

# 辽宁早白垩世今鸟类一新属种 (*Jianchangornis microdonta* gen. et sp. nov.)<sup>1)</sup>

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**摘要:**依据一近完整的相关节的骨骼化石,记述了辽宁建昌早白垩世九佛堂组原始今鸟类一新属种:小齿建昌鸟(*Jianchangornis microdonta* gen. et sp. nov.)。新鸟个体较大,但从骨化程度分析,正型标本可能属于一亚成年个体。具有一些进步特征,如胸骨及龙骨突加长,鸟喙骨具有发育的前鸟喙突以及和肩胛骨关联的关节窝,叉骨“U”字型,愈合荐椎包括9-10枚荐椎,尾综骨短小,第二、三掌骨远端愈合,跗跖骨完全愈合等,表明新属无疑属于今鸟类。在以下特征组合上很容易和已知的早白垩世今鸟类化石相区别:齿骨上至少有16枚细小牙齿,从齿骨前端向后沿齿骨大部密集排列;肩胛骨强烈弯曲;第一掌骨粗壮,较其他掌骨宽;第一指长并且远端延伸明显超过第二掌骨;肱骨+尺骨+第二掌骨与股骨+胫跗骨+跗跖骨的长度比例约为1.1。系统发育分析表明新属属于基干的今鸟类。新发现的材料第二、三掌骨远端愈合很好,但近端却未完全愈合,这一特征尚未见于其他已知鸟类,或许表明今鸟类腕掌骨的愈合和现生鸟类的跗跖骨一样是从远端开始的,不同于反鸟类和其他基干鸟类。建昌鸟的下颌还保存了一个前齿骨,这是继早白垩世红山鸟之后的另一例报道,可能进一步表明这一结构在今鸟类中曾普遍出现。新鸟肩带、胸骨和前肢的特征显示了和现代鸟类相近的飞行能力,其后肢、脚趾的比例以及趾爪的形态等显示和燕鸟、义县鸟等相似的地栖特征。保存于标本上的鱼类残骸可能显示了建昌鸟食鱼类的习性。今鸟类新属种的发现进一步表明,早白垩世这一进步鸟类类群的分化已不亚于反鸟类,湖滨环境在今鸟类的早期演化中确实扮演了重要的角色。

**关键词:**中国辽宁,早白垩世,今鸟类,新属种

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## A NEW BASAL ORNITHURINE BIRD (*JIANCHANGORNIS MICRODONTA* GEN. ET SP. NOV.) FROM THE LOWER CRETACEOUS OF CHINA

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**Abstract** A new genus and species of a basal ornithurine bird is reported from the Lower Cretaceous

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Jiufotang Formation of Jianchang, Liaoning, China. It is represented by a nearly complete articulated skeleton of a sub-adult individual. It is distinguishable from other known ornithurines by possessing a combination of features including at least 16 small and conical teeth on the dentary, scapula strongly curved, metacarpal I robust and wider than other metacarpals, first manual digit long and extending beyond distal metacarpal II, and length ratio of humerus+ulna+metacarpal II to femur+tibiotarsus+tarsometatarsus is approximately 1.1. Phylogenetic analysis indicates that the new taxon is a basal ornithurine. *Jianchangornis* represents the second Early Cretaceous bird with the preservation of a predeontary bone, which may further confirm that a predeontary could be a feature common to Mesozoic ornithurines. The advanced features of the pectoral girdle, sternum and wings of the new bird indicate its powerful flight capability, and the hindlimb bone and toe proportions as well as the ungual morphology suggest a terrestrial locomotion similar to those of *Yanornis* and *Yixianornis*. The associated fish fragments may indicate a piscivorous diet consistent with the dentation of the new bird. The discovery of a new basal ornithurine further shows that the diversification of the Ornithurae is probably no less than the enantiornithes, and the near lakeshore adaptation had definitely played a key role in the early ornithurine radiation.

**Key words** Liaoning, China; Early Cretaceous; Ornithurae; new genus and species

## 1 Introduction

Ornithurines represent the most derived group of birds that coexisted with the enantiornithine and more basal avians in the Early Cretaceous. Several taxa have been reported from both the Yixian and Jiufotang formations of the Jehol Group in northeastern China, including *Liaoningornis* (Hou, 1997a), *Chaoyangia* (Hou and Zhang, 1993), *Songlingornis* (Hou, 1997b), *Yanornis*, *Yixianornis* (Zhou and Zhang, 2001; Clarke et al., 2006), *Hongshanornis* (Zhou and Zhang, 2005) and *Archaeorhynchus* (Zhou and Zhang, 2006). Despite the fact that these basal ornithurines show a great variation of body size, locomotive and dietary adaptations, they seem to well distinguish from other contemporary birds in possessing a more powerful flight capability and showing a trend of specialization for an adaptation of near lakeshore terrestrial life while other birds were dominated by arboreal forms. Furthermore, among Early Cretaceous ornithurines, earlier and more basal forms from the Yixian Formation (125 Ma) seem to be relatively small in size compared to more derived ones from the Jiufotang Formation (120 Ma).

