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# 尾羽龙(*Caudipteryx*)的新材料及其重要骨骼特征的补充和修订[1)]

周忠和[1] 汪筱林[1,2] 张福成[1] 徐 星[1]

(1 中国科学院古脊椎动物与古人类研究所 北京 100044)
(2 中国地质大学地球科学与资源学院 北京 100083)

尾羽龙和原始祖鸟一起被认为是最早发现的带有真正鸟类羽毛的恐龙(Ji et al., 1998),迄今已发现的尾羽龙包括邹氏尾羽龙(*Caudipteryx zoui*)和董氏尾羽龙(*Caudipteryx dongi*)两种(周忠和、汪筱林,2000),前者包括保存在中国地质博物馆的NGMC 97-4-A和NGMC 97-9-A两件标本,而后者依据的材料仅为保存在中国科学院古脊椎动物与古人类研究所的V 12344。以上标本都不是十分完整。本文依据最近新发现的两件几乎完整的尾羽龙标本,对该属的一些重要形态特征进行补充和修订,以期对其系统关系的讨论及其他相关理论问题的研究提供新的信息和佐证。

新发现的两件尾羽龙标本分别保存在辽宁省北票古生物博物馆(BPM 0001)和中国科学院古脊椎动物与古人类研究所(IVPP V 12430)。这两件标本虽都属成年个体,但与已描述的标本相比,个体略小(表1;图版I～II)。由于董氏尾羽龙和邹氏尾羽龙的主要区别是前者具有较小的胸骨,BPM 0001虽然个体较董氏尾羽龙小,但胸骨较大,暂归入邹氏尾羽龙种。而IVPP V 12430标本因没有保存骨化的胸骨,暂时定名为尾羽龙待定种(*Caudipteryx* sp.)。

**重要特征的补充和修订** 两件新的尾羽龙标本都保存了几乎完整的头骨(图1～2;图版III)。牙齿仅限于前颌骨,每侧各具一个细长并弯曲的牙齿,其他牙齿较小或退化。鼻孔较眶前窗大,这一特征和鸟类比较相似(图版III, A)。上颌骨上除具有一个圆形的气孔外,还具有一个位置靠前的气窝。泪骨"Y"形,并具有一个较大的气窝。方颧骨既和方骨相接也和鳞骨相连,这一特征和一般的兽脚类恐龙相似。

尾羽龙可能具有约12枚颈椎,最后一枚颈椎具有较长的颈肋。胸椎的数量较少,可能只有9枚,这一数量少于最原始的鸟类(图版V)。所有新标本的胸肋上都保存了钩状突(图版IV～V),IVPP V 12430标本保存了至少6枚钩状突,分别和前6枚胸肋相连。这些钩状突在位置和形态上与朝阳鸟(侯连海、张江永,1993)、孔子鸟以及窃蛋龙(Clark et al., 1999)等都较为相近。尾羽龙具有22枚尾椎,最后几节没有愈合成尾综骨(图3;图版VI),但尾椎的形态和窃蛋龙较为相似。尾椎没有组成坚固的杆状结构,相反,两件新的标本都

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显示，尾椎呈弯曲保存。

尾羽龙的新标本没有保存完整的叉骨。BPM 0001 的肩胛骨前缘保存了一个细小的骨片，可能代表了叉骨的一支（图 4；图版 IV）。肩胛骨和乌喙骨在 IVPP V 12430 上没有愈合。乌喙骨具有发达的二头肌结节以及一个椭圆形的上乌喙孔；上乌喙孔位于乌喙骨近端的中央，而在始祖鸟和恐爪龙中，该孔的位置比较靠内（Ostrom, 1976）。

在前肢上，两件新标本所揭示的最重要特征是手指指节的数量。Ji et al.（1998）认为，尾羽龙具有和一般的兽脚类以及始祖鸟和孔子鸟一样的“2-3-4”指式。受其影响，周忠和和汪筱林（2000）在研究董氏尾羽龙时，虽然只在第三指上观察到两节指节，但认为这可能是由于第三指的远端两节没有被暴露所致的，而且为了保存羽毛，也没有作进一步的修理。新的两件标本经仔细修理后证明，第三指确实只保存了两节指节。因此，尾羽龙的手指指式应为“2-3-2”而不是“2-3-4”（图 5；图版 VII）。换句话说，第三指已经退化了爪节，而只保留了近端的两节很短的指节，而且这两节指节的总长比其他任何一节指节还要短。这一特征和一些进步的鸟类如始反鸟（侯连海等，1999）相似，而不同于已知的兽脚类恐龙和最原始的鸟类。

新的尾羽龙标本还保存了关节最好的腰带，进一步证明耻骨和窃蛋龙类一样，呈前腹向伸展（图版 VIII），而不同于驰龙类（Norell and Makovicky, 1997; Burnham et al., 2000）和所有的鸟类。

在后肢上，腓骨和跟骨直接相连（图版 IX）。第一蹠骨和第二蹠骨的内后侧面关节，表明第一趾节和其他趾节至少具有一定的对握的特性（图版 X），这一现象与依据董氏尾羽龙所获得的结论相一致。

