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***Jeholornis* compared to *Archaeopteryx*, with a new understanding of the earliest avian evolution**

Received: 17 September 2002 / Accepted: 17 March 2003 / Published online: 15 April 2003
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Abstract The recently reported *Jeholornis* represents the only known bird with a complete long skeletal tail except for *Archaeopteryx*. Two newly discovered specimens referable to *Jeholornis* provide some important new information about its anatomy. The tail of *Jeholornis* is much longer than that of *Archaeopteryx* and comprises a maximum of 27 caudal vertebrae compared with only 23 in *Archaeopteryx*. More interestingly, the tail feathers are shaped more like those of dromaeosaurs than those of *Archaeopteryx*. We conclude that the common ancestor of birds must have a more primitive tail than that in *Archaeopteryx*, confirming the side branch position of *Archaeopteryx* in the early avian evolution. The synsacrum is composed of six sacrals, representing a transitional stage between *Archaeopteryx* and more advanced birds. The scapula of *Jeholornis* has a dorso-laterally exposed glenoid facet, and the coracoid has a supracoracoid foramen. The presence of a pair of fenestrae in the sternum of *Jeholornis* has further implications for the air-sac system in early birds.

Electronic Supplementary Material Supplementary material is available for this article if you access the article at <http://dx.doi.org/10.1007/s00114-003-0416-5>. A link in the frame on the left on that page takes you directly to the supplementary material.

Introduction

Jeholornis is a recently reported basal bird, which appears to be less advanced than any other known bird except for *Archaeopteryx*. Its stomach was found to contain over 50 seeds of unknown plants, representing the first direct

evidence for seed-eating adaptation in the Mesozoic (Zhou and Zhang 2002a).

