Description of a new enantiornithine bird from the Early Cretaceous of Hebei, northern China

Fucheng Zhang, Per G.P. Ericson, and Zhonghe Zhou

Abstract: This paper describes a new enantiornithine fossil bird, *Vescornis hebeiensis*, nov. sp. from the Early Cretaceous of China. We refer *Vescornis* to the crown clade Euenantiornithes based on several characteristics observed in the thoracic girdle and wing. *Vescornis* also exhibits characteristics that separate it from other enantiornithine birds, such as the short alular phalanx, the vestigial manual claws, and the well-developed and long foot claws. These features suggest an adaptation towards an improved flight capability, while the ability of *Vescornis* to climb is reduced compared with many other enantiornithine birds.

Résumé : Cet article décrit un nouvel oiseau fossile, *Vescornis hebeiensis*, sp. nov. (groupe des Enantiornithes), du Crétacé précoce en Chine. Nous référons *Vescornis* au clade maître Euenantiornithes d'après plusieurs caractéristiques observées dans la ceinture thoracique et les ailes. *Vescornis* démontre aussi des caractéristiques qui le distinguent des autres oiseaux du groupe des Enantiornithes : la courte phalange de l'alula, les griffes manuelles atrophiées et les griffes longues et bien développées des pieds. Ces caractéristiques suggèrent une adaptation à une meilleure capacité de vol alors que l'habilité de *Vescornis* à grimper est réduite si on la compare à de nombreux autres oiseaux du groupe des Enantiornithes.

[Traduit par la Rédaction]

Introduction

From an evolutionary perspective, birds (Class Aves) consist of several large clades, of which only one, Ornithurae, has survived to recent time (Martin 1983; Zheng 1995; Feduccia 1999). Several distinct groups of birds became extinct during the Late Cretaceous, not necessarily at the K–T boundary, as was the case in many other categories of organisms. One of these, and probably the most successful as judged from the fossil record, was the enantiornithine birds. The enantiornithines may have been the geographically most widespread, the taxonomically and ecologically most diverse, and, possibly, the most abundant group of birds in the Mesozoic (e.g., Chiappe 1995; Feduccia 1999; Zhang et al. 2001). The members of this group seem most often to have occupied terrestrial habitats, but they are also known from marine environments (Chiappe et al. 2002).

Several enantiornithine birds have been described from Early Cretaceous formations in China (Wang et al. 2000), most notably the Jiufotang Formation (*Sinornis*, *Cathayornis*, *Boluochia*, *Cuspirostrisornis*, *Eocathayornis*, *Largirostrornis*, *Longchengornis*, *Longipteryx*) and the Yixian Formation (*Eoenantiornis*, *Liaoxiornis, Longirostravis*) in the Liaoning Province in the northeastern part of the country (Sereno and Rao 1992; Zhou 1995; Hou 1997; Hou and Chen 1999; Hou et al. 1999; Zhang et al. 2001; Zhou 2002; Hou et al. 2004).

Herein, we describe a new enantiornithine bird from the northern Hebei Province, China (Fig. 1). It comes from the Early Cretaceous Yixian Formation, (Wang et al. 2000). Among vertebrates, the bird-bearing sediments have mostly yielded fish remains, and the number of bird fossils collected so far is rather low—the described avian taxa from the deposits are *Jibeinia luanhera* (Hou 2000) and *Protopteryx* (Zhang and Zhou 2000). The correlations of the deposits in Hebei and Liaoning are mainly based on biostratigraphic comparisons, yet there is no isotope dating supporting the correlations.

Systematic palaeontology

Aves   Linnaeus, 1758
Enantiornithes Walker, 1981
Euenantiornithes Chiappe, 2002
Vescornis hebeiensis, nov. sp.

ETYMOLOGY: The genus name "*Vescornis*" is derived from the Latin prefix "vesc" (thin, attenuated), indicating the short and undeveloped alular digit and other ungual phalanges of

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Fig. 1. Map of the Hebei Province indicating the locality of Senjitu, where the specimen of *Vescornis hebeiensis* was found.
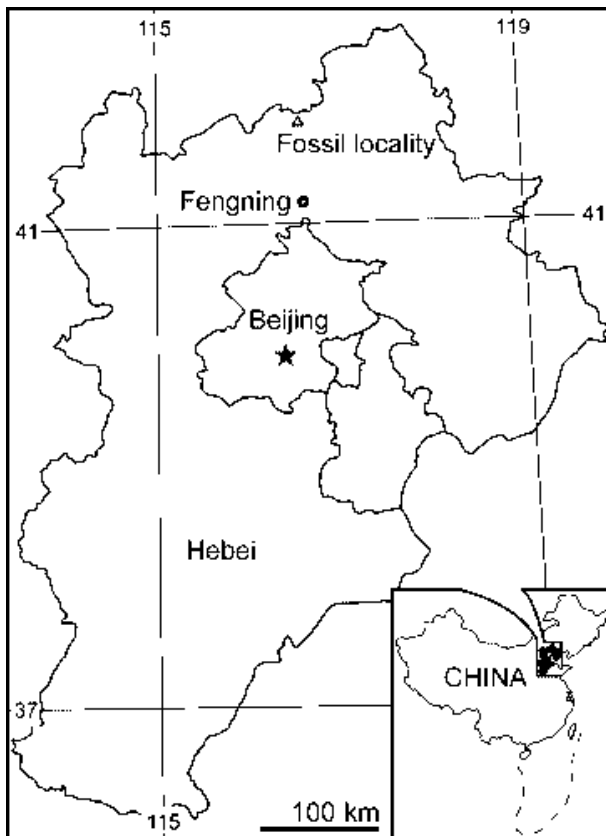
the manus. Species name "*hebeiensis*" is derived from the locality of this bird, the Hebei Province.