**讨论** 新发现的两件尾羽龙标本个体相对较小，但前肢与后肢的比例却相对较大，这可能表明，前肢在个体发育中相对发育较早。

尾羽龙最初被认为是和鸟类关系最近的兽脚类恐龙（Ji et al., 1998），后被多数学者认为和窃蛋龙的关系最近，包括依据分支系统学分析的结果（Sereno, 1999; Norell, pers. comm.），而另有一些学者认为它是次生失去飞行能力的古鸟（Feduccia, 1999; Jones, pers. comm.）。新发现的两件尾羽龙化石虽然保存了一些前所未知的鸟类特征，如，手指的指式为“2-3-2”而不是“2-3-4”，鼻孔大于眶前窗，较少的胸椎数，第一脚趾具有对握的特点等等，但在总体上尾羽龙仍然和恐龙更为相似，因此笔者仍然相信尾羽龙属于带羽毛的恐龙而不是失去了飞行能力的古鸟。当然，分支系统学是建立在哲学上不可检验或者证伪的简约性原理之上的，因此，任何关于尾羽龙的系统学的结论都不是最后的裁决。新材料中发现的更多的与鸟类相似的特点或许提醒我们，关于尾羽龙是龙还是鸟的争论可能还远远没有结束。

尾羽龙所具有的“2-3-2”的指式尚未见于任何已知的恐龙，但在早期鸟类中，始反鸟具有相似的特点（侯连海等，1999）。而更原始的始祖鸟和孔子鸟却还保留“2-3-4”的原始指式。在更进步的鸟类如华夏鸟和中国鸟中，由于第三指的进一步退化，已发育为“2-3-1”的指式。考虑到尾羽龙所具有的发育的初级飞羽以及前肢捕食功能的退化，第三指的退化也不足为奇。尾羽龙所具有的这一和鸟类相似的特点，还从另一方面证明鸟类和兽脚类恐龙前肢的三个手指确实具有同源的关系。第三指的退化在恐龙和早期鸟类的演化中至少独立出现过多次。

**关键词**　辽宁北票，早白垩世，尾羽龙，骨骼特征
**中图法分类号**　Q915.865

# IMPORTANT FEATURES OF *CAUDIPTERYX* - EVIDENCE FROM TWO NEARLY COMPLETE NEW SPECIMENS

ZHOU Zhong-He[1]　WANG Xiao-Lin[1,2]　ZHANG Fu-Cheng[1]　XU Xing[1]

(1 *Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences* Beijing 100044)

(2 *College of Earth Science and Resources, China University of Geosciences* Beijing 100083)

**Abstract**　Two nearly complete specimens of *Caudipteryx* preserved a lot more new information about its skeletal anatomy. It has some unexpected bird characters such as the manual digital format of "2-3-2" as in advanced birds rather than the previously recognized "2-3-4" as in *Archaeopteryx*, *Confuciusornis* and most theropods, the ungual of the third manual digit is lost; in the skull the nasal opening is larger than the antorbital fenestra, the tail is composed of 22 unfused caudals, there exist only 9 dorsal vertebrae, there are about 12 cervical vertebrae. On the other hand, both new specimens confirm that the pubis of *Caudipteryx* is antero-ventrally rather than posteriorly oriented; the fibula contacts the calcaneum; the quadratojugal contacts both the squamosal and the quadrate. The teeth of *Caudipteryx* are restricted to the premaxilla in all known specimens. The scapula is expanded at the distal end. The coracoid has a prominent biceps tubercle and possesses an elliptic supracoracoid foramen. Both new specimens appear to confirm that the first metatarsal articulates with the postero-medial surface of the second metatarsal and the hallux of the foot is at least partially reversed, therefore suggesting that the ancestor of *Caudipteryx* had probably possessed the arboreal capability. The reduction of the third manual digit in *Caudipteryx* also provides further evidence for the homology of the three manual digits in birds and theropod dinosaurs although the reduction of the third digit had obviously appeared many times in the history of dinosaurs and birds. Although *Caudipteryx* is still accepted as a feathered dinosaur, its newly discovered remarkable bird-like characters probably indicate that its phylogenetic position remains a debatable issue.

**Key words**　Liaoning, Early Cretaceous, *Caudipteryx*, skeletal anatomy

## 1　Introduction

*Caudipteryx* was described together with *Protarchaeopteryx* as the first two feathered dinosaurs with true feathers (Ji et al., 1998), but it has been argued by some as a flightless bird (Feduccia, 1999). The second species of *Caudipteryx* (*C. dongi*) has been based on an incomplete individual (Zhou and Wang, 2000). *C. dongi* is distinguishable from *C. zoui* mainly by a relatively smaller sternum. Two nearly complete new specimens have recently been collected, which provide a lot more important new information about its anatomy, and shed new light on the discussion of its systematic position and the origin of the flight of birds. These two new specimens are the Beipiao Paleontological Museum specimen in Liaoning Province (BPM 0001) and the Institute of Vertebrate Paleontology and Paleoanthropology specimen in Beijing (IVPP V 12430) respectively. Both contain a complete skull and nearly completely articulated postcranial skeleton (Pls. I~ II). They are slightly smaller than the other known specimens of *Caudipteryx* (Table 1). BPM 0001 preserved a sternum that is larger than that of *C. dongi*, it is therefore referred to *C. zoui*. The IVPP V 12430 specimen does not preserve an ossified sternum, in other aspects of major skeletal elements it is similar to both *C. zoui* and *C. dongi*. It is referred to *Caudipteryx* sp. in this paper.