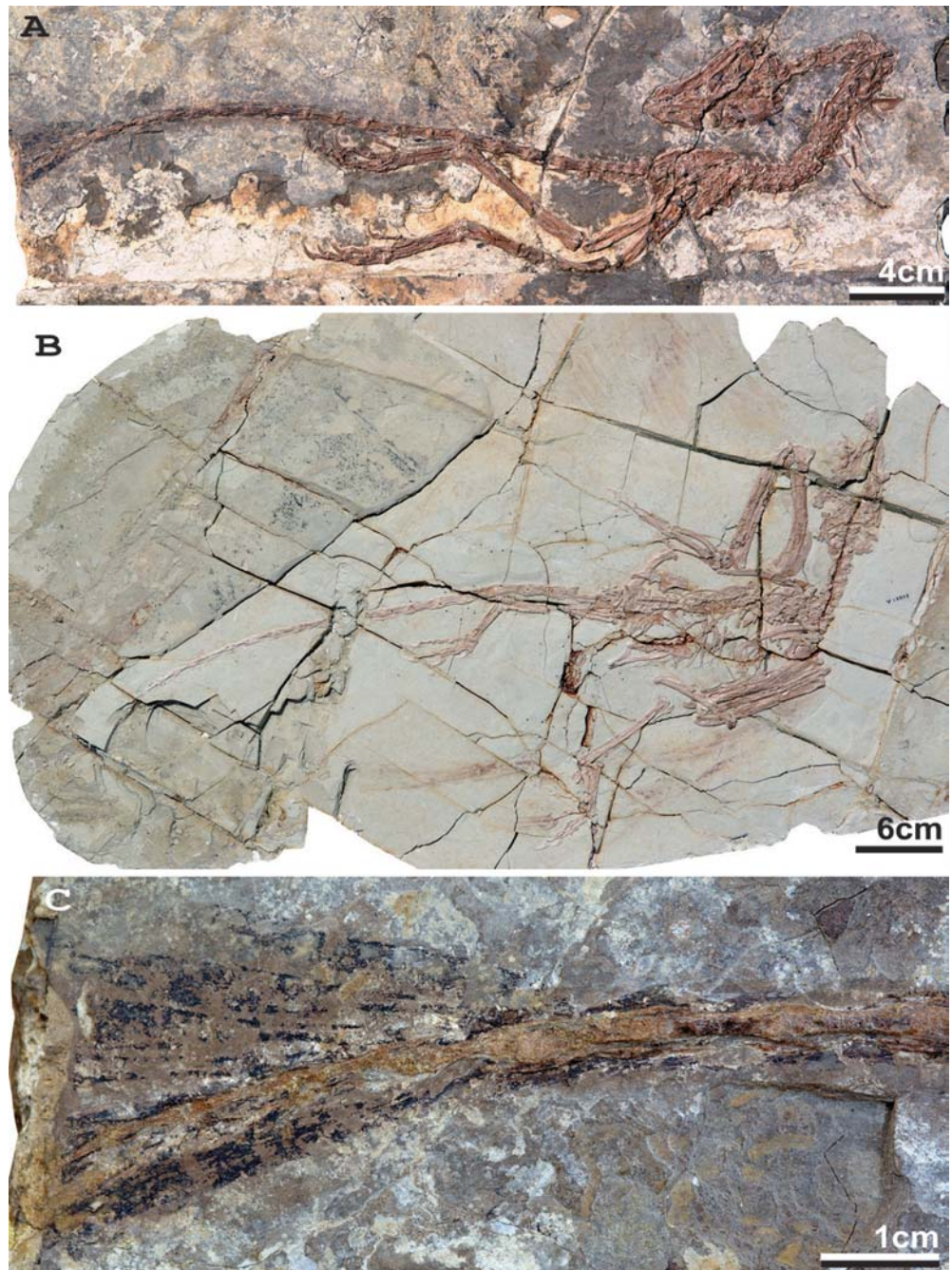
One of the most remarkable features of *Jeholornis* is its unreduced long skeletal tail. Except for *Archaeopteryx* and *Jeholornis*, the only other bird known to have a long skeletal tail is *Rahonavis* from the Late Cretaceous of Madagascar (Forster et al. 1998); however, this was not completely preserved, and hence the exact number of its caudal vertebrae remains unknown. The holotype of *Jeholornis* preserved 22 caudal vertebrae; however, the fact that there are only two short caudal vertebrae before the 20 elongated caudal vertebrae raises suspicions that the tail was probably not completely preserved. The two new specimens of *Jeholornis* described here have preserved a nearly completely articulated tail comprising more caudal vertebrae than that of the holotype.

Both new specimens are from the Jiufotang Formation in Chaoyang, western Liaoning, northeast China (Fig. 1A,B), where the holotype of *Jeholornis* and the associated feathered dromaeosaurs (Norell et al. 2002; Xu et al. 2003) and birds such as *Sapeornis* (Zhou and Zhang 2002b), *Longipteryx* (Zhang et al. 2001) and *Yanornis* (Zhou and Zhang 2001) have all been discovered. They are housed in the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) in Beijing. One is a nearly completely articulated individual (IVPP V13553) and the second lacks the forelimb and pectoral girdle (IVPP V13550). Both specimens are significantly smaller than the holotype and, since many juvenile features can be observed (such as the less well-defined extremities of long limb bones, the unfused vertebrae, relatively large skull), they probably represent two juvenile individuals. In other major features and proportions they are consistent with the description of *Jeholornis prima*, and thus they are classified to the same taxon.

These new materials also provide much new information about other aspects of this basal bird, such as the scapula, coracoid, thoracic vertebrae, synsacrum, pneumaticity of the postcranial bones, complete pedal digits and impression of feathers (see Fig. 1).

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Fig. 1A–C Two new specimens of *Jeholornis prima*. **A** an incomplete skeleton (IVPP V13350); **B** a nearly complete skeleton (IVPP V13353); **C** fan-shaped distal tail feather (IVPP V13350)



The exact age of the bird-bearing Jiufotang Formation is unknown; however, it is generally believed to be Aptian (Wang and Zhou 2002), which is slightly younger than the Santana Formation of Brazil (Albian).

