

辽宁早白垩世会鸟一新种¹⁾

Pauline PROVINI¹ 周忠和² 张福成²

(1 巴黎高等师范学院地球科学系 巴黎 75230)

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

摘要: 记述了辽宁朝阳大平房早白垩世九佛堂组湖相地层中发现的会鸟化石一新种, 窄脊会鸟 (*Sapeornis angustis* sp. nov.)。尽管新种正型标本属于一亚成年个体, 但除个体较小外, 还在许多特征上很容易与属型种(朝阳会鸟)相区别。例如, 不超过6枚荐椎, 肱骨的三角脊和气窗均较细窄, 三角脊远端的背突不显著尖锐, 鸟喙骨具有较长的肩峰突, 叉骨枝较细, 叉骨突较短, 第一掌骨以及耻骨突均相对较短等。和始祖鸟以及其他已报道的会鸟标本一样, 新种材料没有保存胸骨, 肋骨上也未见钩状突起, 推测这两种结构可能在个体发育的晚期才开始骨化, 上述标本均为发育早中期的个体。会鸟新种的发现为这一基干的原始鸟类提供了新的解剖特征, 并表明在会鸟的演化过程中存在个体的逐步增大以及一些形态特征的特化现象。这一新的发现还为分析早白垩世陆地生态系统的鸟类多样性增添了新的资料。

关键词: 中国辽宁, 早白垩世, 会鸟, 新种

中图法分类号: Q915.865 **文献标识码:** A **文章编号:** 1000-3118(2009)03-0194-14

A NEW SPECIES OF THE BASAL BIRD *SAPEORNIS* FROM THE EARLY CRETACEOUS OF LIAONING, CHINA

Pauline PROVINI¹ ZHOU Zhong-He² ZHANG Fu-Cheng²

(1 Earth Science Department, Normal Superior School Paris 75230, France pauline.provini@ens.fr)

(2 Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences Beijing 100044 zhonghe@yeah.net)

Abstract A new species of the avian *Sapeornis* is described based on a specimen discovered from the Early Cretaceous lacustrine Jiufotang Formation in Dapingfang, Chaoyang, Liaoning Province, North-east China. The new species *Sapeornis angustis* is relatively small compared to the type species, *S. chaoyangensis*, and distinguishable from the latter in possessing 5–6 sacrals, a distinct narrow humeral deltopectoral crest with a less acute dorso-distal process, narrower furcular rami, a shorter hypocleidum, a relatively longer Metacarpal I and a shorter pubic symphysis. Like in *Archaeopteryx* and other known specimens of *Sapeornis*, the new species preserves no uncinate process or sternum, suggesting that both structures are ossified in a late stage of development and none of the known specimens of *Archaeopteryx* and *Sapeornis* is fully adult. The discovery of a new species of *Sapeornis* provides more anatomical information about this basal avian, and documents the trend of size increase and some morphological specializations in its evolutionary history. Furthermore, it also adds to our understanding of the differentiation and diversity of birds in the Early Cretaceous terrestrial ecosystem.

Key words Liaoning, China; Early Cretaceous; *Sapeornis*; new species

1) 国家重点基础研究发展规划项目(编号:2006CB806400)和创新研究群体基金项目(编号:40121202)资助。

收稿日期:2009-03-04

1 Introduction

In the last two decades, the excavations from the lacustrine Early Cretaceous Jehol Group that comprises the Dabeigou, Yixian and Jiufotang formations in northern Hebei, western Liaoning and southeastern Nei Mongol, northeastern China have provided an extraordinary number of well-preserved fossils, representing nearly all major clades of vertebrates, invertebrates and plants (Chang et al., 2003; Zhou et al., 2003; Zhou, 2006). Among the Jehol Biota, representatives of major avian lineages in the Mesozoic, i. e., the Enantiornithes, Ornithurae and several more basal groups, have recently been reported, providing key evidence in the discussion of the evolutionary radiation of early birds, only slightly later than *Archaeopteryx* (Swisher et al., 2002; He et al., 2004, 2006). As a result, our understanding of the diversifications of early birds in size, morphology, diet, flight, locomotion and habitat during the Early Cretaceous have been greatly increased.

Sapeornis is the largest bird known from the Early Cretaceous and characterized by an extremely elongated wing, compared to a relatively short hindlimb, and the shape of the non-strut like coracoid that is comparable to that of *Archaeopteryx* and non-avian theropods. Phylogenetically, *Sapeornis* is, among early birds, more derived only than *Archaeopteryx* (Elzanowski, 2002; Mayr et al., 2005, 2007), *Rehonavis* (Forster et al., 1998) and *Jeholornis* (Zhou and Zhang, 2002a, 2003a), representing one of the most basal birds in the Mesozoic (Zhou and Zhang, 2006) and the most basal member of the Pygostylia (Chiappe, 2002). Until now, only one species of *Sapeornis* (*S. chaoyangensis*) is recognized despite the discovery of over a dozen specimens referable to the genera. Recently our examination of a newly found specimen referred to *Sapeornis*, IVPP V 13396 housed at the Institute of Vertebrate Paleontology and Paleoanthropology has shown that it can be well distinguished from the type species, and several of its distinct characters warrants the erection of a new species of the genus. A detailed anatomical description and comparison between this and *S. chaoyangensis* is provided in this paper, with a discussion on its implications for our understanding of the early avian diversifications.

2 Systematic paleontology

Aves Linnaeus, 1758

Pygostylia Chiappe, 2002

Sapeornithiformes Zhou & Zhang, 2006

Sapeornithidae Zhou & Zhang, 2006

***Sapeornis* Zhou & Zhang, 2002**

Type species *Sapeornis chaoyangensis* Zhou & Zhang, 2002.

***Sapeornis angustis* sp. nov.**

(Figs. 1–8)

Holotype IVPP V 13396 (collection of the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China), a sub-adult individual of a nearly complete and articulated skeleton mainly in ventral view (Fig. 1).

Etymology The species name “angustis” comes from the Latin “angustis” meaning “narrow”. Indeed, in the studied specimen, the deltopectoral crest of the humerus shows an exceptionally narrow dorsal margin of the fenestra. Furthermore, “angustis” also means “difficult”, “hard”, probably as the last moment the bird went through, considering the particularly dramatic position of the specimen, with the left hand overlapping its jaws.

Locality and horizon Dapingfang, Chaoyang, Liaoning Province; Jiufotang Formation (Zhou, 2006). Early Cretaceous, Aptian; approximately 120 Ma (He et al., 2004).

