The First Mesozoic Heterodactyl Bird from China

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Abstract: ***Dalingheornis liweii*** **gen. et sp. nov., a new enantiornithine bird was collected from the early Cretaceous Yixian Formation in northeastern China. It is the first record of a highly specialized heterodactyl foot in Mesozoic birds. The Y-shaped furcula with short hypocleidum is different from that of other enantiornithines. The minor metacarpal is robust and longer than the major metacarpal. A long bony tail composed of 20 caudal vertebrae with chevrons resembling those of dromaeosaurids and thus, highlighting again the evolutionary relationship between birds and non-avian theropods. Well-preserved alula feathers and a heterodactyl foot provide strong evidence for the arboreal habit of** ***Dalingheornis*****.**

Key words: Early Cretaceous, heterodactyl, enantiornithine, ***Dalingheornis liweii*****, China**

1 Introduction

Enantiornithines were the dominant birds nearly worldwide throughout the entire span of the Cretaceous (Chiappe, 1995; Feduccia, 1996). The adaptive radiation of opposite birds is little known besides the disparity of rostral morphology in *Boluochia* (Zhou, 1995), *Longipteryx* (Zhang et al., 2001), *Longirostravis* (Hou et al., 2004), and the presence of stomach contents that reflect a diversity of diets. Like the structure of rostrum, differentiation of the locomotor apparatus further expand the ecological opportunities of birds, and the morphology of feet and legs tell us much about avian ecology (Gill, 1994). But unfortunately, all known enantiornithines were anisdactyl or undescribed. *Dalingheornis* represents a new diversification of the pattern of feet.

2 Systematic Paleontology

Aves Linnaeus, 1758

Enantiornithes Walker, 1981

Dalingheornis liweii gen. et sp. nov.

Etymology: The genus name refers to the river where the fossil located, and *ornis* from the Greek word 'bird'. The species name is dedicated to Yang Liwei, China's first astronaut.

Holotype: CNU VB2005001 (Capital Normal University), a nearly completely articulated skeleton with feathers.

Locality and Horizon: Dawangzhangzi, Lingyuan, western Liaoning, China. Yixian Formation, Early Cretaceous (~125 Ma) (Swisher, 2002; Zhou et al., 2003).

Diagnosis: A small enantiornithine bird with the following derived characters: short premaxilla and mandibular symphysis; sharp and sparse teeth. Neck relatively short, consisting of 10 high, short cervical vertebrae; Interclavicular angle about 60°, hypocleidum short. Humerus longer than femur; minor metacarpal robust, and longer than major metacarpal; first phalanx of major digit shorter than the second phalanx. Tail composed

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of 20 caudal vertebrae with elongate chevrons, pygostyle lacks. Heterodactyl foot (the hallux and the second toe direct backwards, the third and the fourth toes point forwards) with large curved unguals.

Measurement (mm): Length of skull, 20; Length of humerus, 14; Length of ulna, 14; Length of coracoid, 6; Length of scapula, 8; Length of furcula, 5; Length of metacarpus II and III, 6; Length of first manual digit, 4; Length of major digit, 8; Length of femur, 11; Length of tibia, 16; Length of tasometatarsus, 9; Length of tail, 17.5; Length of ilium, 8; Length of pubis, 8; Length of ischium, 4.

3 Description

Over 20 primitive Mesozoic birds have been reported from the Jehol Biota (Hou, 1997; Ji et al., 1999; Zhang et al., 2001; Zhou and Zhang, 2001, 2002a, 2003; Hou et al., 1999, 2002; Ji, 2003; Gong, 2004; Lü and Hou, 2005; Lü and Ji, 2005). *Dalingheornis* is about the size of *Liaoxiornis* (Hou and Chen, 1999). The well-preserved new specimen (Plate I-1) provides a demonstration about the differentiation of locomotor apparatus in Mesozoic birds.

The skull bones are thin but well-ossified. The premaxilla is short and bears at least 4 large teeth; its nasal process extends only to the dorsal edge of the antorbital fenestra. The maxilla is more robust, with 5–6 scattered teeth. The large, broad nasal bone lies between the antorbital fenestra and the orbit. The lachrymal is long and triangular.