HOLOTYPE: An almost complete, articulated skeleton impression split in a slab (the location of the counterslab is unknown). Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences, collection number 130722 (Fig. 2).

LOCALITY AND HORIZON: Senjitu, Fengning County, Hebei Province, China. Yixian Formation (Early Cretaceous).

DIAGNOSIS: First phalanx of digit I of manus reduced and slender, less than half of the major metacarpal in length and diameter. Ungual phalanges of digits I and II in the manus small and vestigial. Coracoid slender, with a length to width ratio approaching 3, which distinguishes it from all other known Early Cretaceous enantiornithines.

DESCRIPTION:

Skull and mandible: The skull is badly crushed and damaged, which prevents a detailed anatomical study. However, some of its elements are articulated and in their natural places, providing the possibility of identifying them (Fig. 3).

The skull is mainly exposed in ventral view, but the right lateral side of it seems exposed more than the other side. In the anterior end of the skull, the dorsal–lateral side of premaxilla body exposes a curved outline; posterior to the body, two fine bars may represent its maxillar process or palatinal process. The dentary is covered on the tomial edge, which

makes it impossible to determine whether the premaxilla has teeth.

The maxilla is large. The nasal process of the maxilla is delicate and rises from the middle part of the bone. The premaxillar process has a spiculated end. The jugal process is wide, unlike the condition in *Archaeopteryx* and modern birds. Only one tooth is preserved in the maxilla.

The jugal bone is delicate and has an expanded articular end. Other skull elements, interpreted as being the parasphenoid, pterygoid, palatine, and lacrimal, are represented by diffuse outlines (Fig. 3).

The size of foramen magnum is about twice the diameter of the occipital condyle, and its margin is thick and robust. The occipital condyle is well developed and round. The basioccipital has an approximately round outline and is laterocaudally connected to the exoccipital with a distinct crest. At the anterior end, the basioccipital shares a concave boundary with the basitemporal plate. The supraoccipital is heavily crushed immediately caudal to the foramen magnum, and part of it has the inner surface exposed.

At the posterior and outermost corner of the braincase, there are two distinct and curved ridges that may be the posterior margin of the parietal. At the left side of the skull, anterior to the supposed parietal, there is a long, outward curved and delicate ridge that we interpret as the supraorbital margin of the frontal, since no other skull element is as long and curved as this.

The mandible is exposed in ventral view, except the left ramus, of which the medial side is visible, and the right ramus, of which the lateral side is exposed. In the anteriormost region, the dentary seems round in outline, unlike in most other birds, suggesting that the two halves of the mandible are only loosely connected in the symphysial region. There are some fossae in the anterior region of the dentary. The ventrocaudally projecting process is not as long as in some extant birds. *Vescornis* has a long Meckelian groove like in *Archaeopteryx* (Elzanowski and Wellnhofer 1996), *Allosaurus* (Martin 1976), Dromaeosauridae (Sues 1977), and Troodontidae (Currie 1987). Anteriorly, this groove reaches at least to the region between the first and second teeth, while it diminishes posteriorly and finally disappears at the distal end of posterior process. The anterior part of the dentary is narrow and deep, and almost half of this region is occupied by the Meckelian groove. The Meckelian groove divides the dentary into two parts. The dorsal one is the convex subdental part, and the ventral one forms a ridge, much like the condition in *Archaeopteryx* Elzanowski and Wellnhofer 1996). It seems that the only difference between the Meckelian grooves of *Vescornis* and *Archaeopteryx* is that it is relatively wider in the former taxon (Fig. 3).

There are five and three teeth preserved in the right and left dentary, respectively, but there seem to have been six teeth in each dentary originally. The alveoli decrease gradually in diameter from the anterior to the posterior end of the dentary. Unlike in *Archaeopteryx*, the teeth of *Vescornis* are sparsely arranged; the interdental space is about four times the diameter of the tooth. It is difficult to determine if an interdental plate is present or not. The teeth of *Vescornis* (including the maxillar tooth) are small, no more than 0.5 mm in length from the tip to the socket, which gives the impression that they are cone-shaped. All teeth are arranged in a