Comparison between *Jeholornis* and *Archaeopteryx*

In the skull, the most distinctive difference between *Jeholornis* and *Archaeopteryx* is the reduction of the teeth (see Electronic Supplementary Material). In *Archaeopteryx*, teeth are present in the premaxilla, maxilla

and dentary (Martin 1991; Wellnhofer 1992). However, there are only three very small teeth present in the lower jaw of the holotype (IVPP V13274). In the IVPP V13350 specimen, two small teeth are present in the lower jaw, but none are present in the premaxilla or maxilla, as is also the case in the IVPP V13553 specimen. Both the upper and lower jaws of *Jeholornis* are shorter, deeper and more robust than in *Archaeopteryx*, indicating its specialized seed-eating adaptation (Zhou and Zhang 2002a). Both birds share a large triangle-shaped antorbital fenestra. The lachrymal of *Jeholornis* has two fenestrae that are absent in *Archaeopteryx*.

Table 1 Comparison between *Jeholornis* and *Archaeopteryx* in ratios of some major skeletal element lengths

	<i>Jeholornis prima</i> (IVPP V13353)	<i>Archaeopteryx lithographica</i> (Solnhofen specimen)
Forelimb/hindlimb	1.26	1.02
Humerus/femur	1.52	1.19
Ulna/humerus	1.02	0.87
Manus/ulna	1.06	1.46
Carpometacarpus/ulna	0.47	0.55
Manual digit II/ulna	0.59	0.91
Second phalanx/first phalanx of manual digit II	0.92	1.37
Tibia/femur	1.19	1.28
Tail/ilium	7.41	6.32
Tail/hindlimb	1.58	0.94
Tail/forelimb	1.25	0.92
Coracoid/scapula	0.59	0.48

The neck of *Jeholornis* is as short as in *Archaeopteryx* and is probably composed of fewer than 10 cervical vertebrae. In both birds the cervical ribs are present. The number of the thoracic vertebrae is 14, similar to that of *Archaeopteryx* (Martin 1991). Pneumatic foramina are observed in a number of thoracic vertebrae of *Jeholornis* (Fig. 2A). Pneumaticity has also been reported in cervical and thoracic vertebrae of *Archaeopteryx* (Britt et al. 1998).

IVPP V13553 preserved a complete synsacrum (Fig. 2B, E). It is composed of six fused sacral vertebrae in contrast to *Archaeopteryx*, which has five unfused sacral vertebrae (Martin 1991). The synsacrum is composed of seven sacral vertebrae in *Sapeornis*, *Confuciusornis* and *Protapteryx* (Zhang and Zhou 2000), eight in *Cathayornis* (Zhou 1995) and nine in *Yanornis* (Zhou and Zhang 2001).

The number of caudal vertebrae in *Archaeopteryx* has generally been believed to be between 21 and 23 (Wellnhofer 1992) although a smaller number has been proposed for the Solnhofen specimen (Elzanowski 2001). The holotype of *Jeholornis* has been reported with 22 caudal vertebrae, which lies in the same range of caudal vertebrae as *Archaeopteryx*. Surprisingly, the two new specimens have preserved a skeletal tail comprising more caudal vertebrae than that of *Archaeopteryx*. In the IVPP V13353 specimen, there are 20 elongated caudal vertebrae and four anterior short caudal vertebrae; combined to make a total of 24 caudal vertebrae (Fig. 1B). In the IVPP V13350 specimen, 22 elongated caudal vertebrae are preserved and there are five short caudal vertebrae preserved in articulation (Fig. 2C); the total number of the caudal vertebrae is therefore 27 (Fig. 1A), more than in any known *Archaeopteryx* specimen. The number of elongated caudal vertebrae after the transition point is between 20 and 22 in *Jeholornis* but is less than 20 in *Archaeopteryx*.

The tail of *Jeholornis* not only has more caudal vertebrae than that of *Archaeopteryx*, it is also relatively much longer than in *Archaeopteryx*. The tail is shorter than both the forelimb and hindlimb in *Archaeopteryx*; however, in *Jeholornis* the tail is about 125% and 158% of the length of the forelimb and hindlimb, respectively (Table 1).