## 2 Descriptions

The following description is mainly based on information from the two new specimens of *Caudipteryx*. New and revised anatomical characters are the focus:

**Skull** Both new specimens (IVPP V 12430 and BPM 0001) preserved nearly complete skulls. The frontal is expanded and has a supraorbital rim as in primitive birds such as *Archaeopteryx* (Wellnhofer, 1974, 1993) and *Confuciusornis* (Hou et al., 1995). The nasals are contacting each other nearly along the full length but remain unfused. The premaxilla has a short nasal process and short maxillar process. The two premaxillae are unfused. Teeth are only preserved in the premaxilla and lost in the dentary and the maxilla; this character is consistent in all known *Caudipteryx* specimens. The teeth are needle-shaped and constricted at the base as in birds. All the teeth are restricted to the anterior half of the ventral margin of the premaxilla. In the BPM 0001 specimen the premaxilla preserved a remarkably long and slender tooth (Fig. 1; Pl. III, A). In the IVPP V 12430 specimen each premaxilla also preserved a large and curved tooth (Fig. 2; Pl. III, B); the rest of the teeth on the premaxilla are reduced and much smaller. Nutrient foramen or grooves are visible in the lateral premaxilla, the maxilla and the dentary.

The nasal opening, the antorbital fenestra and the orbit are best preserved in the BPM 0001 specimen. It is interesting to note that the nasal opening is larger than the antorbital fenestra (Fig. 1; Pl.III, A), which is similar to birds but not to most theropod dinosaurs such as ornithomimids, dromaeosaurs and troodontids. The nasal opening is posteriorly bordered by the branched nasal; it is elliptical in shape, its length is about twice that of its height.

The maxilla is slightly longer than the jugal as in most theropods; it contains a rounded pneumatic fenestra in the middle and a pneumatic fossa in the anterior part. The jugal has a long and posteriorly directed dorsal ascending process, which tapers distally. The lacrymal is "Y"-shaped; both of its dorso-posterior and anterior processes taper distally. The lacrymal appears to bear a rounded pneumatic fossa on the top.

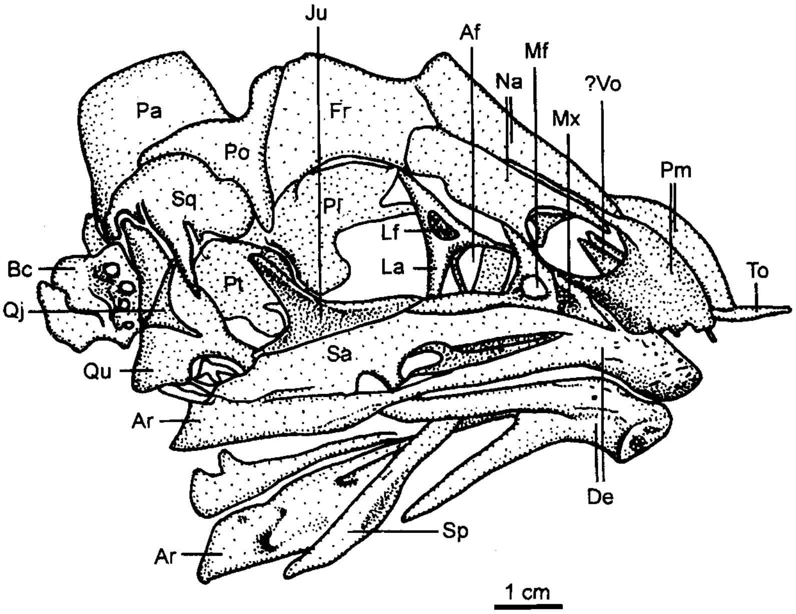

Fig. 1 Skull of *Caudipteryx zoui* (BPM 0001)

简字说明 Abbreviations: Af, antorbital fenestra 眶前窗； Ar, articular 关节骨； Bc, brain case 脑颅； De, dentary 齿骨； Fr, frontal 额骨； Ju, jugal 颧骨； La, lacrymal 泪骨； Lf, lacrymal fossa 泪骨的气窝； Mf, maxillar fenestra 上颌骨的气窗； Mx, maxilla 上颌骨； Na, nasal 鼻骨； Pa, parietal 顶骨； Pl, palatine 腭骨； Pm, premaxilla 前颌骨； Po, postorbital 眶后骨； Pt, pterygoid 翼骨； Qj, quadratojugal 方颧骨； Qu, quadrate 方骨； Sa, surangular 上隅骨； Sp, splenial 夹板骨； Sq, squamosal 鳞骨； To, tooth，牙齿； ? Vo, ?vomer 犁骨

The postorbital is separately preserved in the IVPP V 12430 specimen (Fig. 2; Pl. III, B). It is generally similar to that of dromaeosaurs and primitive birds. The ectopterygoid is also well preserved in the same specimen; it is hooked in shape.

The quadratojugal abuts the lateral surface of the quadrate in the BPM 0001 specimen, which is consistent with the original description of *Caudipteryx*. As in dromaeosaurs and primitive birds such as *Confuciusornis*, the quadratojugal has a short posterior process and two long and slender ascending processes; the latter two processes extend dorsally and anteriorly respectively and form an angle of about 90 degrees. The quadrate appears to be in articulation with the pterygoid in both the BPM 0001 and the IVPP V 12430 specimens; it is vertical, long and expanded at the base; it has a single head that articulates with the squamosal as best shown in the BPM 0001 specimen (Fig. 1; Pl.III, A). The squamosal has a long and pointed ventral process that appears to be in contact with the ascending process of the quadratojugal as previously suggested. In primitive birds such as *Archaeopteryx* and *Confuciusornis*, the quadratojugal lost contact with the squamosal although it also abuts on the quadrate. The lower jaw has a large mandibular fenestra as in oviraptorids. The dentary is forked posteriorly; its ventral branch tapers posteriorly and