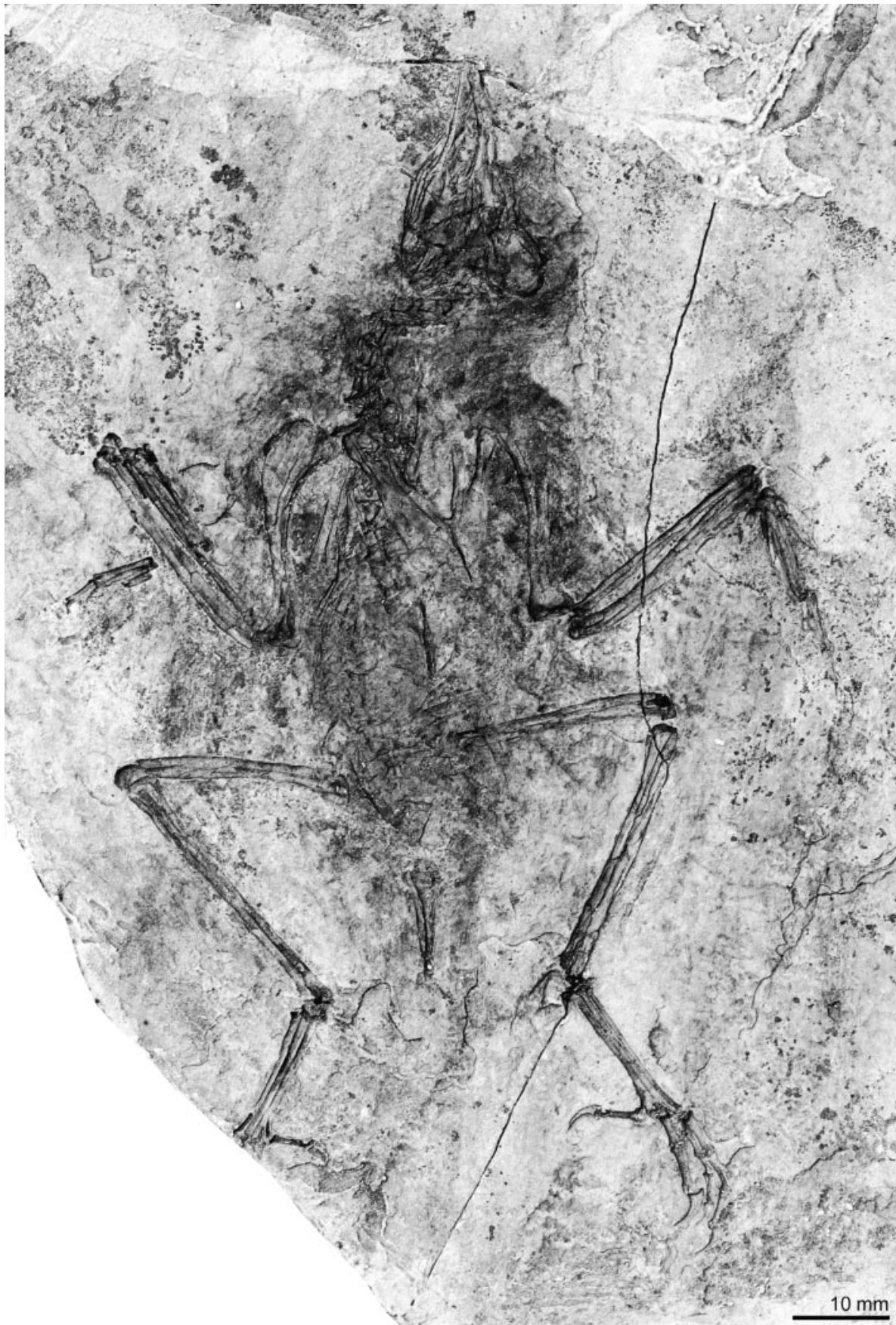**Fig. 2.** *Vescornis hebeiensi* in ventral view, preserved in impression.