The other major difference between *Jeholornis* and *Archaeopteryx* in the caudal series is that the chevrons of *Jeholornis* are much more elongated, and are connected along most of the caudal series, resulting in a more solid tail (Zhou and Zhang 2002a). In this aspect, it bears more resemblance to the dromaeosaurs (Norell and Makovicky 1999; Xu et al. 2000) than to any other bird.

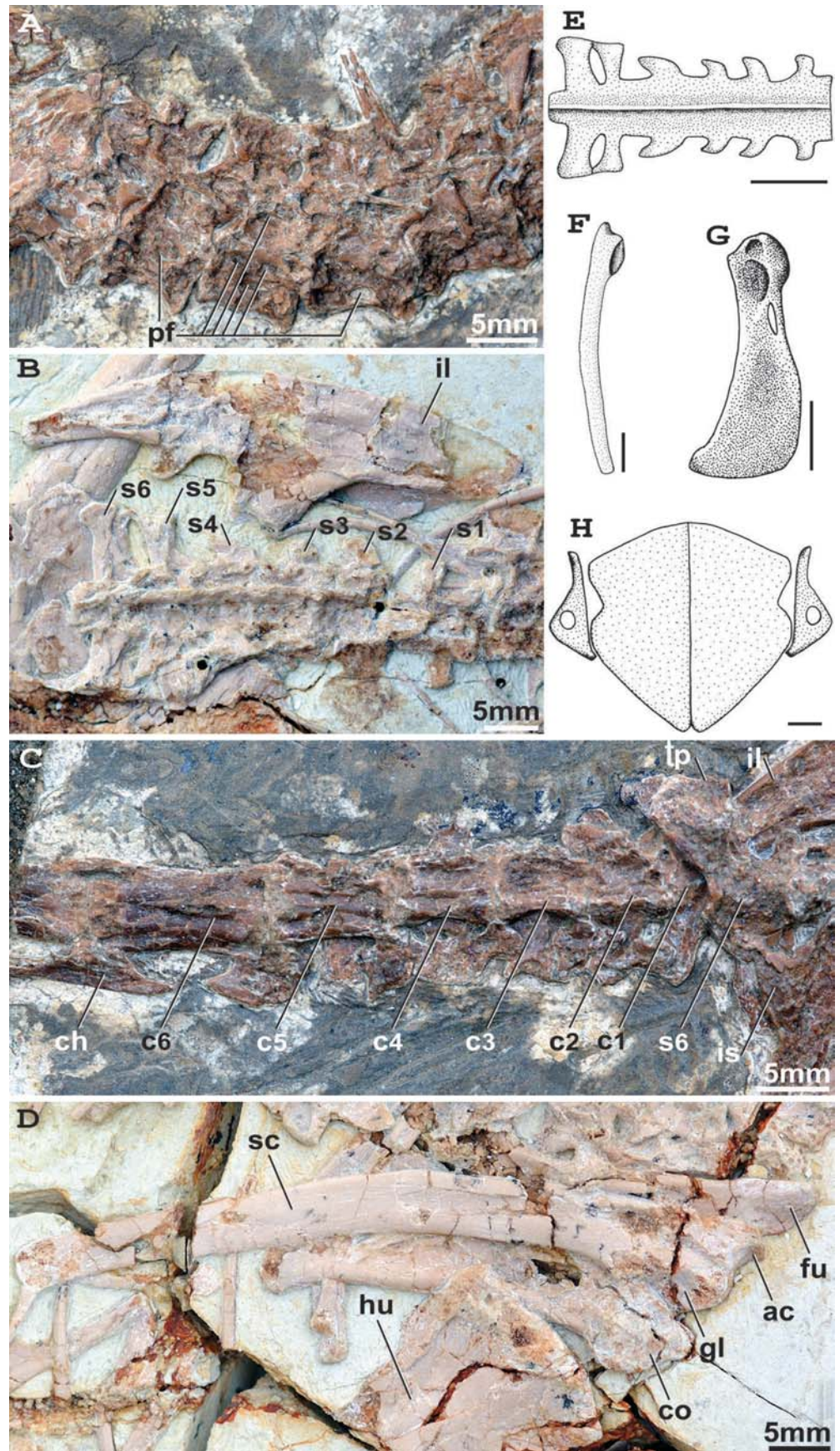
Archaeopteryx has a short sternum, which lacks a lateral trabecula. Re-examination of the sternum of *Jeholornis* shows sutures between the two sternal plates, similar to some dromaeosaurs and probably *Archaeopteryx* too (P.A. Wellnhofer, personal communication). The sternum of *Jeholornis* also represents the most basal bird with a lateral trabecula (Fig. 2H) and, further, the lateral trabecula possesses a rounded fenestra (Zhou and Zhang 2002a).