The neck is composed of ten cervical vertebrae. There are 10 cervicals; all of them are short and high. The centrum is amphicelous; the head of cervical ribs can be seen on both sides. The first cervical has a horseshoe shaped neural arch; the neural spine of the second cervical is high and long. There are 11 dorsal vertebrae, and the number of dorsal vertebrae is 12 in *Protopteryx* (Zhang and Zhou, 2000), 11or 12 in *Confuciusornis*, and 11 in *Iberomesornis*. Compared with the cervicals, the dorsal vertebrae are slightly elongated and have higher neural arches. There are 8 sacral vertebrae, all of which are unfused. About 20 caudals constitute the long tail. With the exception of several proximal caudals, the rest are elongated with rod-like extensions of the chevrons as in dromaeosaurid dinosaurs (Ostrom, 1969; Currie, 1995; Norell and Makovichy, 1999; Xu, 2000), *Archaeopteryx*, *Jeholornis* (Zhou and Zhang, 2002b) and other early birds. There are 9 pairs of well-preserved ribs, and four pairs of sternal ends of the ribs are arranged compactly anterior to the proximal end of the lateral process of sternum.

The scapula is more than half the length of the humerus, and the shaft is straight and strap-like with a truncate distal end. The coracoid is slightly shorter than the scapula and expands distally to form a broad sternal end with a slightly convex margin; the sternal half is concave medially and little convex laterally. The thin and Y-shaped furcula has a short hypocleidum as in *Neuquenornis* (Chiappe and Calvo, 1994), whereas those of other known enantiornithines bear a much longer one. The two clavicular rami form an angle of about 60° (Plate I-2).

The sternum provides the best evidence that the individual is a juvenile. Only the rod-shaped lateral process of the sternum lying between the third and fourth ribs can be seen, and the distal end of the lateral process is forked (Plate I-2).

The humerus is approximately the size of the ulna, the proximal end curves inward, and two condyles are obviously present at the distal end. The ulna is more robust than the radius, curving slightly at the proximal end. The radius is straighter than the ulna, and the ratio of the shaft width of the ulna to that of the radius is about 3:2. There are at least three ossified carpals, and the short-conical shaped medial one is the largest, the middle one is square, and the lateral one is the smallest and pisiformed. The major metacarpal (metacarpal II) and minor metacarpal (metacarpal III) are the same in width and similar in morphology, and the intermetacarpal space between the major and minor metacarpals is very narrow. The first phalanx of the alular digit is short, only half the length of metacarpal II and III, a feature that differs largely from that of *Archaeopteryx* (Wellnhofer, 1993) and *Confuciusornis* (Hou et al., 1999), in which the bones have a 1:1 ratio. The major digit has three phalanges, the intermediate phalanx is longer than the proximal phalanx, and this condition is similar to that of some early birds (e.g., *Archaeopteryx*, *Confuciusornis*) and is contrary to that of other known enantiornithines.

All the components of the pelvic girdle are ossified and the structure is relatively simple. The pubis is slender and fused distally. The ilium is equal in length to the pubis like *Archaeopteryx* and other primitive birds. The preacetabular iliac blade is longer than the postacetabular ilium. The ischium is wide and short, and simplified in comparison to *Archaeopteryx* and *Confuciusornis*.

Like several of the longer forelimb bones, the distal ends of the femur and tibiotarsus, and the proximal end of tarsometatarsus are cartilaginous. As in *Archaeopteryx* and *Confuciusornis*, the femur is shorter than the humerus. The astragalus and calcaneum are still cartilaginous and unfused to the distal end of the tibia. The tibia is longer than the humerus and lacks the proximal cnemial crest. The tarsometatarsus is more than half the length of tibiatarsus; Metatarsi II–IV fused proximally, and metatarsal II is

curved medially in the distal end; among the three major metatarsals, metatarsal III is the longest and relatively straight, metatarsal IV is less prominent than metatarsi II and III. The three trochleae for digits 2–4 are cartilaginous and simple. The trochleae for digits 2 and 3 are obviously broader than that for digit 4, the trochlea of metatarsal III lies more adjacent to that of metatarsal IV than to that of metatarsal II, and there is an obvious space between trochleae II and III. In general, the distal end of the tasometatarsus (Plate I-3, 4) exhibits more similarity to modern heterodactyl birds than to syndactyl or other patterns of feet. The pedal phalanges of the left foot are preserved articulately, but the four toes are displaced uniformly from their usual position to medial side. The toes are arranged in pairs, the third toe and the fourth toe cluster close together and point forward, the second toe lying adjacent to the hind toe together points backward, and the claw of the second toe appears to have the same orientation as that of the hind toe, which would not be the case if it was an accidentally reversed forward-pointing toe. We have not observed such a kind of pedal morphology in any other of the numerous articulated or distorted bird fossils from Jehol Biota. It seems reasonable for us to deduce a heterodactyl foot in the new bird but not an accidental. The toes are relatively long; the first digit is the same length as the tarsometatarsus, while the other three digits are longer.