Fig. 3. Head of *Vescornis hebeiensis* in ventral view. 1, atlas; 2, axis; a, angular; b, basioccipital; d, dentary; fm, foramen magnum; h, hyoid; j, jugal; la, lacrimal; m, maxilla; mg, Meckelian groove; mpp, maxillar process of premaxilla; np, nasal process; oc, occipital condyle; p, premaxilla; pa, palatine; pi, parietal; pr, prearticular; ps, parasphenoid; pt, pterygoid; s, splenial; smf, supraorbital margin of frontal; su, surangular; t, tooth; ul, ulna. Note: all photos in Figs. 3–10 were taken from the peel of the fossil that only preserved bone impressions.
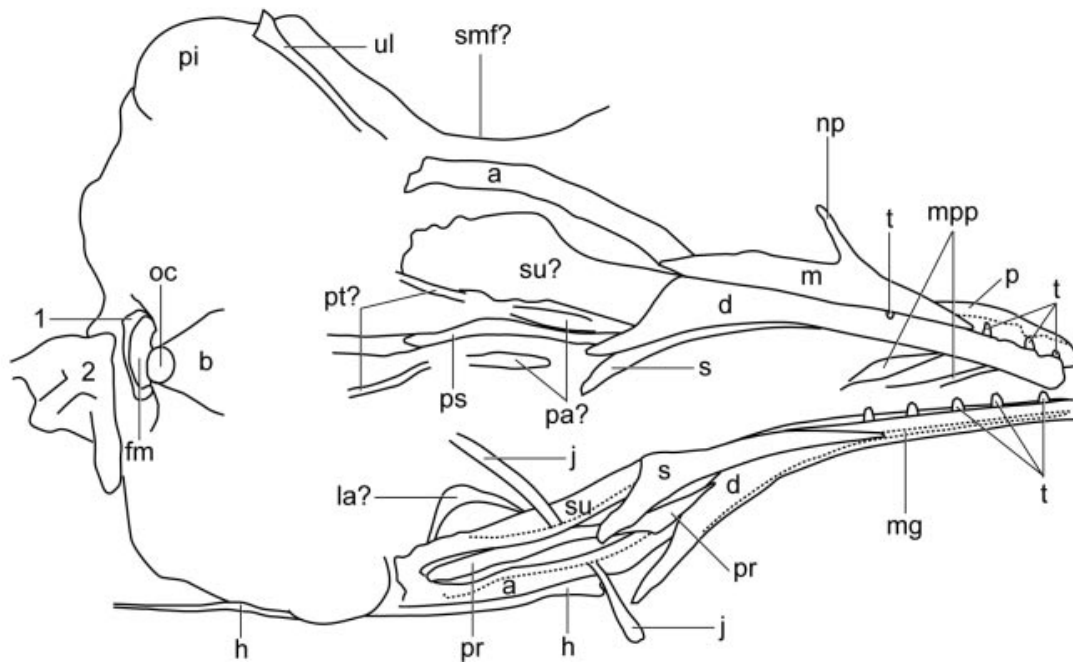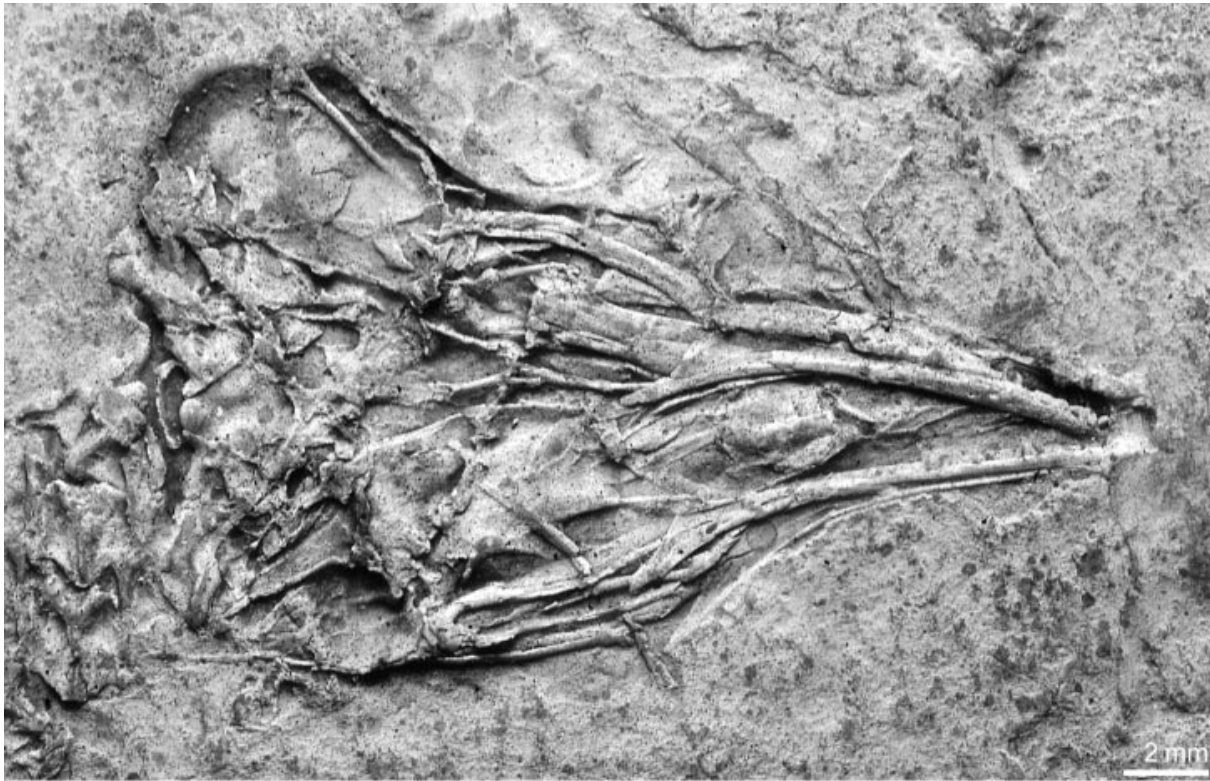
straight row, although the anterior three seem slightly backward.

The splenial is about three-fifth of the dentary in length. It has a long and sharply angled anterior arm. The posterior arm is relatively short and slightly rounded compared with the anterior one. There is a 2:1 ratio between the lengths of

the anterior and the posterior arms, which differs from the 4:3 ratio observed in *Archaeopteryx* (Elzanowski and Wellnhofer 1996).

The anterior part of the prearticular is lancet-shaped, as in *Archaeopteryx* (Elzanowski and Wellnhofer 1996), but unlike in modern birds and theropods, in which the prearticular is rounded. Posterior to the anterior, lancet-shaped part of the bone is a delicate, round neck, which equals the blade part in length. Although the remaining part of the prearticular is heavily crushed, the thickness of the posterior region seems to taper posteriorly.

Of the surangulars, the left is exposed in a lateral view, and the right in a lateral–ventral view. The surangular in *Vescornis* is broad and sturdy, especially in its posterior part, and, like in *Archaeopteryx* (Elzanowski and Wellnhofer 1996), it has a descending edge that connects it to the quadrate.

Judged from its outline, the angular seems to be a long, narrow and slightly curved, strap-shaped bone. The anterior part of the angular seems slightly wider in lateral view than the rest of the bone.

The outline of the quadrate is difficult to determine. The hyoid is partly preserved; it is delicate and long and has an expanded anterior end.