Diagnosis A relatively small-sized *Sapeornis*, also distinguishable from *Sapeornis chaoyangensis* in possessing a maximum of 6 sacrals, a distinctively narrow humeral deltopectoral crest, with the dorso-distal portion of the deltopectoral crest tapering into a less acute process, relatively narrow furcular rami and a shorter hypocleidum, a relatively long Metacarpal I which is about one third the length of Metacarpal II, and a shorter pubic symphysis.



Fig. 1 Photo of the holotype of *Sapeornis angustis* sp. nov. (V 13396) mainly in ventral view

Description and comparison Cranial bones; the skull and mandibles of the new specimen are nearly completely preserved; however, their cranial portions are overlapped by the left

hand. The skull is laterally exposed and moderately high. Two mandibles are visible from lateral side. The dentary is marked by some nutrient foramina near the dorsal margin; it is posteriorly forked, and about half the length of mandible. Teeth are absent in the dentary, and there is no mandibular fenestra as in other *Sapeornis* specimens. The right mandible is medially exposed, showing a long and slender splenial bone that tapers both cranially and caudally.

Axial skeleton: the vertebral column is composed of well-articulated cervical, thoracic, sacral and caudal vertebrae (Fig. 1). At least nine cervicals are preserved in the specimen. The middle cervicals are more elongate than those of the cranial and caudal part of the neck. The cervicals appear to be heterocoelous as in other specimens of *Sapeornis* (Zhou and Zhang, 2003b). Eleven thoracic vertebrae are visible; however, there appear to be one to two most cranial thoracic vertebrae that are overlapped by the coracoid. Therefore, the estimated number of the thoracic vertebrae is twelve to thirteen, which is consistent with that of other known *Sapeornis* specimens. The thoracic vertebrae do not show pleurocoels and seem to have biconcave central articulation as in other primitive birds, as well as in other known specimens of *Sapeornis* (Zhou and Zhang, 2003b).

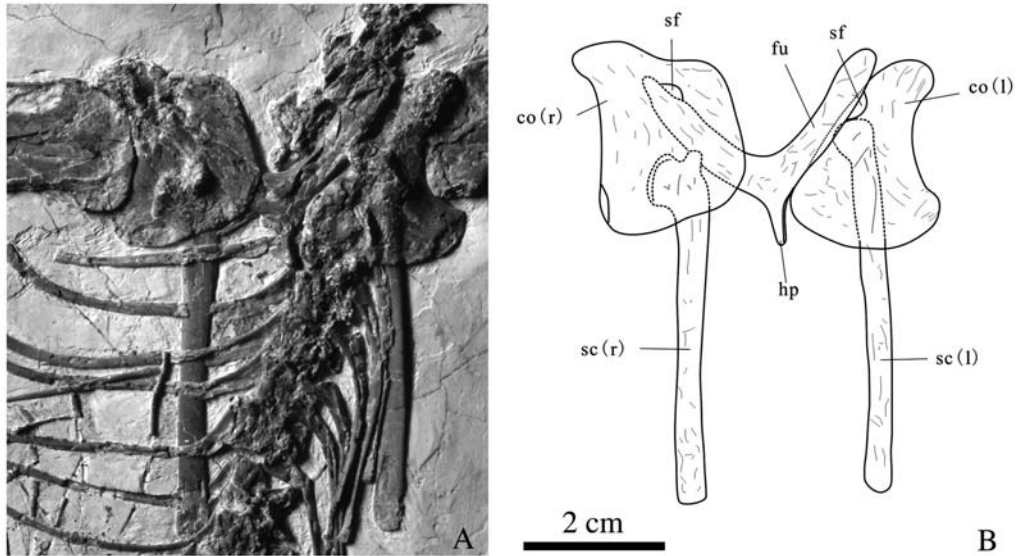


Fig. 2 Pectoral girdle of *Sapeornis angustis* sp. nov. (V 13396)

A. photo; B. linedrawing; co(1). left coracoid 左乌喙骨; co(r). right coracoid 右乌喙骨; fu. furcula 叉骨; hp. hypocleidum of the furcula 叉骨突; sc(1). left scapula 左肩胛骨; sc(r). right scapula 右肩胛骨; sf. supracoracoid foramen of the right coracoid 右乌喙骨的上乌喙孔

The sacral vertebrae are not ossified into the synsacrum, probably because of the juvenile status of the individual. Five sacrals are exposed, but we estimate that the total number of sacrals is six, as the last sacral is probably overlapped by the left ischium and pubis. In other known specimens, the synsacrum is composed of seven sacrals. There exist seven free caudal vertebrae that are in articulation. They are short and small compared to the preceding sacral vertebrae. The transverse processes of the caudals are long, caudally directed, and become progressively shorter caudally. The lack of a pygostyle might suggest that the distal portions of the caudal series are not preserved, as the pygostyle is present in the other known specimens of *Sapeornis* (Zhou and Zhang 2002b, 2003b).

The cervical ribs seem to be much reduced, with only two cervical ribs observable, and they are very short and slender. Thoracic ribs are nearly completely preserved. Twelve pairs of

thoracic ribs can be seen on the specimen (Fig. 1). They are mostly long, slender and slightly curved, particularly near the distal end. The tuberculum area is about twice as wide as the distal end (Fig. 2). No uncinat process or sternal rib is recognized, as in other known specimens of *Sapeornis*.

About fifteen to sixteen pairs of the gastralgia can be counted (Fig. 1). The gastralgia are more slender and shorter than the thoracic ribs. They are generally needle-shaped and taper distally, and they become progressively short towards the caudal end.

Pectoral girdle: the scapula and coracoid of both left and right sides are exposed ventrally (Fig. 2). As the coracoid overlaps the scapula, it is impossible to examine the articulation between them and determine whether they are fused or not (Fig. 2). The scapula is only about half the length of the humerus. It is straight, and its width is consistent from its proximal to distal end, which is neither pointed nor expanded distally.

The coracoid is broad, short and non-strut-like. It shows a distinctive acrocoracoid process as in *C. chaoyangensis*. A small supracoracoid foramen is visible on the medial part of the right coracoid (Fig. 2). The two clavicles are fused into a broad "V"-shaped furcula. The furcular ramus is wide and craniocaudally compressed, and does not significantly taper distally. The hypocleidum is present unlike in non-avian theropods (Norell et al., 1997; Xu et al., 2000, 2003). It is slender and slightly shorter than that of *Sapeornis chaoyangensis* and further shorter than that of enantiornithines (Zhang and Zhou, 2000; Chiappe and Walker, 2002; Zhou et al., 2005). However, it is longer than that of the basal ornithurine *Hongshanornis* (Zhou and Zhang, 2005). No sternum or its impression has been preserved, as is the case in other known specimens of *Sapeornis*. We assume that it is not ossified in all known *Sapeornis* specimens, i. e., none of them is fully adult.