The pelvis of *Jeholornis* is generally similar to that of *Archaeopteryx* in the degree of the posterior inclination of the pubis. However, the ischium of *Jeholornis* has a better-developed proximal dorsal process than in *Archaeopteryx* and, in this respect, it is more similar to enantiornithines and some other basal birds such as *Sapeornis* and *Confuciusornis* (Martin et al. 1998).

Compared with *Archaeopteryx*, *Jeholornis* shows many derived features related to flight adaptation. As in *Confuciusornis* (Chiappe et al. 1999), the scapula of *Jeholornis* has a dorso-laterally facing glenoid facet (Fig. 2D, F); in *Archaeopteryx*, the glenoid facet is laterally faced. The coracoid is strut-like in *Jeholornis*, while it is short and non-strut-like in *Archaeopteryx* and *Sapeornis* (Zhou and Zhang 2002b). The new materials indicate that *Jeholornis* also has a supracoracoid foramen (Fig. 2G), as does *Archaeopteryx*. The carpometacarpus is well fused proximally in *Jeholornis*, but is less well fused in *Archaeopteryx*. The third metacarpal of *Jeholornis* is strongly bow-shaped, providing a strong support for the attachment of the primary feathers.

In *Archaeopteryx* the forelimb is about the same length as the hindlimb; however, in *Jeholornis* the forelimb is about 126% that of the hindlimb (Table 1); the manus in *Jeholornis* is also relatively much shorter and robust than in *Archaeopteryx* (see Electronic Supplementary Material).

Fig. 2A–H *Jeholornis prima*. **A** Thoracic vertebrae in lateral view (IVPP V13353); **B** synsacrum in dorsal view (IVPP V13353); **C** proximal caudal vertebrae in lateral view (IVPP V13350); **D** scapula in dorsal view (IVPP V13353); **E** reconstruction of synsacrum in dorsal view (IVPP V13353); **F** reconstruction of scapula in lateral view (IVPP V13353); **G** reconstruction of coracoid in dorsal view (holotype, IVPP V13274); **H** reconstruction of sternum in dorsal view (holotype, IVPP V13274). Abbreviations: *ac* acromion, *ch* chevron, *co* coracoid, *c1–c6* the first through sixth caudal vertebrae (the transition point is between the fifth and sixth), *fu* furcula, *gl* glenoid, *hu* humerus, *il* ilium, *is* ischium, *pf* pneumatic foramen, *sc* scapula, *s1–s6* first through sixth sacral vertebrae, *tp* transverse process. Scale bars in parts **E–H** are 1 cm long



The two new specimens of *Jeholornis* preserved completely articulated pes. Although the hallux is reversed and the claws are large and curved, indicative of arboreal capability, the toe proportions are not characteristic of more advanced perching birds with distinctively longer penultimate phalanges (Zhou and Farlow 2001). It is notable that the first digit is short compared with *Archaeopteryx* with a relatively small claw. A free tarsal in IVPP V13553 is probably a juvenile feature.