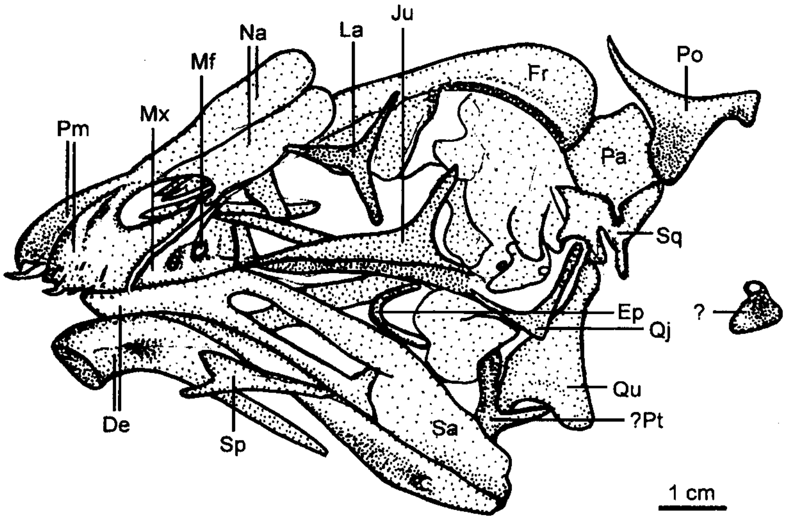

Fig.2 Skull of *Caudipteryx* sp. (IVPP V 12430)

简字说明 Abbreviations: De, dentary 齿骨；Ep, ectopterygoid 外翼骨；Fr, frontal 额骨；Ju, jugal 颧骨；La, lacrymal 泪骨；Mf, maxillar fenestra 上颌骨的气窗；Mx, maxilla 上颌骨；Na, nasal 鼻骨；Pa, parietal 顶骨；Pm, premaxilla 前颌骨；Po, postorbital 眶后骨；?Pt, ?pterygoid 翼骨；Qj, quadratojugal 方颧骨；Qu, quadrate 方骨；Sa, surangular 上隅骨；Sp, splenial 夹板骨；Sq, squamosal 鳞骨

curved ventrally. The splenial is long and strap-shaped.

**Vertebral column** There are estimated 12 cervical vertebrae; all have a pair of spine-like cervical ribs and elongate postzygopophysis; the last cervical vertebra has a pair of long ribs which are approximately half the length of the dorsal ribs. There appear to be only 9 thoracic vertebrae and dorsal ribs as in more advanced birds while primitive bird *Archaeopteryx* has 13 and *Confuciusornis* has 12 thoracic vertebrae. The dorsal vertebrae lack deep pleurocoels. Among the dorsal ribs, the fourth is the longest. Three distinct uncinate processes are preserved in the *Caudipteryx dongi* specimen (IVPP V 12344), and at least four oberserved in the Beipiao specimen (BPM 0001)(Pls. I, IV) and 6 in the IVPP V 12430 specimen (Pl. V). In the IVPP V 12430 specimen the 6 uncinate processes are attached to the anterior 6 dorsal ribs; and the second, third and fourth uncinate processes are longer than the other uncinate processes. The uncinate processes are flat, slightly curved and expanded at the ventral ends; they articulate with the dorsal ribs at about the middle position as in ornithurine bird *Chaoyangia* (Hou and Zhang, 1993); they are also similar to that of *Confuciusornis* and oviraptorids in shape (Clark et al., 1999). Sternal ribs were preserved associated with the sternum, they are straight and flatter than the dorsal ribs.

The tail is nearly completely preserved in both the IVPP V 12430 and BPM 0001 specimens. The tail was not preserved as a straight rod as in dromaeosaurs; on the contrary, the tail is curved in both new specimens. The number of caudals was

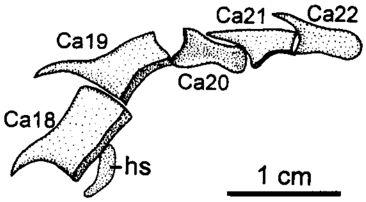

Fig.3 Posterior caudal vertebrae of *Caudipteryx* sp. (IVPP V 12430)
简字说明 Abbreviations: Ca18～22, caudal vertebrae 18～22 第18～22 节尾椎；hs, haemal spine 脉弧

counted as 22 in NGMC 97-4-A specimen; this is confirmed in the IVPP V 12430 specimen. None of the caudals are fused, the pygostyle that was recently reported in oviraptorids (Barsbold et al., 2000) is absent in *Caudipteryx* (Fig.3; Pls. I～II, VI); however, their terminal caudals are generally similar in shape; their posterior vertebrae all have an elongated prezygopophysis. The haemal spines of the anterior three caudals are nearly equally long and slender. Other haemal spines decrease in height and size posteriorly. The fourth to eighth haemal spines are shorter but are slender too. The rest haemal spines are more anteroposteriorly expanded than more anterior ones. The prezygopophysis becomes progressively longer from twelfth to twenty-second caudals (Pl.VI).

**Pectoral girdle** The scapula is straight and has a slightly expanded distal extremity. The scapula appears to be fused with the coracoid in the BPM 0001 specimen, but they are separated in the IVPP V 12430 specimen, in which the coracoid has a facet for the articulation of the scapula. The scapula and the coracoid form an angle of about 90 degrees as in *Archaeopteryx* and some maniraptorian theropods (Xu et al., 1999). The scapula lacks a prominent acromion process as in *Archaeopteryx* and *Confuciusornis*. The coracoid has a prominent biceps tubercle as in *Archaeopteryx* and many theropod dinosaurs. The coracoid preserved a supracoracoid nerve foramen in both the BPM 0001 and IVPP V 12430 specimens; the elliptic foramen is situated near the proximal end of the middle of the coracoid (Fig.4; Pls. IV～ V). In *Deinonychus* and *Archaeopteryx* the supracoracoid foramen is more medially situated (Ostrom, 1976).