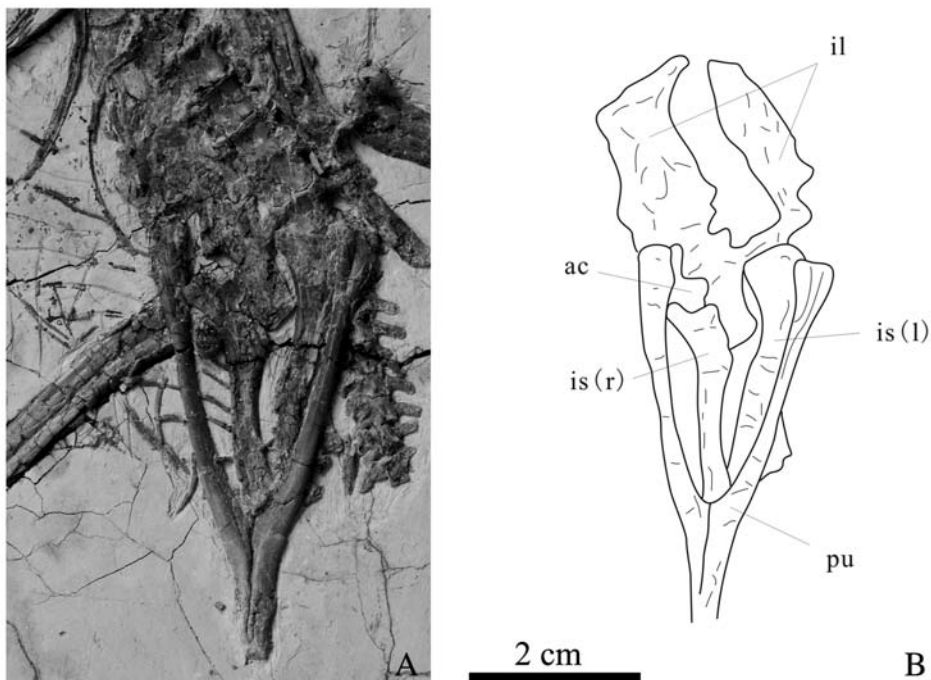


Fig. 3 Pelvic girdle of *Sapeornis angustis* sp. nov. in ventral view (V 13396)

A. photo; B. linedrawing; ac. acetabulum 髌臼; il. ilium 髌骨; is(l). left ischium 左坐骨; is(r). right ischium 右坐骨; pu. pubis 耻骨

Pelvic girdle: the pelvis is more or less completely preserved (Fig. 3). The ilium, ischium, and pubis are not fused with each other as in other Early Cretaceous birds. The pubis is caudally directed as in all birds and some non-avian theropods. The two long and rod-shaped pubes are ventrally preserved and symphysized (but not fused) distally in a “V”-shape, lacking a pubic foot. The pubic symphysis is about one-third the length of the pubis, which is similar to the case of other known *Sapeornis* (Zhou and Zhang, 2002b, 2003b)

The two ischia are laterally preserved, but not symphysized distally (Fig. 3). They are about half as long as the pubis, but are more robust, much comparable to those of *Archaeopteryx* and *Confuciusornis* (Martin et al., 1998; Chiappe et al., 1999). The right ischium shows a prominent dorsal ascending process proximally and tapers slightly towards the distal end as in other known specimens of *Sapeornis*.

The two ilia are well preserved as well, displaying a larger and expanded pre-acetabulum wing and a smaller and rod-shaped post-acetabulum wing that does not taper distally. It is also notable that the transverse processes of the sacrals are tightly attached to the ilia and it is hard to determine if they are fused with them or not.

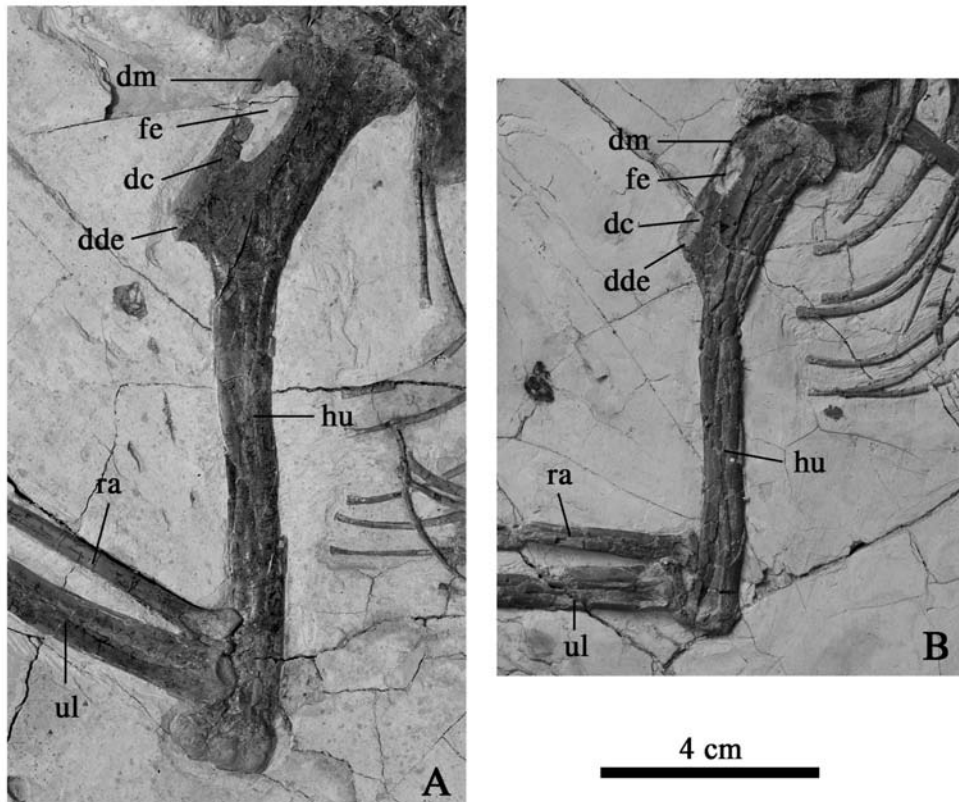


Fig. 4 Comparison of the right humerus in ventral view

A. *Sapeornis chaoyangensis* (V 13276, Zhou and Zhang, 2003b); B. *Sapeornis angustis* sp. nov. (V 13396); dc. deltopectoral crest 三角脊; dde. dorso-distal end of the deltopectoral crest 三角脊的远背端; dm. dorsal margin of the fenestra 气窗背缘; fe. fenestra 气窗; hu. humerus 肱骨; ra. radius 桡骨; ul. ulna 尺骨

