zheng G (1996) Ornithology. Beijing Normal University Press, Beijing

Zhou Z (1995) Discovery of early Cretaceous birds in China. Cour Forchungsinst Senckenb 181:9–23

Zhou Z, Farlow JO (2001) Flight capability and habits of *Confuciusornis*. In: Gauthier J, Gall LF (eds) New perspectives on the origin and early evolution of birds. (Special publication of the Peabody Museum of Natural History) Yale University, New Haven, N.J. pp 237–254

Zhou Z, Hou L (1998) *Confuciusornis* and the early evolution of birds. Vertebr PalAsiat 36:136–146

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

Zhou Z, Wang X, Zhang F, Xu X (2000) Important features of *Caudipteryx* – evidence from two nearly complete new specimens. Vertebr PalAsiat 38:241–254