No furcula is completely preserved in either of the new specimens. In BPM 0001, the slender bone in front of the scapula probably represents one branch of the furcula (Fig.4; Pl. IV).

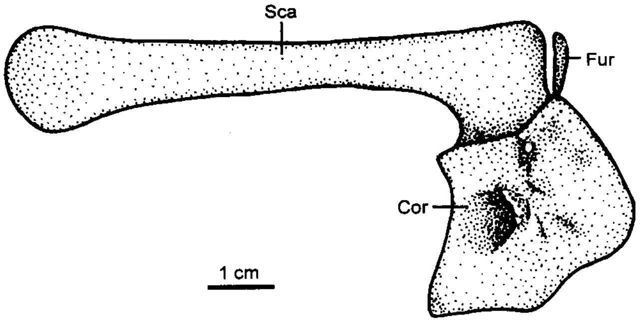

Fig.4 Pectoral girdle of *Caudipteryx zoui* (BPM 0001), right in lateral view
简字说明 Abbreviations: Cor, coracoid 乌喙骨；Fur, furcula 叉骨；Sca, scapula 肩胛骨

**Forelimbs** The most significant feature that has been revealed from the new materials of *Caudipteryx* is the phalangeal format of the manus. It was previously recognized as "2–3–4 " as in many theropods and the primitive birds *Archaeopteryx* and *Confuciusornis*. The short third manual digit in the type of *Caudipteryx dongi* had been regarded as the result of insufficient preparation (Zhou and Wang, 2000); however, all the two new specimens of *Caudipteryx* and further observation of the type of *C. dongi* show that the third digit is a lot more reduced and contains only two short phalanges (Fig. 5; Pls. VII~ VIII), the first phalanx is longer than the second one. The total length of the third digit is shorter than any other phalanges of the manual digits. The third digit also abuts tightly on the first phalanx of the second digit as in advanced birds. It is also noteworthy that the ungual of the third digit is lost. Primitive birds *Archaeopteryx*, *Confuciusornis* and *Eoenantiornis* (Hou et al., 1999) all retained three unguals in the wing as in their theropod ancestors. The unguals in the first and second digits are shorter than the penultimate phalanges; they are less curved than in *Archaeopteryx* and *Confuciusornis* and most theropods. As in *Archaeopteryx* and *Confuciusornis* and most theropods the second phalanx is longer than the first in the second digit, indicating that *Caudipteryx* still retained part of its ancestral grasping pattern in the manus.

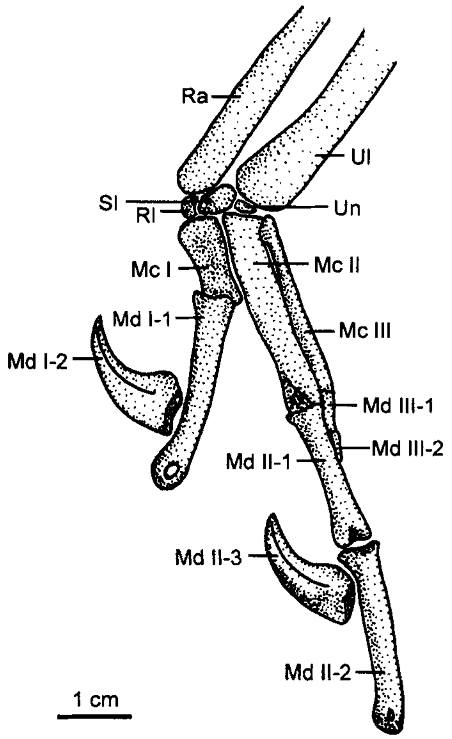

Fig. 5 Manus of *Caudipteryx* sp. (IVPP V 12430)

简字说明 Abbreviations: Mc I~III, metacarpals I~III 第1~3掌骨; Md I~III-1~3, phalanges 1~3 of manual digits I~III 第一~三指骨的第1~3指节; Ra, radius 桡骨; Rl, radiale 桡腕骨; Sl, semilunate bone 半月形腕骨; Ul, ulna, 尺骨; Un, ulnare 尺腕骨

Three carpals are recognizable near the distal end of the radius and ulna in the IVPP V 12430 specimen. The carpals are not fused with the metacarpals, therefore the carpometacarpus is absent in *Caudipteryx*. The semilunate bone is the largest; it sits on both the first and second metacarpals. There is a small carpal distal to the ulna; it probably represents the ulnare; it lacks the metacarpal incision as in birds. Another small carpal distal to the radius is recognized as the radiale (Fig. 5; Pl. VII).

The manus is longer than the radius as in maniraptorian dinosaurs and the most primitive birds *Archaeopteryx* and *Confuciusornis*. In more advanced birds the manus is close to or slightly shorter than the radius (Zhou, 1995). The third metacarpal is laterally compressed; it is shorter and significantly narrower than the second metacarpal.