Forelimb: the forelimbs of IVPP V 13396 are extremely elongated compared with the hindlimbs (Table 1). The humerus has a very long deltopectoral crest, which is about one-third the

Table 1 Measurements of some skeletal elements of *Sapeornis angustis* sp. nov. (V 13396) and the holotype of *Sapeornis chaoyangensis* (V 12698) (mm)

| | V 12698 | V 13396 |
|--|--------------------|-------------------|
| Skull (length) | | 54.5 |
| Scapula (length) | 75(1)*, 75(r) | 52.4(1), 52.4(r) |
| Scapula (width) | | 4.0(1), 3.9(r) |
| Coracoid (length) | 40(r)* | |
| Coracoid (maximal width) | | 22.2 |
| Furcula (width) | 43.1 | 42.3 |
| Hypocleidum (length) | 10.1* | 13.1 |
| Hypocleidum to end of rami | 37.3* | 30.1 |
| Humerus (maximal length) | 126.5(1), 129.6(r) | 93.9(1), 93.1(r) |
| Humerus (deltopectoral crest length) | 48.9(1) | 34.6(1), 29.4(r) |
| Humerus (deltopectoral crest proximal width) | 22.3(1) | 16.3(1), 17.3(r)* |
| Humerus (deltopectoral crest distal width) | 19.5(1) | 15.4(1), 16.0(r) |
| Humerus (fenestra maximal length) | | 9.4(1), 9.1(r) |
| Humerus (fenestra maximal width) | | 3.0(1), 3.5(r) |
| Humerus (distal end width) | 14.7(1), 17.8(r) | 11.6(1), 12.0(r) |
| Ulna (maximal length) | 133.1(1), 135.1(r) | 91.5(1), 88.0(r) |
| Ulna (proximal end width) | 12.3(1)* | 9.0(1), 9.4(r) |
| Ulna (midshaft width) | 9.4 | 6.2(1), 5.5(r) |
| Ulna (distal end width) | 7.3(1) | 5.7(1), 8.1(r) |
| Radius (maximal length) | 133(1), 131.9(r) | 91.1(1), 88.0(r) |
| Radius (proximal end width) | 4.7(1) | 7.7(1), 7.7(r) |
| Radius (midshaft width) | 4.1 | 4.6(1), 4.6(r) |
| Radius (distal end width) | 7.1(1) | 3.7(1), 4.1(r) |
| Carpometacarpus (length) | 61.9(1) | 42.3(1), 41.5(r) |
| Metacarpal I (length) | 14.3(1) | 14.2(1), 11.9(r) |
| Metacarpal II (length) | 57.1(1) | 42.8(1), 41.3(r) |
| Metacarpal II (width of midshaft) | | 5.3(1), 5.3(r) |
| Metacarpal III (length) | 54.6(1) | 36.0(1) |
| Manual digit I-1 (length) | 33.6(1) | 24.1(1), 24.7(r) |
| Manual digit I-2 (length) | 19(1)* | 10.6(1)*, 13.7(r) |
| Manual digit II-1 (length) | 30(1), 32.2(r) | 22.3(1), 23.4(r) |
| Manual digit II-2 (length) | 27.7(1) | 21.7(1), 21.7(r) |
| Manual digit II-3 (ungual) (length) | 18(1)* | 13.1(1), 13.7(r) |
| Ilium (length) | 56(1)* | 30.4(r) |
| Ischium (length) | 42.1(1) | |
| Pubis (length) | 85.4(1), 87(r) | 57.3(1), 58.5(r) |
| Pubic symphysis | 27.9 | 19.1 |
| Femur (length) | 80.4(1) | 58.2(1), 58.3(r) |
| Femur (proximal width) | 11.5(1) | 9.2(1) |
| Femur (distal width) | 9.1(1) | 6.5(1), 6.5(r) |
| Tibiotarsus (length) | 83.6(1) | 68.5(1), 68.4(r) |
| Tibiotarsus (proximal width) | | 9.3(1), 10.1(r) |
| Tibiotarsus (distal width) | | 7.7(1), 7.7(r) |
| Fibula (length) | 72.4(1)* | 65.7(1) |
| Tarsometatarsus | 44.6(1) | 30.0(1), 33.1(r) |
| Metatarsal II (width) | 2.6(1) | 2.1(1), 2.1(r) |
| Metatarsal III (width) | 2.6(1) | 3.4(1), 3.2(r) |
| Pedal digit I-1 | | 12.7(1), 13.1(r) |
| Pedal digit I-2 | | 13.7(1), 13.7(r) |

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

total length of the humerus (Fig. 4). The deltopectoral crest is long, with a straight dorsal margin. Its dorso-distal portion does not taper into an acute angle, unlike in *Sapeornis chaoyangensis*. The humerus has a distinctive proximodistally elongated fenestra at the proximal end. It is short and its width is only about one third of its length. The dorsal margin of the fenestra is very narrow (Fig. 4).

The ulna is about the same length of the humerus, as in *Jeholornis* (Zhou and Zhang, 2002a). The ulna does not seem to be curved along its proximal two thirds as seen in many other basal birds, yet this feature might be an artefact of preservation. The distal end of the ulna is as wide as the midshaft. The radius is relatively straight and rod-shaped.

The manual elements are articulated (Fig. 5). The total length of the manus is about the same as that of the ulna. Metacarpal I is short, straight, and about one third the length of metacarpal II. Metacarpal I is not fused with the carpometacarpus, although both are tightly attached to each other. Compared to Metacarpal III, Metacarpal II is slightly longer and extends distally past it. By contrast, in all known enantiornithine birds, Metacarpal III extends distally past Metacarpal II (Zhang and Zhou, 2000; Chiappe and Walker, 2002; Zhou et al., 2005). The midshaft width of Metacarpal II is more than twice that of Metacarpal III. Metacarpal III is mediolaterally compressed. Metacarpals II and III are unfused distally; they are both straight and so tightly attached to each other that there is no intermetacarpal space.