Axial skeleton: Nine cervical vertebrae are visible, but it is likely that the cervical region consists of 10–11 vertebrae. Near the foramen magnum of the skull, the atlas is visible in a caudoventral view. The narrow arcus has two relatively small and robust caudolateral processes; there is no ventral process, which is present in some extant birds, such as wild turkey. The axis is short and broad with prominent posterior articular processes. The dens axis is broad and strong, and slightly triangular in ventral view. The area just anterior to the dens and connecting it posteriorly to the proximal part of the ventral process is sturdy and quadrangle in shape. The ventral process of the axis is small compared with those in the following cervical vertebrae (Fig. 4).

Like the axis, all other postatlantal cervical vertebrae are preserved in ventral view. They are all rather short and broad, with heterocoelous articulations both posteriorly and anteriorly. The anterior and posterior zygapophyses, as well as the costal processes are well developed, except in the third and forth vertebrae. Along the side of the latter vertebrae, there is a long and continued bone plate connecting the prezygapophysis and postapophysis; the ventral parts of the cranioventral fovea and anterior articulate facet are visible in ventral view. The bodies of at least the 2nd to the 8th cervical vertebrae have long ventral processes (keels). In modern birds, ventral processes are generally present only in the anteriormost cervical vertebrae (e.g., from 2nd to 4th or 5th). All cervical vertebrae after the fifth have their costal processes, and their distal ends reach the middle of the vertebral body, respectively. As in most extant birds the cervical vertebrae get successively shorter and broader backwards (Fig. 4).

The single, well-preserved thoracic vertebra identified appears to have an opisthocoelous articulation and the lateral side of the corpus excavated (Fig. 5).

There are eight sacral vertebrae. They are not completely fused as shown by the large space between the articulations of the fourth and fifth, and fifth and sixth, vertebrae,

Fig. 4. Cervical vertebrae of *Vescornis hebeiensis* in ventral view. 1, atlas; 2, axis; 3–9, cervical vertebrae 3–9; cap, caudal articular processes; clp, caudolateral process; de, dens; oc, occipital condyle; vp, ventral process.
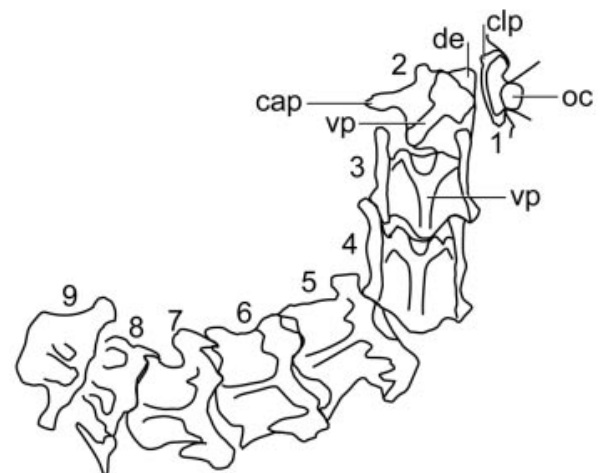

respectively. The first four vertebrae seem to have fused, however. All corpi that can be observed have a shallow ventral synsacral sulcus. The sixth sacral vertebrae has well-developed transversal processes, which are similar in length to the width of the vertebral body (Fig. 6).

No free posterior vertebrae are preserved. The pygostyle is ventrolaterally compressed and has a deep medial excavation along the ventral side of the anterior end. The articulation surface is concave in ventral view. A ridge formed by the fused transversal processes runs along the lateral sides of the pygostyle, and another ridge formed by the fused ventral processes runs along the posterior margin of the bone, like in modern birds. The apex of the pygostyle is round and simple, without any lamellae developed (Fig. 6).

Thoracic girdle and sternum: Both coracoids are exposed in anterior view. The coracoid is elongate and narrow, with a broad sternal articulation, but the lateral margin is not expanded as in other enantiornithines, e.g., *Protopteryx* (Zhang and Zhou 2000). As in other enantiornithines, the lateral margin is convex, and there is no indication of the presence of a procoracoid process. The scapular articulation cannot be