A recently discovered bird from the Jiufotang Formation in Jianchang, Liaoning Province is comparable to *Yanornis* in size and bone proportions. However, it also preserved a few features that also seem to be most primitive among ornithurines, such as the presence of a long first wing digit. It also preserved a predeontary bone that is previously only reported in *Hongshanornis* (Zhou and Zhang, 2005) among Early Cretaceous birds. The new discovery thus provides important new information for understanding the early diversification of ornithurines as well as the complex pattern of character evolution in this avian group.

## 2 Systematic paleontology

**Aves Linnaeus, 1758**

**Pygostylia Chiappe, 2002**

**Ornithurae Haeckel, 1866**

**Ord. and Fam. indet.**

***Jianchangornis microdonta* gen. et sp. nov.**

(Figs. 1–7; Table 1)

**Holotype** IVPP V 16708 (collection of Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China), a sub-adult individual of a nearly complete and articulated skeleton (Figs. 1, 2).

**Etymology** The genus name is derived from Jianchang County where the holotype was



Fig. 1 Photo of the holotype of *Jianchangornis microdonta* gen. et sp. nov. (IVPP V 16708)

collected, and the species name indicates the small teeth on the dentary.

**Locality and horizon** Jianchang, Chaoyang, Liaoning Province; Jiufotang Formation. Early Cretaceous, Aptian; approximately 120 Ma (He et al., 2004).

**Diagnosis** A relatively large-sized basal ornithurine, distinguishable from other known ornithurines in possessing a combination of characters including: at least 16 small and conical teeth on the dentary, scapula strongly curved, robust “U”-shaped furcula, a robust and wide metacarpal I, first manual digit extending beyond distal metacarpal II, and length ratio of humerus+ulna+metacarpal II to femur+tibiotarsus+tarsometatarsus about 1.1.

**Description and comparison** The skull is laterally exposed while the postcranial bones are mainly dorsally exposed.

**Cranial bones:** most of the cranial bones are incompletely preserved and are disarticulated. As a result, many of the fragmentary bones cannot be appropriately recognized. It is uncertain whether teeth are present on the premaxilla, which is very fragmentary (Fig. 3). The jugal is