The first manual digit comprises two phalanges. The first phalanx is long, slender and curved. Although it is more than half the length of Metacarpal I, it does not extend to the distal end of Metacarpal II. The second phalanx (ungual) is large and curved but is much shorter than the first phalanx. The second manual digit is significantly longer than the carpometacarpus. It is composed of three long phalanges. Unlike in *Archaeopteryx* and *Confuciusornis* (Martin et al., 1998; Chiappe et al., 1999), but like in other specimens of *Sapeornis*, the first phalanx is the largest and most robust one among manual phalanges; it is as wide as Metacarpal II, and is slightly expanded at the distal end. The first phalanx is slightly longer than the second, although the third (ungual) is further shorter. The second phalanx is much more slender, rod-shaped, and more curved than the first phalanx of the first digit, but it tapers distally. The ungual of the second digit is curved and as long as the ungual of the first digit. The third manual digit appears to be incompletely preserved on both the left and right wings. Considering the phalangeal formula of other *Sapeornis* specimens “2-3-2”, the left manus of the new specimen seems only to have preserved the first phalanx, which is tightly attached to the first phalanx of the second digit, while the second phalanx of the third digit is preserved on the right manus, which is slightly shorter than the first (Fig. 5). No ungual is present on the third manual digit, and clearly the third digit is much reduced as in other known specimens of *Sapeornis*.

Hindlimb: the hindlimbs are much shorter compared with the forelimbs, similar to what is seen in other *Sapeornis* specimens as well as in the enantiornithine *Longipteryx* (Zhang et al., 2001).

The femur is stout and curved, with a twisted and prominent head (Fig. 1). The proximal tarsals are well fused with the tibia into a tibiotarsus as in more advanced birds. The fibula is very long and slender. On the left side, it clearly reaches the distal end of the tibiotarsus, as in other known *Sapeornis* specimens as well as in *Archaeopteryx* and *Jeholornis* (Zhou and Zhang, 2003a).

The tarsometatarsus is robust, and not well fused at the proximal end, which can be seen as further evidence of the young age of the specimen. Metatarsals II, III, and IV are straight and not fused with each other throughout their length (Fig. 6). Metatarsal III is slightly longer than Metatarsals II and IV, which are approximately of the same length. Metatarsal II and IV are of about the same width, whereas Metatarsal III is wider.

Pedal digits II, III and IV are approximately of the same length, and are approximately as

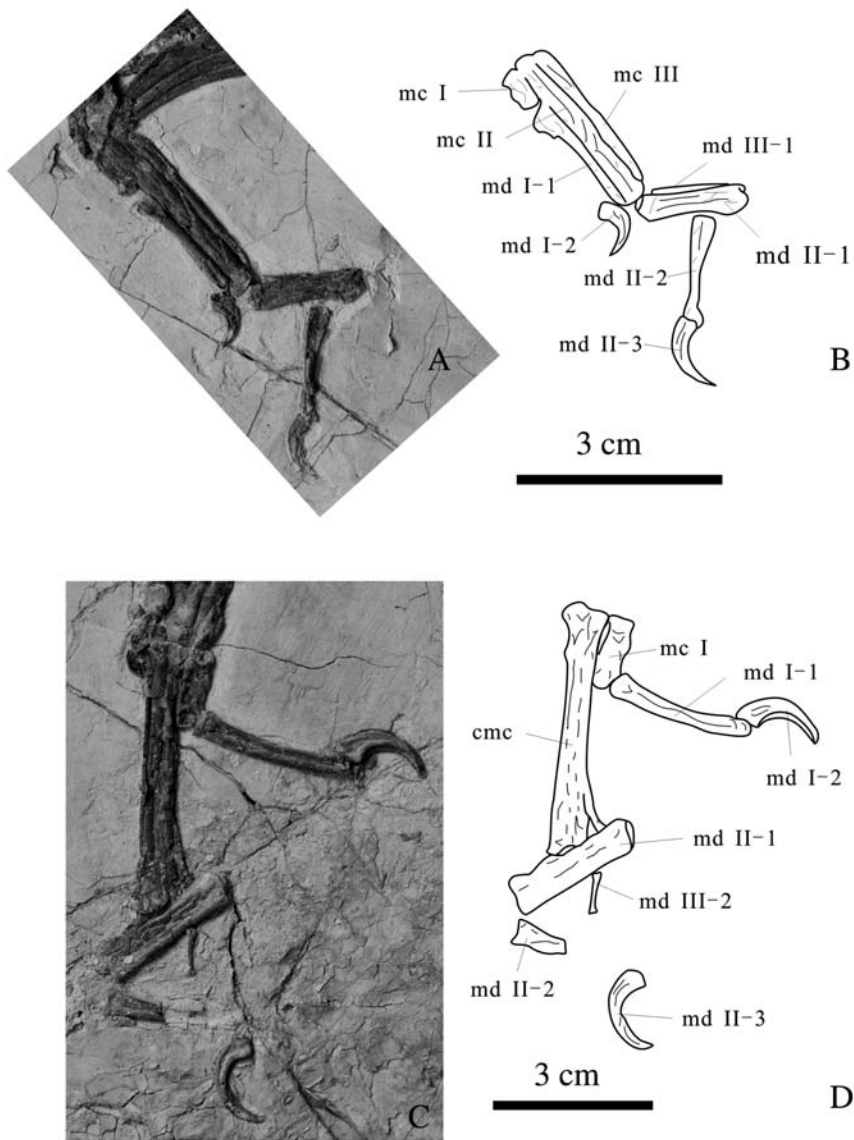


Fig.5 Manus of *Sapeornis angustis* sp. nov. (V 13396)

A. photo of the left manus; B. linedrawing of the left manus; C. photo of the right manus; D. linedrawing of the right manus; cmc. carpometacarpus 腕掌骨; mc I-III. Metacarpal I-III 第一至第三掌骨; md I-1, 2. first and second phalanges of first manual digit 第一指的第1,2指节; md II-1,2,3. first, second and third phalanges of second manual digit 第二指的第1,2,3指节; md III-1,2. first and second phalanges of third manual digit 第三指的第1,2指节

long as the tarsometatarsus. All the unguals are large and semicircular, with sharp and needle-shaped horny sheaths. Digit I is reversed as in nearly all birds. It is long, with two long phalanges of about the same length. Digit II have three phalanges; each is shorter than those of Digit I. The second phalanx of Digit II is slightly longer and more slender than the first phalanx.