**Pelvic girdle** The pelvic girdle is well articulated in the new specimens (Pls. I~II, VIII). The notch in the ventral margin of the pubic peduncle of the type of *Caudipteryx* was interpreted as characteristic of opisthopubic pelves (Ji et al., 1998). However, based on the description of *C. dongi* it was suggested that the pubis is antero-ventrally oriented as in oviraptorids and some advanced maniraptorian dinosaurs but is different from that of dromaeosaurs, segnosaurids and birds. The two new materials preserved even better articulated pelves, and they all confirm an antero-ventral pubis. The pubis is long and nearly twice the length of the ischium; it also has a short pubic foot. The pubic symphysis is about half the length of the pubis; in primitive birds it is about one third of the length of the pubis or even shorter.

The ilium lacks a large and deep iliac fossa for M. cuppedicus as in oviraptorids (pers. observ.) and early birds. The pubic peduncls is much broader and deeper than the ischiadic peduncle as in dromaeosaurs and birds. The pubic peduncle forms the anterior wall of the acetabulum; it extends further ventrally and posteriorly in birds. The new specimens confirm that the ischium has a triangular shaft that bears a large and pointed obturator process; it is more robust than in dromaeosaurs, oviraptorids and birds.

**Hindlimbs** Nearly completely articulated hindlimbs are preserved in both the Beipiao specimen (BPM 0001) and the IVPP V 12430 specimen. The fibula is completely preserved, it is long and extends to the distal end of the tibia and contacts the calcaneum in all new specimens; it tapers distally and the distal two thirds is needle-shaped (Pls. I~II, IX). The calcaneum is disk-shaped.

The fifth metatarsal is well preserved in the IVPP V 12430 specimen (Pl. II); it is slender and rod-shaped as in primitive birds *Archaeopteryx*, *Confuciusornis* and most maniraptorian theropods; it is less than one third the length of the second metatarsal. The third metatarsal is longer than the other two major metatarsals in both new specimens (Table 1), its mid-shaft is remarkably laterally compressed and is much narrower than the second and fourth metatarsals.

The first pedal digit is well preserved in both new specimens (Pls. I~II, X). In both cases the hallux appears to be at least partially reversed to the rest of the pedal digits. It is also noteworthy that the first metatarsal articulates with the postero-medial rather than the medial surface of the second metatarsal. The distal end of the first metatarsal is ball-shaped, which appears to be an adaptation for the rotation of the hallux.

**Table 1 Measurements of the two new specimens of *Caudipteryx* (BPM 0001 and IVPP V 12430) (mm)**

| | *C. zoui* (BPM 0001) | *C.* sp. (IVPP V 12430) |
|---|---|---|
| Maximum dorsal rib length | 114* | 120 |
| Maximum sternal rib length | 38* | 36 |
| Maximum uncinate process length | | 26 |
| Scapula length | 80 | 80 |
| Scapula mid-shaft width | 7 | 8 |
| Scapula distal width | 17 | 16 |
| Coracoid length | 34 | 35 |
| Coracoid height | 26 | 27 |
| Sternal plate length | 30* | |
| Humerus length | 72 | 69 |
| Humerus mid-shaft width | 7 | 8 |
| Ulna length | 62 | 61 |
| Ulna mid-shaft width | 6 | 6 |
| Radius length | 59 | 56* |
| Radius mid-shaft width | 3.5 | 4 |
| Manus length | 91 | 91 |
| Metacarpal I length | 11 | 11 |
| Metacarapal I proximal end width | 5 | 5 |
| Metacarpal II length | 28 | 28 |
| Metacarpal II proximal end width | 5 | 5 |
| Metacarpal III length | 25 | 23 |
| Metacarpal III proximal end width | 2 | 2 |
| First phalanx of manual digit I length | 25 | 26 |
| Second phalanx of manual digit I length | 16 | 16 |
| First phalanx of manual digit II length | 17 | 19 |
| Second phalanx of manual digit II length | 24 | 24 |
| Third phalanx of manual digit II length | 15 | 15 |
| Ilium length | 115 | 112 |
| Ilium height | 59 | 53 |
| Ischium length | 72 | 72* |
| Pubis length | 124* | 125* |
| Leg total length | 526 | 516 |
| Femur length | 145 | 145 |
| Femur mid-shaft width | 15 | 16 |
| Tibia length | 188 | 183 |
| Fibula length | 188 | 175 |
| Metatarsal I length | 16 | 15 |
| Metatarsal II length | 102 | 102 |
| Metatarsal II mid-shaft width | 8 | 8 |
| Metatarsal III length | 113 | 112 |
| Metatarsal III mid-shaft width | 2 | 2 |
| Metatarsal IV length | 107 | 106 |
| Metatarsal IV mid-shaft width | 7 | 8 |
| Metatarsal V length | 30 | 31 |

Continued

| | *C. zoui* (BPM 0001) | *C.* sp. (IVPP V 12430) |
|---|---|---|
| First phalanx of pedal digit I length | 13 | 12 |
| Second phalanx of pedal digit I length | 12 | 12 |
| First phalanx of pedal digit II length | 23 | 22 |
| Second phalanx of pedal digit II length | 16 | 14 |
| Third phalanx of pedal digit II length | 19 | 17 |
| First phalanx of pedal digit III length | 24 | 23 |
| Second phalanx of pedal digit III length | 19 | 17 |
| Third phalanx of pedal digit III length | 15 | 13 |
| Fourth phalanx of pedal digit III length | 18 | 18 |
| First phalanx of pedal digit IV length | 14 | 12 |
| Second phalanx of pedal digit IV length | 8 | 8 |
| Third phalanx of pedal digit IV length | 6 | 6 |
| Fourth phalanx of pedal digit IV length | 4 | 5 |
| Fifth phalanx of pedal digit IV length | 14 | 14 |

* indicates estimated measurement.