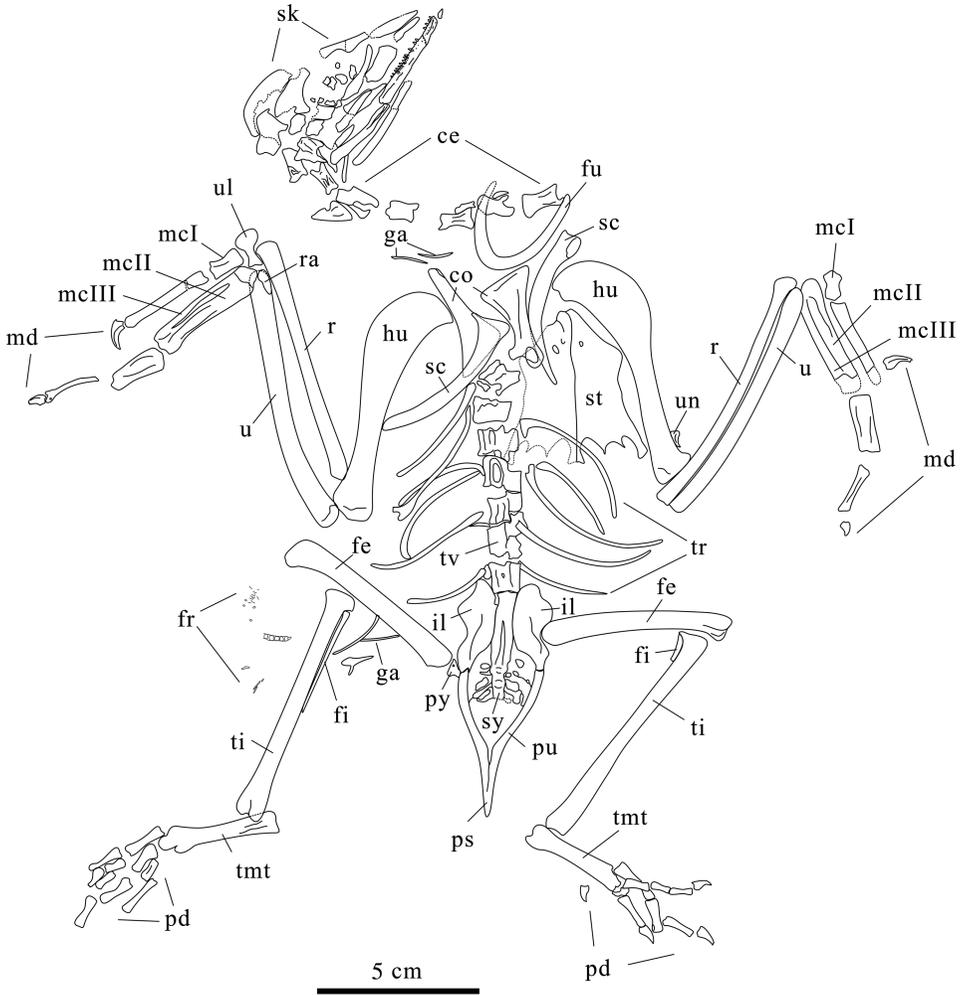


Fig. 2 Linedrawing of the holotype of *Jianchangornis microdonta* gen. et sp. nov. (IVPP V 16708)

ce. cervical vertebrae 颈椎; co. coracoid 乌喙骨; fe. femur 股骨; fi. fibula 腓骨; fr. fish remains 鱼类残骸; fu. furcula 叉骨; ga. gastralia 腹膜肋; hu. humerus 肱骨; il. ilium 髌骨; mcI-III. Metacarpals I-III 第一至第三掌骨; md. manual digits 指骨; pd. pedal digits 趾骨; ps. pubic symphysis 耻骨联合; pu. pubis 耻骨; py. pygostyle 尾综骨; r. radius 桡骨; ra. radiale 桡腕骨; sc. scapula 肩胛骨; sk. skull 头骨; st. sternum 胸骨; sy. synsacrum 愈合荐椎; ti. tibiotarsus 胫跖骨; tmt. tarsometatarsus 跖跖骨; tr. thoracic rib 胸肋; tv. thoracic vertebra 胸椎; u. ulna 尺骨; ul. ulnare 尺腕骨; un. ungual 指爪

rod-shaped and lacks an ascending process. A bone partially overlapped by a cervical vertebra is tentatively recognized as the quadrate, which seems to have a well-developed orbital process. The nasal bone is also incomplete, and is slightly expanded in the middle. Two frontals are preserved and dorsally expanded. The parietal is unfused with the frontal, with a well-developed articulating facet. A pair of small bones are tentatively recognized as the exoccipitals. In the orbital region, several small bones are recognized as the sclerotic bones.

The left mandible is relatively well preserved. The dentary is straight with a blunt rostral end that has a sloping and straight margin. The dentary is not branched at the caudal end. At least 16 teeth can be recognized on the dentary, they are tightly distributed from nearly the cra-