Digit III is completely preserved on the right foot (Fig. 6). The first phalanx is slightly

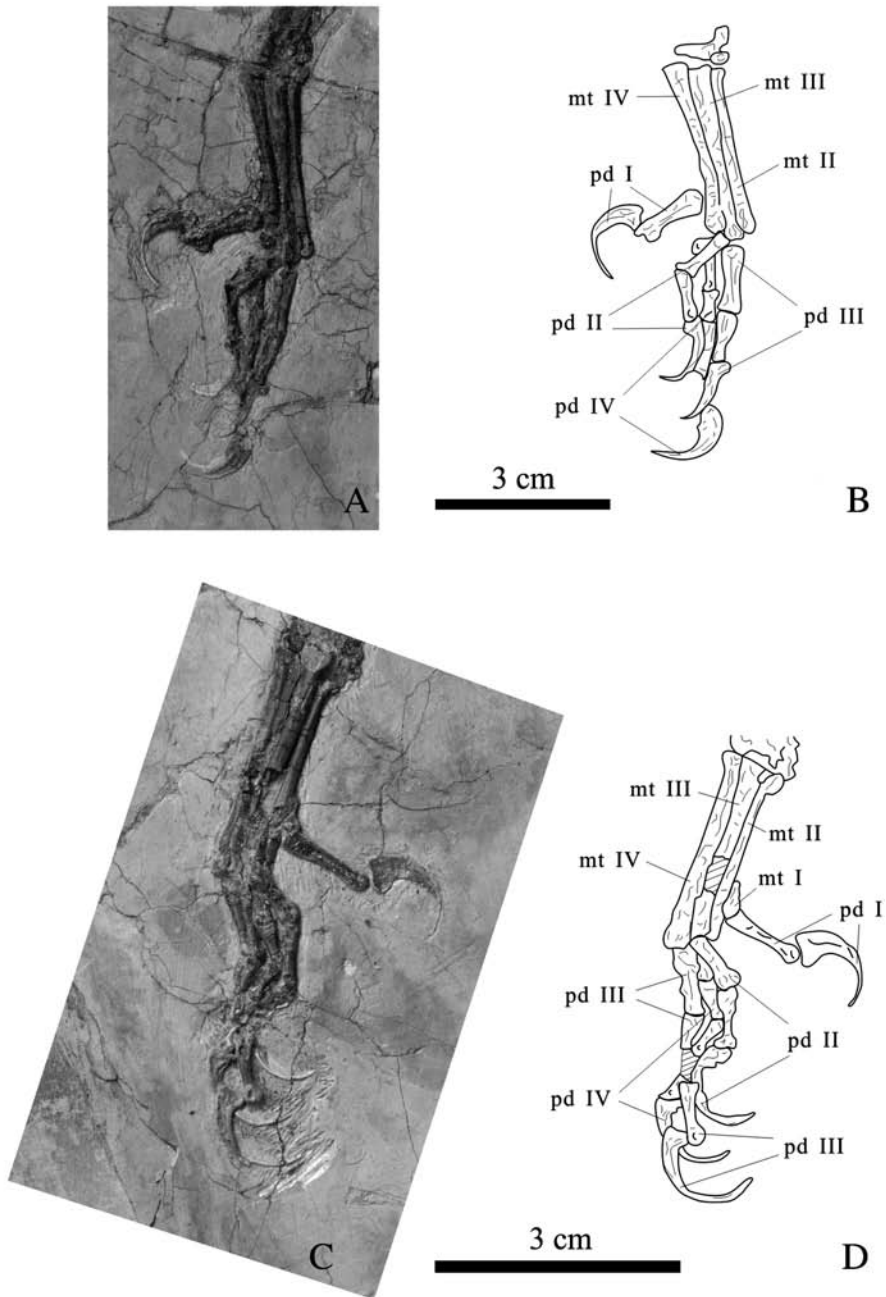


Fig. 6 Foot of *Sapeornis angustis* sp. nov. (V 13396)

A. photo of the left foot; B. linedrawing of the left foot; C. photo of the right foot; D. linedrawing of the right foot; mt I-IV. Metatarsal I-IV 第一至第四跖骨; pd I-IV. pedal digit I-IV 第一至第四趾

longer and more robust than the second and third phalanges. The second phalanx is broken distally and is estimated to approximately of the same length of the third phalanx.

The first four phalanges of Digit IV have approximately the same length. They are shorter

than the phalanges of other digits. The unguals are longer than the penultimate phalanges in all pedal digits.

3 Discussion

IVPP V 13396 can be undoubtedly referred to *Sapeornis*, based on the presence of a combination of a number of distinct anatomical features unique to this genera, such as the toothless mandible, a robust furcula with a short hypocleidum, a broad and non-strut like coracoid, extremely elongated forelimb compared to the hindlimb, a distinct elongated fenestra at the proximal humerus, the 2–3–2 phalangeal formula of the manus, etc.

Although the new specimen is generally similar to other known materials of *Sapeornis*, several distinct features show that it is distinguishable from all known specimens referable to *Sapeornis chaoyangensis*. For example, V 13396 has a maximum of 6 sacrals, the furcular rami are relatively narrower than in other specimens of *Sapeornis*, with a shorter hypocleidum (Fig. 7).

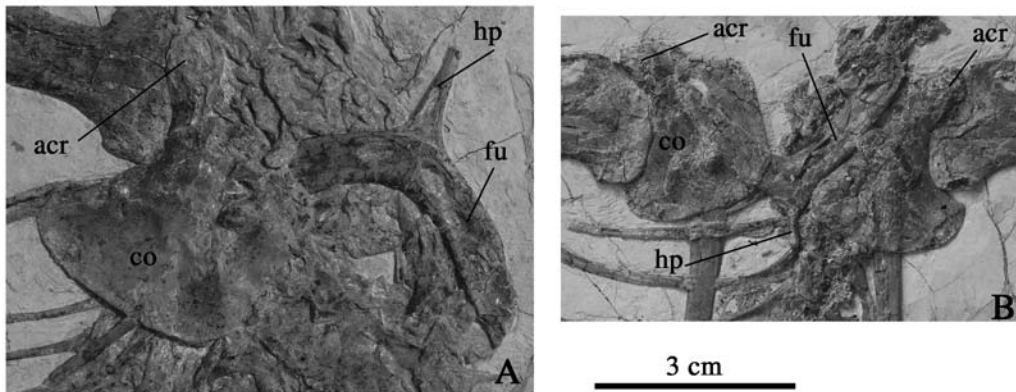


Fig. 7 Comparison of the pectoral girdle

A. *Sapeornis chaoyangensis* (V 13276, Zhou and Zhang, 2003b); B. *Sapeornis angustis* sp. nov. (V 13396); acr. acrocoracoidal process 肩峰突; co. coracoid 乌喙骨; fu. furcular 叉骨; hp. hypocleidum of the furcula 叉骨突