## 3 Discussions

Based on the measurements of the total leg length (526 mm in BPM 0001 and 516 mm in IVPP V 12430), both new specimens are slightly smaller than all known specimens of *Caudipteryx zoui* (540 mm in NGMC 97-9-A and 550 mm in NGMC 97-4-A) and *C. dongi* (553 mm in IVPP V 12344). However, their leg to arm ratio is smaller than that of other larger *Caudipteryx* specimens, which may indicate that the arm was developed earlier than the leg in the development of *Caudipteryx*.

*Caudipteryx* was initially described as one of the first two feathered dinosaurs with true bird feathers. It has been acclaimed as one of the most critical evidence supporting the hypothesis of the dinosaurian origin of birds; however, because of many of its ambiguous characters its phylogenetic position has been hotly debated. It has recently been suggested to be a relative of oviraptorids (Sereno, 1999) or a flightless bird (Feduccia, 1999).

The newly discovered specimens of *Caudipteryx* provide a lot yet unknown important information about the anatomy of this maniraptorian. It obviously possesses more bird characters than previously recognized. For instance, the teeth are constricted at the base, the antorbital fenestra is smaller than the nasal opening, the uncinate processes are present, the number of the thoracic vertebrae is less than that of *Archaeopteryx* and *Confuciusornis*, the third manual digit is composed of only two reduced phalanges, the third manual digit tightly abuts on the second digit, the hallux is reversed. On the other hand, the quadratojugal is in contact with the squamosal as in dinosaurs but not in birds; the haemal spines are more developed than in *Archaeopteryx*; the sternal plates are unfused; the first phalanx of the first manual digit extends distally to the middle of the first phalanx of the second digit; the pelvis is similar to oviraptorids in having an anteroventrally oriented pubis rather than a retroverted pubis as in dromaeosaurs and birds; the obturator process of the ischium is large; the pubic symphysis is at least half the length of the pubis; the astragalus and calcaneum are separated from the tibia; the tarsometatarsus is unfused. Therefore *Caudipteryx* retained an unexpected combination of primitive and derived characters.

Phylogenetic analysis of *Caudipteryx* indicates that it is more closely related to oviraptorids than to any other dinosaurs or birds (Sereno, 1999; Norell, pers. comm.). The unexpected distribution of many bird characters in maniraptorian dinosaurs probably indicates that in a sense we are now getting further close to the transition between birds and their immediate ancestors. On the other hand, it must be pointed out that cladistic result is based on the assumption of the principle of parsimony which is, however, philosophically untestable. Therefore, although with the discoveries of more unexpected bird-like characters in *Caudipteryx* we still believe it is a feathered dinosaur because of its overwhelming similarity to dinosaurs it must be admitted that we have no compelling evidence to exclude it from being a flightless bird; in other words, theoretically there is no single dinosaurian character in *Caudipteryx* that could not have been reversed from its presumable avian ancestor. Furthermore, the presence of true avian feathers together with the remarkable avian manual digital format and the possible reversed hallux force us to be open minded on the issue of its phylogenetic position.

The uncinate process is present in nearly all modern birds. Such structures were regarded as unique to birds and indicative of skeletomuscular capacity for inhalatory filling of abdominal air sacs (Ruben et al., 1997). The oldest known ornithurine bird with such structure is the Early Cretaceous *Chaoyangia* from Liaoning, northeast China. Oviraptorids (Clark et al., 1999) and the oldest known beaked bird *Confuciusornis* also have similar uncinate processes, which may indicate that this structure is not a synapomorphy for birds but rather that it had appeared in birds and theropods a lot more times than we expected. Although uncinate processes have previously been reported in various dinosaurs the recent description of uncinate processes in oviraptorids and dromaeosaurids (Clark et al., 1999) and its presence in *Caudipteryx* add further evidence for the close affinity of birds and theropod dinosaurs. The uncinate processes in both oviraptorids and *Caudipteryx* are hardly distinguishable from those of birds such as *Chaoyangia* and *Confuciusornis*.

The first metatarsal articulates with the postero-medial side of the second metatarsal. The hallux appears to be at least partially reversed as compared to the rest of the digits as in birds but not in any other known dinosaurs. This character can probably be explained as a retained ancestral trait. If *Caudipteryx* was a true feathered theropod rather than a secondarily flightless bird, then we would have to believe that at least some maniraptorian dinosaurs might have already had arboreal capability that was believed by many as critical to the origin of the avian flight, thus providing further evidence for the arboreal hypothesis of the origin of the flight of birds.

The phalangeal format (“2–3–2”) of the manus of *Caudipteryx* is unique among maniraptorian dinosaurs, which normally have a format of “2–3–4” as in early birds *Archaeopteryx* and *Confuciusornis*. The manus of *Caudipteryx* retained only two unguals, each in the first and second digits, and the third digit contains two reduced phalanges as in some more advanced early birds such as the Early Cretaceous enantiornithine *Eoenantiornis* (Hou et al., 1999). Other early enantiornithine birds such as *Cathayornis* and *Sinornis* only retained one phalanx in the third digit as in modern birds (Zhou, 1995). The reduction of the third digit is obviously related to the attachment of the primary feathers. As in birds the third digit is tightly attached to the second digit. Since *Caudipteryx* is interpreted as a theropod dinosaur, therefore the loss of the distal two phalanges occurred independent of the similar reduction in the early evolution of birds.