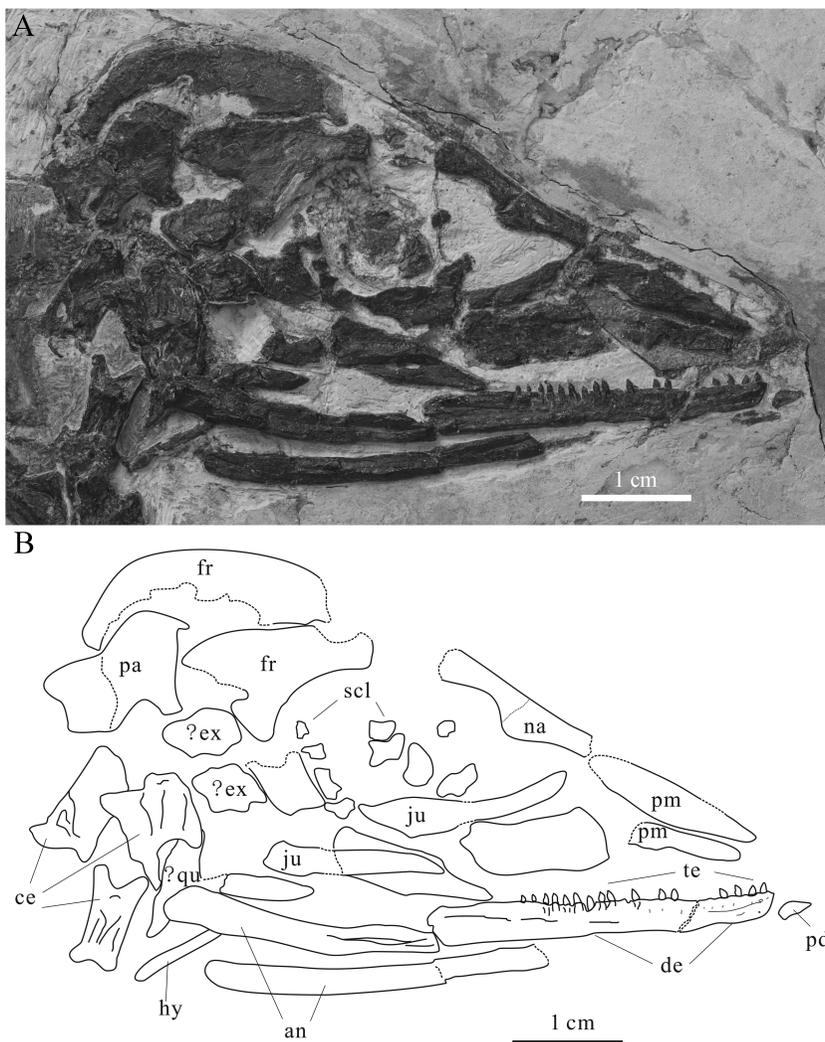


Fig. 3 Skull of the holotype of *Jianchangornis microdonta* gen. et sp. nov. (IVPP V 16708)

A. photo; B. linedrawing; an. angular 隅骨; ce. cervical vertebrae 颈椎; de. dentary 齿骨; ?ex. ? exoccipital ?外枕骨; fr. frontal 额骨; hy. hyoid bone 舌骨; ju. jugal 颧骨; na. nasal 鼻骨; pa. parietal 顶骨; pd. prementary 前齿骨; pm. premaxilla 前颌骨; ?qu. ? quadrate ?方骨; scl. sclerotic bones 巩膜骨; te. teeth 牙齿

nialmost end to about one third the caudal end of the dentary. Since some teeth are missing, the total account of the dentary teeth is greater than 16 and may reach 20. The teeth are of approximately the same size and are generally small and conical in shape. No serration is observed on the margin of the tooth. The angular is slightly curved and robust, and is slightly shorter than the dentary. No mandibular fenestra is present. The right mandible only preserved its caudal half including part of the edentulous portion of the dentary. A small bone near the rostral end of the dentary that slightly tapers cranially is recognized as a prementary. A pair of small foramen on the cranial margin of the rostral dentary possibly host for the ligamental articulation with the prementary.

Axial skeleton: the vertebral column is not completely preserved. However, eight cervicals

are recognized. Neither the atlas nor the axis seems to be preserved. The cervicals are elongated and seem to have a weakly heterocoelous central articulation. Cervical ribs are reduced as short and spine-shaped.

Seven posterior thoracic vertebrae are preserved in articulation; they are robust and seem to have a biconcave central articulation. Longitudinally distributed lateral depressions are developed on the thoracic centrum. The xiphisternum is dorsally exposed with a shallow spinal crest along its middle portion, it appears to be comprised of 9–10 sacra, but it is unclear whether or not it was fused with the ilia that extend cranially to the last thoracic vertebra. The transverse processes of the last five sacra are united distally to form fenestrae between two neighboring processes. The pygostyle is displaced to a position proximal to the left femur; it is small and roughly triangle-shaped. No free caudals are recognized.

The thoracic ribs are slender and moderately curved. The last pair of thoracic ribs are less curved and significantly shorter than more cranial ones. No uncinat process is observed. Gastralia are observed.



Fig. 4 Pectoral girdle of *Jianchangornis microdonta* gen. et sp. nov. (IVPP V 16708)

lt. lateral trabecula of sternum 胸骨的侧突; ris. rostral internal spine 内吻突;  
see Fig. 2 for other abbreviations

Pectoral girdle: the scapulae are disarticulated from the coracoids (Fig. 4). The right scapula is dorsally exposed, it is strongly curved and much shorter than the humerus, with a dorso-laterally directed glenoid facet. The caudal half of the scapular shaft tapers distally towards a pointed end. There exists a longitudinal concavity on the dorsal surface of the cranial scapula. The acromion is short and blunt. The left scapula is ventrally exposed. The left coracoid is well preserved in dorsal view. It has a well-developed sternocoracoidal impression. Distally the coracoid shows a well-developed facet for articulation with the sternum, but lacks a distinctive medial angle (angulus medialis). The coracoid possesses a prominent procoracoidal process, a distinctive scapular cotyle for articulation with the scapula, and concave medial and lateral margins. The acrocoracoidal process is pointed. The right coracoid is ventrally exposed. The furcula is cranially exposed; it is "U"-shaped, with robust clavicular rami tapering slightly towards their distal ends. It lacks a hypocleidum or a midline tubercle.