Feathers are mostly preserved as carbonizations. All types of feathers are developed; the alula (Sanz et al., 1996; Zhang and Zhou, 2000) and remiges (especially seconderies) are well preserved (Plate I-2). The rectrices are long and are situated on either side of the tail; the terminal rectrices are the longest.

4 Discussion

The enantiornithine status of *Dalingheornis liweii* is indicated by the presence of a V-shaped furcula with hypocleidum, the slender and reduced metatarsus IV, and the slightly longer minor metacarpal compared with the major metacarpal. *Dalingheornis* is thought to be a juvenile individual due to: (i) the large size of the skull in proportion to the body; (ii) the ends of most long bones are still cartilaginous; (iii) the sternum consists of two separate lateral processes that have not fused into one plate as in adults.

In modern birds, feet are of several types (anisodactyl, syndactyl, zygodactyl, heterodactyl, pamprodactyl), depending on the arrangement of the toes and/or the particular functions the feet perform, and they are commonly used as characters for distinguishing groups of birds. Fossil birds with heterodactyl feet have been reported from Cenozoic of France and Germany (Mayr, 1999, 2005). Toes are held in usual position by muscles, and the presence of heterodactyl feet is consistent to some extent with the peculiar configuration of flexor muscles and insertions, that is, M. flexor digitorum longus only inserts on digit III and IV, and M. flexor hallucis longus inserts on hallux and the second toe (George and Berger, 1966). Considering from this respect, it is also reasonable to deduce heterodactyl foot in *Dalingheornis*. It is the first record of perching heterodactyl feet in Mesozoic birds, and this feature is strong evidence for the arboreal habit of this bird. The presence of the alula that is essential for low-speed flight and maneuverability in modern birds (Sanz et al., 1996), which confirms again the arboreal nature of this new bird. The presence of the plesiomorphic long bony tail with elongate chevrons provides new evidence to support the relationship between birds and dromaeosaurids and adds to the emerging mosaic pattern of early bird evolution.

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References

Chiappe, L.M., 1995. The first 85 million years of avian evolution. *Nature*, 378: 349–354.

Chiappe, L.M., and Calvo, J.O., 1994. *Neuquenornis volans*, a new Enantiornithes (Aves) from the Upper Cretaceous of Patagonia (Argentina). *J. Vert. Paleontol.*, 14(2): 230–246.

Currie, P.J., 1995. New information on the anatomy and relationships of *Dromeaosaurus albertensis* (Dinosauria: Theropoda). *J. Vert. Paleontol.*, 15: 576–591.

Feduccia, A., 1996. *The Origin and Evolution of Birds*. New Haven: Yale University Press, 139–194.

George, J.C., and Berger, A.J., 1966. *Avian Myology*. New York: Academic Press, 380–463.

Gill, F.B., 1994. *Ornithology*, 2nd ed. New York: W. H. Freeman and Company, 13–22.

Gong Enpu, Hou Lianhai and Wang Lixia, 2004. Enantiornithine bird with diapsidian skull and its dental development in the Early Cretaceous in Liaoning, China. *Acta Geologica Sinica* (English edition), 78: 1–7.

Hou, L., 1997. *Mesozoic Birds of China*. Nantou, Taiwan, China: Feng-Huang-Ku Bird Park Press, 43–223 (in Chinese with English abstract).

Hou Lianhai and Chen Piji, 1999. *Liaoxiornis delicatus* gen. et sp. nov., the smallest Mesozoic bird. *Chin. Sci. Bull.*, 44: 834–838.

Hou, L., Martin, L.D., Zhou, Z., Feduccia, A., and Zhang, F., 1999.

A diapsid skull in a new species of the primitive bird *Confuciusornis*. *Nature*, 399: 679–682.

Hou Lianhai, Zhou Zhonghe, Zhang Fucheng and Gu Yucai, 2002. *Mesozoic Birds from Western Liaoning in China*. Shenyang: Liaoning Science and Technology Publishing House, 5–82 (in Chinese with English abstract).

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

Ji, Q., Chiappe, L. M., and Ji, S., 1999. A new Late Mesozoic confuciusornithid bird from China. *J. Vert. Paleontol.*, 19(1): 1–7.