Although the forelimbs are extremely elongated compared to the hindlimbs, the ratio of forelimb/hindlimb in V 13396 is not as great as in *S. chaoyangensis*. Both the fenestra at the proximal humerus and its dorsal margin in V 13396 are narrower compared to those of *S. chaoyangensis* (Fig. 8). The ulna is about as long as the humerus in V 13396 while the ulna is slightly longer in *S. chaoyangensis* (Table 1). The tibiotarsus is longer than the pubis, whereas it is about the same length in other known *Sapeornis* specimens. The pubic symphysis in V 13396 is relatively shorter than in V 13276.

Nevertheless, V 13396 is smaller than other known specimens of *Sapeornis*, and some other evidence suggests that it probably represents a subadult individual. For instance, the sacral vertebrae are not yet well ossified into a synsacrum; both the carpometacarpus and tarsometatarsus are not well ossified proximally. And the extremities of many long bones are not well defined. In addition, no sternum is observed.

All of those characters might raise the question whether V 13396 is a new species of *Sapeornis* or a juvenile specimen of *S. chaoyangensis*. Indeed, many differences observed are based on the proportions of the bones and those features could be explained by the growth of the animal and its allometric laws. However, it is also notable that the sternum is absent in all other known specimens of *Sapeornis*, including those with well ossified skeletal elements. Until now,

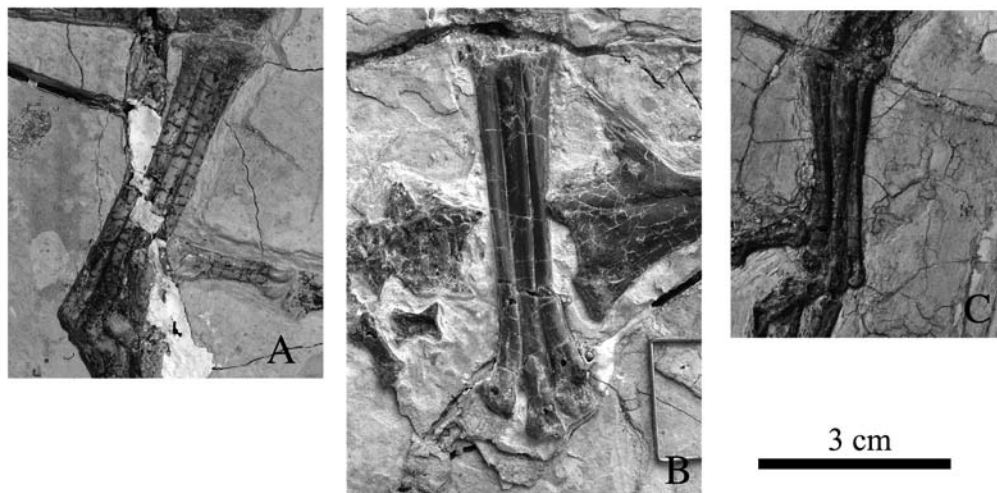


Fig. 8 Comparison of the foot

A, B. *Sapeornis chaoyangensis* (V 13276, Zhou and Zhang, 2003b), A. right foot, B. left tarsometatarsus;
C. left tarsometatarsus of *Sapeornis angustis* sp. nov. (V 13396)

no sternum has been discovered from any known specimens of *Archaeopteryx* (Mayr et al., 2005, 2007). In contrast, an ossified sternum is present in nearly all other known Early Cretaceous avian specimens, including the more primitive long tailed *Jeholornis* (Zhou and Zhang, 2002a, 2003a) and many non-avian theropods (Hwang et al., 2002; Xu et al., 2003). Similarly, the uncinat process has not been found in any specimen of *Sapeornis* and *Archaeopteryx*. However, it has been observed in some new *Jeholornis* and many non-avian theropods (Clark et al., 1999; Norell and Makovicky, 1999; Zhou and Wang 2000; Zhou et al., 2000; Lü, 2002; Hwang et al., 2002; Xu et al., 2003) as well as many more derived Early Cretaceous birds. Thus, we propose that the sternum and uncinat process probably ossified late in development of *Sapeornis* and *Archaeopteryx*. Therefore, it is very likely that none of the known specimens of *Sapeornis* or *Archaeopteryx* is full adult. More discoveries of these early avians are certainly necessary for a more complete understanding of their anatomy.

Therefore, even if V 13396 is a subadult, it might also be the case for the known specimens of *S. chaoyangensis*. Furthermore, although many differences are based on proportions, some contrasts are less likely linked to the juvenile character of the specimen, for example, in V 13396, the thoracic ribs are less curved than in other known specimens of *Sapeornis*, which indicates that V 13396 probably had a less laterally expanded rib cage. Furthermore, the number of sacral vertebrae seem to be no more than 6 compared to 7 in *S. chaoyangensis*. Therefore, we can safely conclude that this specimen belongs to a new species of *Sapeornis*.

The discovery of a new species of the basal avian *Sapeornis* further demonstrates the remarkable differentiation of morphology, size, diet, flight and habitat of Early Cretaceous birds from the Jehol Biota of Northeast China despite the competition from pterosaurs (Wang et al., 2005) and other vertebrates for a similar ecological niche.

Acknowledgements We thank Gareth Dyke for comments on the manuscript, Zhiheng Li for help with the illustrations, and Yan Li for fossil preparation. This research was funded by the Major Basic Research Projects (2006CB806400) of MST of China, the National Natural Science Foundation of China (40121202), and a travel fund from Normal Superior School, France.