The sternum is dorsally exposed. It is longer than wide and has a distinctive rostral internal spine. It also has a pair of lateral trabeculae that extend latero-caudally, with slightly expanded distal ends. Medial trabeculae are present but do not appear to enclose a fenestra. The caudal portion of the sternum appears more laterally expanded than the cranial portion. A keel extending along the full length of the sternum also appears to be observable despite the fact the sternum is dorsally exposed.

**Table 1** Measurements of some skeletal elements of *Jianchangornis microdonta* gen. et sp. nov. (IVPP V 16708) (mm)

Skull length	72	Manual digit II-1 length	18(1) <sup>+</sup> , 20(r) <sup>+</sup>
Synsacrum length	34	Manual digit II-2 length	16(1) <sup>+</sup> , 16(r) <sup>+</sup>
Synsacrum maximum width	18 <sup>*</sup>	Manual digit II-3 length	6(1) <sup>+</sup> , 4.5(r) <sup>+</sup>
Pygostyle length	5.5	Manual digit III-ungual length	5.5(r) <sup>+</sup>
Scapula length	47(1) <sup>+</sup> , 53(r)	Ilium length	38(1)
Coracoid length	32(1), 30(r) <sup>+</sup>	Pubis length	51(r) <sup>+</sup>
Coracoid maximum width	17(1)	Pubic symphysis length	17 <sup>+</sup>
Furcula height	30	Femur length	60(1), 59(r)
Furcula maximum width	26 <sup>*</sup>	Tibiotarsus length	76(1), 75(r)
Humerus length	76(1), 75(r)	Fibula length	26(1) <sup>+</sup>
Humerus midshaft width	7(1), 7(r)	Tarsometatarsus length	37(1), 35(r) <sup>+</sup>
Humerus distal end width	12(1), 13(r)	Pedal digit I-2 length	5.5(r) <sup>+</sup>
Ulna length	83(1), 82(r)	Pedal digit II-1 length	12(1)
Ulna midshaft width	5(1), 4(r)	Pedal digit II-2 length	11(1)
Radius length	78(1), 81(r)	Pedal digit II-3 length	6(1) <sup>+</sup>
Radius midshaft width	3(1), 3(r)	Pedal digit III-1 length	15(r)
Metacarpal I length	10(1), 10(r)	Pedal digit III-2 length	11(r)
Metacarpal I midshaft width	5(1), 4.2(r)	Pedal digit III-3 length	10(r)
Metacarpal II length	33(1), 34(r)	Pedal digit III-4 length	7(r) <sup>+</sup>
Metacarpal II midshaft width	5(1), 4.5(r)	Pedal digit IV-2 length	8(r)
Metacarpal III length	36(1), 32(r) <sup>+</sup>	Pedal digit IV-3 length	6(r)
Metacarpal III midshaft width	2.2(1), 2.2(r)	Pedal digit IV-4 length	7(r)
Manual digit I-1 length	29(1), 25(r) <sup>+</sup>	Pedal digit IV-5 length	6(r) <sup>+</sup>
Manual digit I-2 length	9(1) <sup>+</sup> , 9(r) <sup>+</sup>		

\* Estimated measurement; + preserved measurement; l and r indicate left and right sides.

Forelimbs: the forelimbs are preserved in dorsal view. The right humerus is well ossified and shows a strap-like head and large deltopectoral crest with a convex margin. The deltopectoral crest is more than one third the total length of the humerus. Proximally, no capital incision is visible. Distally, the humerus is slightly medio-laterally expanded. The left humerus is less well ossified at both proximal and distal ends. The ulna is slightly longer than the radius, and significantly longer than the humerus.