Feather impressions are not preserved in the holotype of *Jeholornis*, but are found in both the IVPP V13550 and IVPP V13553 specimens. In the IVPP V13550 specimen, the tail feathers are relatively well preserved (Fig. 1C). It is notable how the long tail feathers are attached to the distal caudal vertebrae in a way very similar to that of non-avian theropods *Caudipteryx* (Ji et al. 1998) and *Microraptor* (Xu et al. 2003), i.e., they form a more or less fan-shaped rectrice at the distal end of the tail. It is probably noteworthy that both *Caudipteryx* and *Microraptor* have been suggested to be flightless birds by some researchers (Feduccia 1999; L.D. Martin, personal communication). In the IVPP V13553 specimen, wing feathers are relatively well preserved (Fig. 1B). The exact number of the primary and secondary feathers is difficult to estimate, but the wing feathers are asymmetric and long.

Discussion

Jeholornis is undoubtedly one of the most important discoveries of early birds after *Archaeopteryx*, as it is only the second known bird with a complete long tail (which also bears much resemblance to dromaeosaurs, demonstrating a close relationship between birds and dromaeosaurs regardless of whether dromaeosaurs are dinosaurs or secondarily flightless birds).

The number of sacral vertebrae of *Jeholornis* (6) is larger than that in *Archaeopteryx* (5), but fewer than in other known birds, and may represent a link between the most primitive bird and those more advanced forms such as *Sapeornis*, *Confuciusornis* and *Protopteryx*, which have seven sacra.

Jeholornis has more caudal vertebrae (maximum of 27) than *Archaeopteryx* (maximum of 23) and this may imply that the common ancestor of birds had at least 27 caudal vertebrae. The tail of *Jeholornis* is also much longer than that of *Archaeopteryx* (Table 1). It has been proposed that *Archaeopteryx* probably represents a side-branch in early avian evolution (Martin 1983; Hou et al. 1996; Feduccia 1999). The discovery in *Jeholornis* of a much longer tail comprising more caudal vertebrae than in *Archaeopteryx* appears to lend further credence to this hypothesis.

Despite of the primitive appearance of *Jeholornis*, shared with *Archaeopteryx* in the caudal half of the body (i.e., the pelvis, the hindlimb and the caudal vertebrae), it shows a surprisingly advanced cranial half of the body,

which is more derived than in *Archaeopteryx*, thus confirming a mosaic pattern of morphological evolution common in early birds. These advanced character states include: a scapula with a dorso-laterally exposed glenoid facet, a strut-like coracoid, a sternum with a lateral trabecula with a fenestra; a wing having a well fused carpometacarpus, bowed metacarpal III and a shortened and more robust digit II, which is more suitable for attachment of the primary feathers.

Pneumaticity has been recognized in the skull, cervical and thoracic vertebrae and pelvis of *Archaeopteryx* (Britt et al. 1998; Christiansen and Bonde 2000). *Jeholornis* has not only preserved pneumaticity in various thoracic vertebrae but also in the sternum. The sternum, together with the furcula, is part of a respiratory cycling mechanism between the lungs and the air sacs (Jenkins et al. 1988). The pneumatic sternum may indicate the presence of the interclavicular sac in *Jeholornis*.

Sternal fenestrae are present in all known ornithurine birds such as *Yanornis* and *Yixianornis* (Zhou and Zhang 2001) and most modern birds, but it has not been reported in any dinosaur or enantiornithine bird, although the sternum of enantiornithine *Concornis* is perforated by several foramina (Sanz et al. 1995). The development of the interclavicular sac in *Jeholornis* is related either to its powerful flying ability or its large size, as large flying birds generally have well-developed pneumatic bones, while small fliers have only a few or none (Welty 1982).

Acknowledgements We thank L.D. Martin, P. Currie and L. M. Chiappe for discussions, and X. Wang for help in the field. Y. Li prepared the specimens. This work was supported by the National Natural Science Foundation of China, Special Funds for Major State Basic Research Projects of China (G2000077700) and the Chinese Academy of Sciences.

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