The relative short trunk and long neck of *Caudipteryx* probably provide further evidence that it was a fast running animal. The long neck may also be related to its presumed herbivorous habit as evidenced by the presence of the gastroliths and the reduction of teeth in the dentary and the maxilla in all known specimens.

Finally, the homology of the manual digits of birds and dinosaurs is still a controversial issue in terms of evidence from fossils and development (Wagner and Gauthier, 1999). Since the third digit of *Caudipteryx* is reduced in such a way as in birds that it adds further evidence for the homology of the three manual digits retained in maniraptorian dinosaurs and birds.

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## Explanations of plates

**Plate I** *Caudipteryx zoui* (BPM 0001), × 0.24

**Plate II** *Caudipteryx* sp. (IVPP V 12430), × 0.19

**Plate III** Skulls of (A) *Caudipteryx zoui* (BPM 0001), × 1.2; and (B) *Caudipteryx* sp. (IVPP V 12430), × 1.1

**Plate IV** *Caudipteryx zoui* (BPM 0001), showing the pectoral girdles and partial forelimbs, × 1

**Plate V** *Caudipteryx* sp. (IVPP V 12430), showing the pectoral girdles and complete dorsal ribs, × 0.9

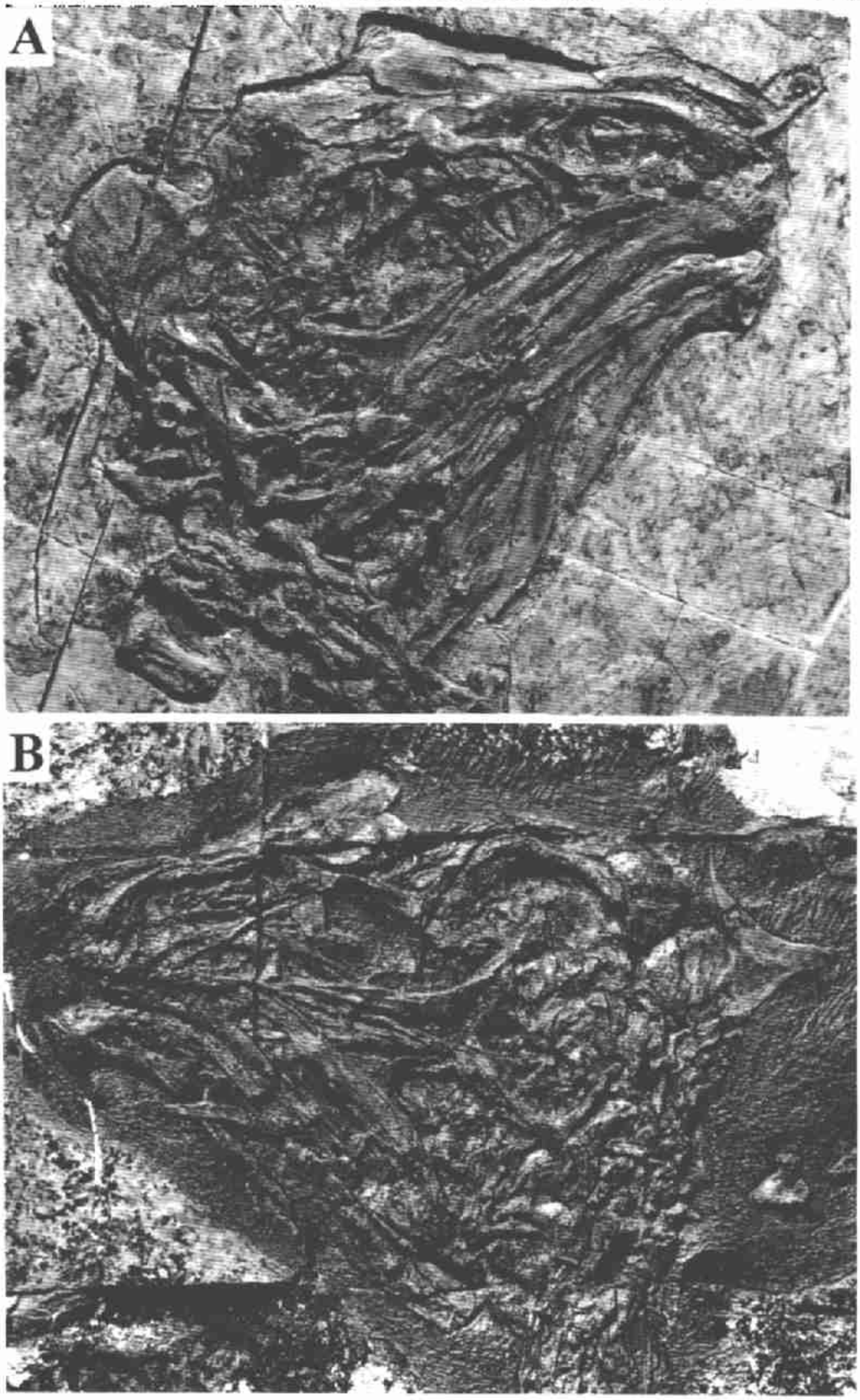
**Plate VI** *Caudipteryx* sp. (IVPP V 12430), showing the posterior caudals and the ilia, × 1

**Plate VII** Manus of *Caudipteryx* sp. (IVPP V 12430), × 2

**Plate VIII** *Caudipteryx zoui* (BPM 0001), showing the pelvis and gastroliths, × 0.7

**Plate IX** Tibiae and the fibulae of *Caudipteryx* sp. (IVPP V 12430), × 0.9

**Plate X** Feet of *Caudipteryx zoui* (BPM 0001), × 0.9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