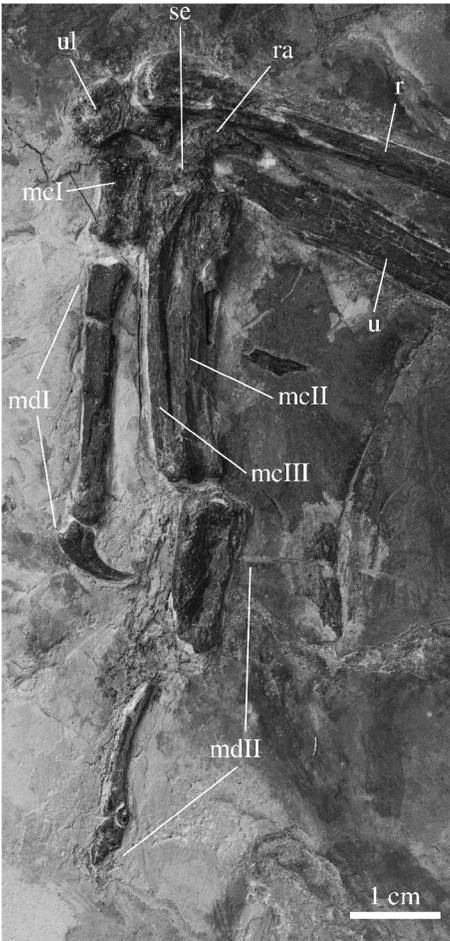


Fig. 5 Left manus of *Jianchangornis microdonta* gen. et sp. nov. (IVPP V 16708), with metacarpals II and III overturned to a cranial view

mdI—II. first and second manual digit 第一和第二指; se. semilunate carpal 半月型腕骨; see Fig. 2 for other abbreviations

two thirds length, but is straight and medio-laterally compressed for the distal one third length. The distal pubes are united into a “Y” shaped symphysis that is approximately one third the total length of the pubis and not distally expanded into a pubic foot. The ischia are not exposed.

**Hindlimbs:** the hindlimbs are nearly completely preserved in articulation. The femur is long and slightly curved, the length ratio of the femur to tibiotarsus is 0.79. The right femur is caudally exposed, showing prominent lateral and medial condyles separated by a deep intercondylar sulcus. The tibiotarsi are preserved in cranial view. The distal end of the right tibiotarsus shows nearly equally-sized and prominent medial and lateral condyles, with a narrow intercondylar incision. The medial condyle tapers slightly medially. The distal end of the tibiotarsus is as wide as or only slightly wider than the shaft. No supratendinal bridge is developed. The fibula is nearly completely preserved on the left side, and extends distally for less than half of the

Metacarpals II and III are nearly straight and cranially exposed, with approximately the same distal extent, but metacarpal II is about twice as wide as metacarpal III that is expanded proximally (Fig. 5). Proximally, metacarpals II and III appear unfused with each other, and not fused with the semilunate carpal either. Metacarpal I is robust and wider than other metacarpals; it is unfused with metacarpal II. The robust ulnare is preserved on the left side, showing a distinctive “V” shaped incision for articulation with the metacarpals as well as an articulation for the ulna. The radiale is much smaller compared to the ulnare. Metacarpals II and III are caudally exposed on the right side. They seem fused at the distal end, but unfused proximally, and form a very narrow intermetacarpal space. It is notable that the distal end of metacarpal III is incomplete, thus appearing shorter than metacarpal II.

The manual phalangeal formula is unknown as the third digit only preserved an isolated unguis located near the distal end of the right humerus. The first manual digit is long and extends past distal metacarpal II. The first phalanx is significantly longer than the second (unguis). The first phalanx of second digit is robust but not caudally curved; it is slightly longer than the second phalanx, which is much more slender. The unguis of the second digit is about the same size as that of the third digit, and both are smaller and less curved than the unguis of the first digit.

**Pelvic girdle:** the pelvis is dorsally exposed. The ilium is in close contact with the synsacrum, but it is unclear if they are fused with each other. The preacetabular portion of the ilium extends cranially to the last thoracic vertebra and is more expanded than the postacetabular one. The pubis is rod-shaped and medially curved for the proximal

length of the tibiotarsus, but only proximally preserved on the right side.

The right foot is not completely preserved distally, but the left foot is nearly complete. The tarsometatarsus is well fused at both proximal and distal ends. It is slightly constricted at the middle portion of the bone. Metatarsal V is absent. Metatarsal III extends more distally than II and IV. The pedal digits are preserved only partly in articulation. On the left side, the three phalanges of the second digit are complete in articulation, with the first phalanx longer than the second, and the third (ungual) is significantly shorter than the proximal two phalanges. On the right side, the third digit is nearly complete in articulation, with the phalanges becoming progressively shorter distally. The fourth digit on the right side seems to have preserved the last four phalanges, with the ungual slightly shorter than the other three nearly equally long phalanges. Unguals of all the four digits are preserved on the left side and are approximately of the same length. They are small compared to other phalanges and are only weakly curved.