Fig. 5. Sternum and thoracic girdle elements of *Vescornis hebeiensis* in ventral view. ca, carina; co, coracoid; fu, furcula; ga, gastralia; hu, humerus; lp, lateral process; ri, rib; sc, scapula; st, sternum; tv, thoracic vertebra.
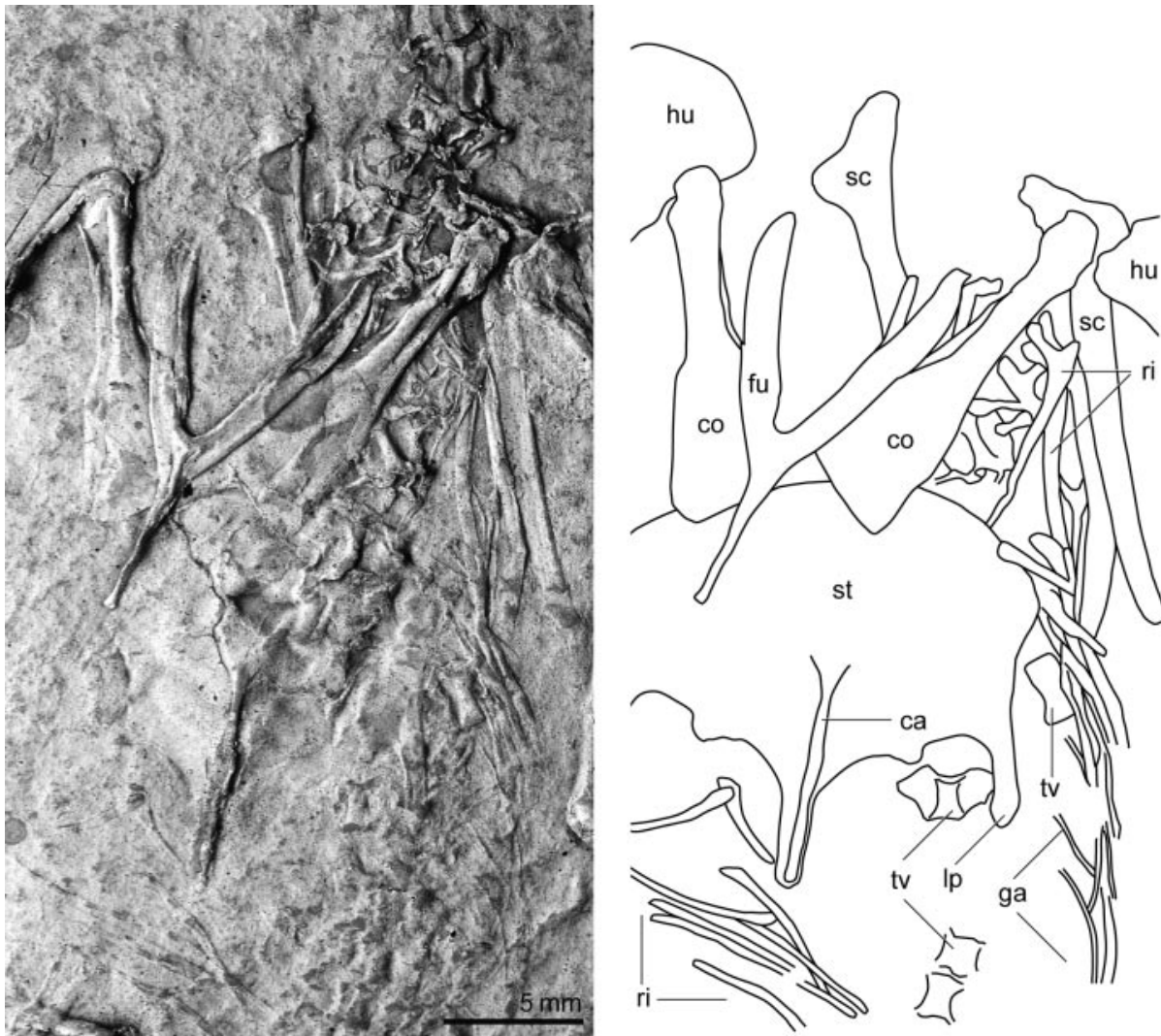
observed, as only the ventral side of the coracoid is exposed. However, it is clear that the coracoid and scapula articulate at an acute angle (Fig. 5).

The scapula is long and narrow, with a shallow, longitudinal depression on the lateral side, similar to that in *Halimornis* (Chiappe et al. 2002). In the anterior end, the acromion and coracoid tuberosity are well developed, and the humeral articular facet is probably less concave than in many other enantiornithines (Chiappe 1996; Chiappe et al. 2002). It cannot be judged whether the shaft is sagitally curved, as in modern birds (Fig. 5).

In agreement with other enantiornithines (Sanz et al. 1995; Zhang and Zhou 2000; Zhang et al. 2001), the furcula is Y-shaped with a prominent hypocleidum that is about half the length of the clavicular rami. The ventral process of the hypocleidum is uneven; its middle region is more developed than other regions. The clavicular ramus is robust with a thin and narrow epicleidium. In anterior view, the clavicular rami are slightly curved medially and separated by an angle of ~ 45°. The rami are not markedly excavated, unlike in *Neu-*

*quenornis* (Chiappe and Calvo 1994), *Concornis* (Sanz et al. 1995) and *Longipteryx* (Zhang et al. 2001).

As in other enantiornithine birds (Zhang and Zhou 2000; Zhang et al. 2001), the sternum is short and broad with the width and length of about equal size. The anterior end is difficult to observe but seems to have a thin margin, which may represent the coracoidal articular sulcus. An ossified keel runs from the middle of the sternum to the posterior end of the medial process. The posterior margin is deeply notched forming two lateral processes and a triangular medial process, as in some other enantiornithines (Zhang and Zhou 2000).

All visible ribs are slender. The sternal ribs are short. The vertebral ribs are relatively long, except the most posterior ones (Fig. 5).

Several gastralia are present in the abdominal part, and they are woven together as in some other birds (Chiappe et al. 1999; Zhang et al. 2001; Zhou and Zhang 2003).