Ji Qiang, Ji Shu'an, You Hailu, Zhang Hongbin, Zhang Nanjun, Yuan Chongxi and Ji Xinxin, 2003. An Early Cretaceous avialian bird, *Shenzhouraptor sinensis*, from western Liaoning, China. *Acta Geologica Sinica* (English edition), 77: 21–27.

Lü Junchang and Hou Lianhai, 2005. A possible long-tailed bird with a pygostyle from the late Mesozoic Yixian Formation, western Liaoning, China. *Acta Geologica Sinica* (English edition), 79: 7–10.

Lü Junchang and Ji Qiang, 2005. A new ornithocheirid from the Early Cretaceous of Liaoning province, China. *Acta Geologica Sinica* (English edition), 79: 157–163.

Mayr, G., 1999. A new trogon from the Middle Oligocene of Céreste, France. *Auk*, 116: 427–434.

Mayr, G., 2005. New trogons from the early Tertiary of Germany. *Ibis*, 147: 512–518.

Norell, M.A., and Makovichy, P., 1999. Important features of the Dromeaosaurid skeleton: information II: information from a newly collected specimen of *Velociraptor mongoliensis*. *Am. Mus. Novit.*, 3282: 1–45.

Ostrom, J.H., 1969. Osteology of *Deininychus antirrhopus*, an unusual theropod dinosaur from the Lower Cretaceous of Montana. *Peabody Mus. Hist. Bull.*, 30:1–165.

Sanz, J.L., Chiappe, L.m., Perez-mereno, B.P., Buscalioni, A.D., Moratalla, J.J., Ortega, F., and Poyato-Ariza, F.J., 1996. An early Cretaceous bird from Spain and its implications for the evolution of avian flight. *Nature*, 382: 442–445.

Swisher, C.C. III, Wang Xiaolin, Zhou Zhonghe, Wang Yuanqing, Jin Fan, Zhang Jiangyong, Xu Xing, Zhang Fucheng and Wang Yuan, 2002. Further support for a Cretaceous age for the feathered-dinosaur beds of Liaoning, China: new $^{40}Ar/^{39}Ar$ dating of the Yixian and Tuchengzi Formations. *Chinese Sci. Bull.*, 47: 135–138.

Wellnhofer, P.A., 1993. Das Siebte Exemplar Von *Archaeopteryx* aus dem Salnhofen Schichten. *Archaeopteryx*, 11: 1–48.

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

Zhang Fucheng, Zhou Zhonghe, Hou Lianhai and Gu Gang, 2001. Early diversification of birds: evidence from a new opposite bird. *Chinese. Sci. Bull.*, 46: 945–949.

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

Zhou Zhonghe, 1995. Discovery of a new enantiornithine bird from the Early Cretaceous of Liaoning, China. *Vertebrata PalAsiatica*, 33(2): 99–113 (in Chinese with English abstract).

Zhou, Z., Barrett, P.M., and Hilton, J., 2003. An exceptional preserved Lower Cretaceous ecosystem. *Nature*, 421: 807–814.

Zhou, Z., and Zhang, F., 2003. *Jeholornis* compared to *Archaeopteryx*, with a new understanding of the earliest avian evolution. *Naturwissenschaften*, 90: 220–225.

Zhou Zhonghe and Zhang Fucheng, 2001. Two new ornithurine birds from the Early Cretaceous of western Liaoning, China. *Chinese Sci. Bull.*, 46: 1258–1264.

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

Zhou, Z., and Zhang, F., 2002b. A long-tailed, seed-eating bird from the Early Cretaceous of China. *Nature*, 418: 405–409.

Explanation of plate

Plate I

1. Complete holotype of *Dalingheornis liweii* gen. et sp. nov. (CNU VB2005001). Scale bar, 5 mm.
2. Pectoral girdle and forelimb of *Dalingheornis liweii* gen. et sp. nov. (CNU VB2005001). ad – alular digit; ca – carpal; co – coracoid; fu – furcula; hu – humerus; lp – lateral process of sternum; mc – minor metacarpal; ra – radius; sc – scapula; sr – sternal ribs; ul – ulna. Scale bar, 5 mm.
3. Foot and tail of *Dalingheornis liweii* gen. et sp. nov. (CNU VB2005001). Scale bar, 1 mm.
4. Line drawing of the foot of *Dalingheornis liweii* gen. et sp. nov. (CNU VB2005001).

Plate I