Feather impressions are also faintly preserved on the holotype, but little detail can be recognized about their structures.

### 3 Discussion

The new bird undoubtedly represents an ornithurine by possessing the following features: synsacrum comprising 9–10 sacrals, pygostyle short, sternum elongated with a keel extending along its full length and a prominent internal rostral spine, scapula strongly curved with a dorso-laterally directed glenoid facet, metacarpals II and III well fused at the distal end, a coracoid with a well-developed procoracoidal process, furcula “U”-shaped and tarsometatarsus completely fused.

*Jianchangornis* is unique among known ornithurines in possessing a long first manual digit extending well beyond distal metacarpal II, which alone can distinguish the new avian from other known ornithurines. In basal avians, like *Archaeopteryx* (Mayr et al., 2005), confuciusornithids have a long first digit with an even longer ungual (Hou et al., 1995; Chiappe et al., 1999; Zhang et al., 2008). In both *Jeholornis* and *Sapeornis* (Zhou and Zhang, 2002a, b), the first digit also extends beyond distal metacarpal II, but the first phalanx is not as elongated as in *Jianchangornis*. In enantiornithines, the only known genus with similarly elongated first manual digit is *Protopteryx* from the Dabeigou Formation in Hebei Province (Zhang and Zhou, 2000). We can thus infer that the reduction of the first manual digit had occurred independently several times in early avian evolution.

Phylogenetic analysis indicates that *Jianchangornis* is a basal ornithurine (Fig. 7). However, adding of this new taxon to the data matrix of an earlier analysis (Zhou et al., 2008) only produces more vague relationships among basal ornithurines. This was probably caused by the

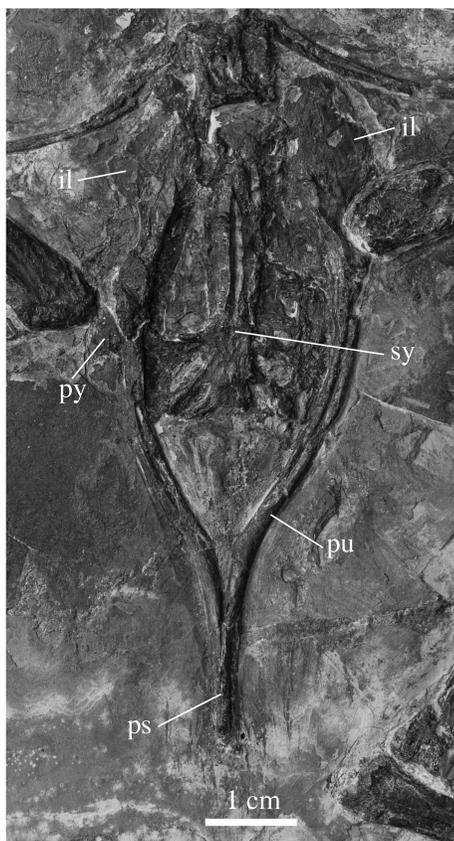


Fig. 6 Pelvic girdle and synsacrum of *Jianchangornis microdonta* gen. et sp. nov. (IVPP V 16708) in dorsal view (see Fig. 2 for abbreviations)

lack of determination of many characters from the crushed specimen as well as the mosaic combination of derived and primitive features in the new taxon.

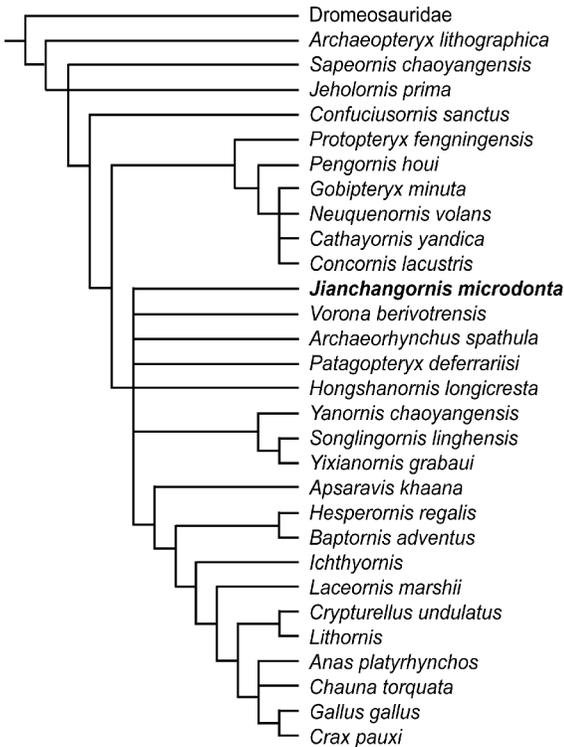


Fig. 7 Phylogeny of *Jianchangornis microdonta* gen. et sp. nov.