References

- Chang M M, Chen P J, Wang Y Q et al., 2003. The Jehol Biota, the Emergence of Feathered Dinosaurs, Beaked Birds and Flowering Plants. Shanghai; Shanghai Scientific and Technical Publishers. 1–208
- Chiappe L M, 2002. Basal bird phylogeny. In: Chiappe L M, Witmer L M eds. Mesozoic Birds Above the Heads of Dinosaurs. Berkeley: University of California Press. 448–472
- Chiappe L M, Ji S, Ji Q et al., 1999. Anatomy and systematics of the Confuciusornithidae (Aves) from the Mesozoic of Northeastern China. Bull Am Mus Nat Hist, **242**: 1–89
- Chiappe L M, Walker C A, 2002. Skeletal morphology and systematics of the Cretaceous euenantiornithes (Ornithothoraces: Enantiornithes). In: Chiappe L M, Witmer L M eds. Mesozoic Birds Above the Heads of Dinosaurs. Berkeley: University of California Press. 240–267
- Clark J M, Norell M A, Chiappe L M, 1999. An oviraptorid skeleton from the Late Cretaceous of Ukhaa Tolgod, Mongolia, preserved in an avian-like brooding position over an oviraptorid nest. Am Mus Novit, (3265): 1–36
- Elzanowski A, 2002. Archaeopterygidae (Upper Jurassic of Germany). In: Chiappe L M, Witmer L M eds. Mesozoic Birds Above the Heads of Dinosaurs. Berkeley: University of California Press. 129–159
- Forster C A, Sampson S D, Chiappe L M et al., 1998. The theropod ancestry of birds: new evidence from the Late Cretaceous of Madagascar. Science, **279**: 1915–1919
- He H Y, Wang X L, Jin F et al., 2006. The $^{40}\text{Ar}/^{39}\text{Ar}$ Ar dating of the early Jehol Biota from Fengning, Hebei Province, northern China. Geochem Geophy Geosyst, **7**: Q04001, doi:10.1029/2005GC001083
- He H Y, Wang X L, Zhou Z H et al., 2004. Timing of the Jiufotang Formation (Jehol Group) in Liaoning, northeastern China and its implications. Geophy Res Lett, **31**(12): L12605
- Hwang S H, Norell M A, Ji Q et al., 2002. New specimens of *Microraptor zhaoianus* (Theropoda: Dromaeosauridae) from Northeastern China. Am Mus Novit, (3381): 1–44
- Lü J C, 2002. A new oviraptorosaurid (Theropoda: Oviraptorosauria) from the Late Cretaceous of Southern China. J Vert Paleont, **22**(4): 871–875
- Martin L D, Zhou Z H, Hou L H et al., 1998. *Confuciusornis sanctus* compared to *Archaeopteryx lithographica*. Naturwissenschaften, **85**: 286–289
- Mayr G, Pohl B, Peters S P, 2005. A well-preserved *Archaeopteryx* specimen with theropod features. Science, **310**: 1483–1486
- Mayr G, Pohl B, Peters D S, 2007. A well-preserved *Archaeopteryx* specimen with theropod features. Zool J Linn Soc London, **149**: 97–116
- Norell M A, Makovicky P J, 1999. Important features of the dromeosaurid skeleton. Part 2, information from newly collected specimens of *Velociraptor mongoliensis*. Am Mus Novit, (3282): 1–45
- Norell M A, Makovicky P J, Clark J M, 1997. A *Velociraptor* wishbone. Nature, **389**: 447
- Swisher III C C, Wang X L, Zhou Z H et al., 2002. Further support for a Cretaceous age for the feathered-dinosaur beds of Liaoning, China; new $^{40}\text{Ar}/^{39}\text{Ar}$ Ar dating of the Yixian and Tuchengzi Formations. Chin Sci Bull, **47**(2): 135–138
- Wang X L, Kellner A W A, Zhou Z H et al., 2005. Pterosaur diversity in Cretaceous terrestrial ecosystems in China. Nature, **437**: 875–879
- Xu X, Zhou Z H, Wang X L, 2000. The smallest known non-avian theropod dinosaur. Nature, **408**: 705–708
- Xu X, Zhou Z H, Wang X L et al., 2003. Four-winged dinosaurs from China. Nature, **421**: 335–340
- Zhang F C, Zhou Z H, 2000. A primitive enantiornithine bird and the origin of feathers. Science, **290**: 1955–1959
- Zhang F C, Zhou Z H, Hou L H et al., 2001. Early diversification of birds-evidence from a new opposite bird. Chin Sci Bull, **46**(11): 945–949
- Zhou Z H, 2006. Evolutionary radiation of the Jehol Biota: chronological and ecological perspectives. Geol J, **41**: 377–393
- Zhou Z H, Barrett P M, Hilton J, 2003. An exceptionally preserved Lower Cretaceous ecosystem. Nature, **421**: 807–814

- Zhou Z H, Chiappe L M, Zhang F C, 2005. Anatomy of the Early Cretaceous bird *Eoenantiornis buhleri* (Aves: Enantiornithes) from China. *Can J Earth Sci*, **42**: 1331–1338
- Zhou Z H, Farlow J O, 2001. Flight capability and habits of *Confuciusornis*. In: Gauthier J, Gall L F eds. *New Perspectives on the Origin and Early Evolution of Birds*. New Haven: Special Publication of the Peabody Museum of Natural History, Yale University. 237–254
- Zhou Z H(周忠和), Wang X L(汪筱林), 2000. A new species of *Caudipteryx* from the Yixian Formation of Liaoning, north-east China. *Vert PalAsiat(古脊椎动物学报)*, **38**(2): 111–127
- Zhou Z H(周忠和), Wang X L(汪筱林), Zhang F C(张福成) et al., 2000. Important features of *Caudipteryx*-evidence from two nearly complete new specimens. *Vert PalAsiat(古脊椎动物学报)*, **38**(4): 241–254
- Zhou Z H, Zhang F C, 2002a. A long-tailed, seed-eating bird from the Early Cretaceous of China. *Nature*, **418**: 405–409
- Zhou Z H, Zhang F C, 2002b. Largest bird from the Early Cretaceous and its implications for the earliest avian ecological diversification. *Naturwissenschaften*, **89**: 34–38
- Zhou Z H, Zhang F C, 2003a. *Jeholornis* compared to *Archaeopteryx*, with a new understanding of the earliest avian evolution. *Naturwissenschaften*, **90**: 220–225
- Zhou Z H, Zhang F C, 2003b. Anatomy of the primitive bird *Sapeornis chaoyangensis* from the Early Cretaceous of Liaoning, China. *Can J Earth Sci*, **40**: 731–747
- Zhou Z H, Zhang F C, 2005. Discovery of a new ornithurine bird and its implication for Early Cretaceous avian radiation. *PNAS*, **102**(52): 18998–19002
- Zhou Z H(周忠和), Zhang F C(张福成), 2006. Mesozoic birds of China—a synoptic review. *Vert PalAsiat(古脊椎动物学报)*, **44**(1): 74–98