Thoracic limb: In the wing, the humerus equals the ante-

Fig. 6. Synsacral vertebrae, pygostyle and pelvic girdle elements of *Vescornis hebeiensis*. fe, femur; fo, pubic foot; il, ilium; is, ischium; pu, pubis; py pygostyle; sv, synsacral vertebrae.
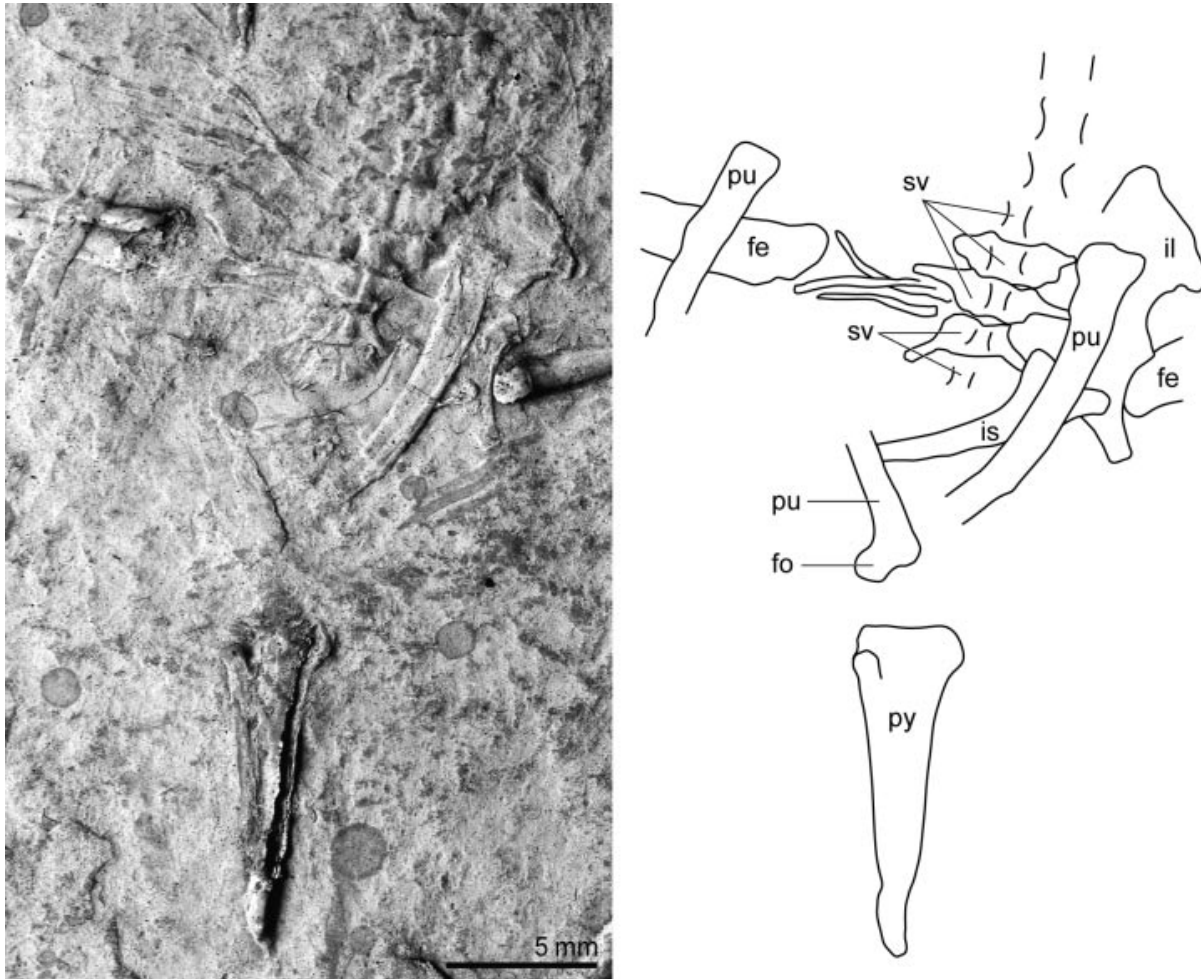
brachium (radius and ulna) in length, while the carpometacarpus is somewhat shorter (Figs. 7, 8).

The shaft of the humerus is slightly S-shaped. The pectoral crest area is large compared with the relatively short shaft of humerus. The proximal end of the humerus is anteriorly concave, with a prominent ventral tubercle and a well-developed, cranioventrally projecting bicipital crest. Although no transversal ligamental groove occurs in the cranioproximal surface of the bicipital crest, a small fossa for muscular attachment is present in this region, as in other enantiornithines (Chiappe et al. 2002). The distal condyles are mainly located on the anterior side of the bone. The dorsal condyle is small when compared with that in modern birds. Another distinct enantiornithine feature of the humerus is that the longitudinal axis of the dorsal condyle is almost perpendicular to the axis of the shaft. The ventral condyle is slightly longer than the dorsal one, but not as wide. The ventral epicondyle, and its nearby area, is well developed and anteriorly expanded, unlike in modern bird (Figs. 7, 8).

The ulna is considerably more robust than the radius. The proximal part of the ulna is slightly curved, and the olecranon seems slightly poorly developed in caudoventral view. There is a crest between the distal area of the proximal cotylae and

the shaft of the ulna. A longitudinal depression along the posterior border of the radius may be similar to the axial groove observed in some enantiornithine birds (Chiappe and Calvo 1994), but could also result from a postmortal compression of the radius' shaft. At the distal end of ulna, the condyles and tuberosities are not as developed as in modern birds (Figs. 7, 8).

The radius is thin and straight, with the distal part slightly curved. The proximal end of radius is slightly expanded and seems to have a simple articular face (Figs. 7, 8).

The ulnare bone appears to be V-shaped with the long and short crura well developed, as in modern birds. The radiale is a rather compressed bone with the distal articulation surfaces divided by a low ridge (Figs. 7, 8).