Phylogenetic analysis was conducted by using NONA 2.0 and WinClada, all characters were unordered; a total of 205 morphological characters are used according to Zhou et al. (2008), the data matrix is modified from Zhou et al. (2008); tree length = 506; CI = 0.52;

RI = 0.74, the cladogram is based on the strict consensus tree from 70 most parsimonious trees

low, 2001) and pedal unguis morphology strongly suggest that *Jianchangornis* shared a terrestrial locomotion with most Lower Cretaceous ornithurines.

*Jianchangornis* represents the second Early Cretaceous bird with the preservation of a predatory. *Hongshanornis* was the first Early Cretaceous and also the most basal bird with such a structure (Zhou and Zhang, 2005), which may further confirm that the predatory could be a feature common to Mesozoic ornithurines (Martin, 1987).

It is notable that the new taxon has well-fused distal metacarpals II and III; however, metacarpals II and III are proximally neither completely fused with each other nor well fused with the semilunate carpal, which is unknown in other Early Cretaceous birds. Although the proximal carpometacarpus might have been better fused in a fully adult individual, the observation may suggest that the ossification of the carpometacarpus starts from the distal end in ornithurines as is the case of the tarsometatarsus in extant birds, in contrast to enantiornithines and other more basal avians.

*Yanornis* represents the first known Chinese Early Cretaceous bird with definite evidence

*Jianchangornis* is most similar to *Yanornis* (Zhou and Zhang, 2001) in body size (Table 1). It is smaller than *Jeholornis* and *Sapeornis*, but is larger than other known ornithurines such as *Yixianornis*, *Archaeorhynchus* (Zhou and Zhang, 2006), *Hongshanornis* (Zhou and Zhang, 2005) and *Liaoningornis* (Hou et al., 1996) as well as all known enantiornithines including the largest enantiornithine *Pengornis* (Zhou et al., 2008). Its length ratio of the femur to tibiotarsus (0.79) is most similar to that of *Yixianornis* (0.78), and greater than that of *Yanornis* (0.67) but smaller than that of *Archaeorhynchus* (0.88). Its length ratio of metatarsal III/tibiotarsus is 0.47, which is similar to that of both *Yixianornis* (0.48) and *Yanornis* (0.49). The length ratio of the forelimb (humerus+ulna+metacarpal II) to hindlimb (femur+tibiotarsus+tarsometatarsus III) is 1.1, which is also most similar to that of *Yanornis* (1.14), and greater than those of *Yixianornis* (0.98) and *Hongshanornis* (0.79), but smaller than that of *Archaeorhynchus* (1.35). From above comparisons, the new bird is most similar to *Yanornis* in limb bone proportions, except with a relatively longer femur compared to tibiotarsus. These features combined with those of the toe proportions (Hopson, 2001; Zhou and Far-

for piscivorous diet (Zhou et al., 2002; Yuan, 2004) although radical diet switch has also been proposed for the same bird (Zhou et al., 2004). Fish remains including vertebrae, finrays and ribs are preserved near the left femur and tibiotarsus of the holotype of *Jianchangornis*. They can be undoubtedly referred to small teleosts, possibly *Jinanichthys* that is the most common fish from the Jiufotang Formation in the region. Although there is no compelling evidence to argue that they were the diets of the new avian, their extremely fragmentary status, their position not much distant from the stomach region of the bird, as well as the fact that they represent the only other distinctive biological remains associated with the bird on the whole slab, may suggest that this bird was piscivorous as also implied by the characteristics of the dentation on the mandible.

The discovery of a new basal ornithurine with a terrestrial adaptation and possible piscivorous diet further confirms that almost all basal ornithurines had adapted to a near lakeshore environment (Martin, 1983) that is different from that of most other contemporary birds which were dominated by arboreal forms. Such a niche differentiation mostly likely had played a key role in the evolution of ornithurines in the Early Cretaceous or beyond (Hou and Liu, 1984; Hou et al., 1996; Zhou and Zhang, 2005; You et al., 2006). Furthermore, it seems that the differentiation of ornithurines in the Early Cretaceous was almost as great as that of enantiornithines.

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