The alular metacarpal has a curved lateral outline and is short and stout and lacks the extensor process that is present in modern birds. The alular metacarpal is close to the second metacarpal and seems not fused to it. The second metacarpal is straight and the most robust of the three metacarpals. The third metacarpal is slightly curved and extends somewhat more distally than the second. The alular metacarpal is about one-fifth of the second in length and slightly more than half the length of the first phalanx of the first digit (Figs. 7, 8).

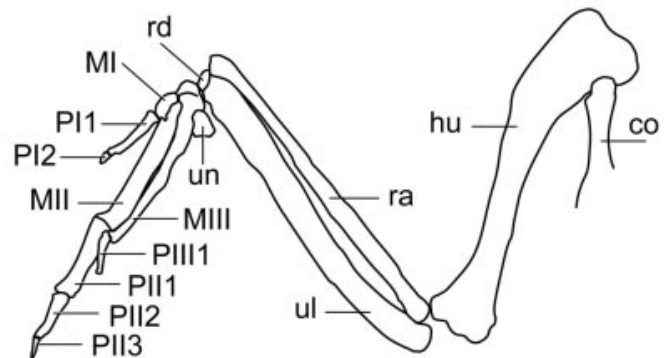The first phalanx of digit I of the manus is slender and

Fig. 7. Left forelimb of *Vescornis hebeiensis.* co, coracoid; hu, humerus; MI, alular metacarpal; MII, second metacarpal; MIII third metacarpal; PI1, first phalanx of digit I; PI2, second phalanx of digit I; PII1, first phalanx of digit II; PII2, second phalanx of digit II; PII3, third phalanx of digit II; PIII1, first phalanx of digit III; ra, radius; rd, radiale; ul, ulna; un, ulnare.

Fig. 8. Right forelimb of *Vescornis hebeiensis.* co, coracoid; hu, humerus; MI, alular metacarpal; MII, second metacarpal; MIII third metacarpal; PI1, first phalanx of digit I; PI2, second phalanx of digit I; PII1, first phalanx of digit II; PII2, second phalanx of digit II; PII3, third phalanx of digit II; PIII1, first phalanx of digit III; ra, radius; rd, radiale; ul, ulna; un, ulnare.
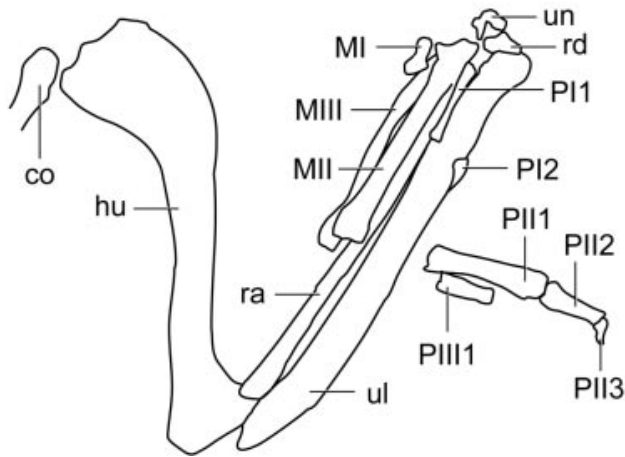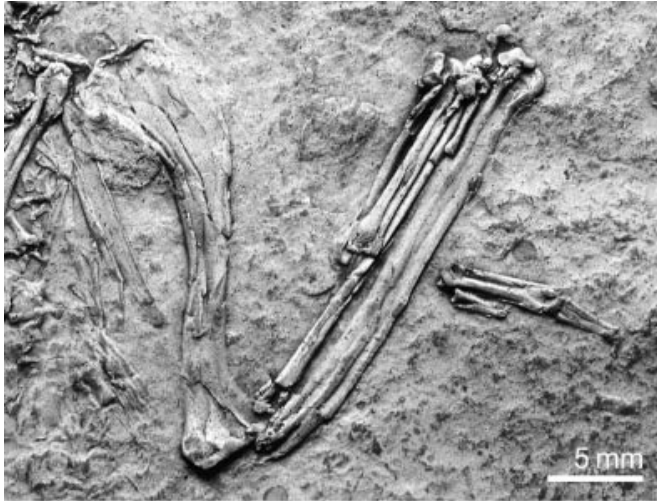
less than half of the second metacarpal in length and diameter. The ungual phalanx of digit I is not as curved as it is in other primitive birds. The proximal phalanx of digit II is the longest; it is broad and robust, suggestive of the condition in extant birds. The intermediate phalanx of digit II is short, only half the length of the proximal one. Compared with the alular digit, the ungual phalanx of digit II is smaller and straighter. The phalanx of digit III is positioned close to the first phalanx of digit II; it is short and tapers in width distally as in extant birds. The phalangeal formula of the manus is 2–3–1 (Figs. 7, 8).

Pelvic girdle and limb: The elements of the pelvic region are not well preserved. Two fragments are identified as being mid-parts of the left and right pubes, respectively. Only the outline of the ilium is preserved. The proximal end of the ischium is expanded, as in other enantiornithine birds. In general, the pelvic elements contribute little anatomical information (Fig. 6).

The femur is slender and slightly craniocaudally curved. Both femora are exposed in medial view, and it is thus not possible to determine if they possess the posterior trochanter typical of many Mesozoic taxa (Chiappe 1996). The greater trochanter is poorly developed, as in many other Mesozoic taxa, including the enantiornithines. The distal end has a distinct popliteal fossa that seemingly is separated from the intercondylar groove by a transverse ridge. The condyles are rounded, and the medial condyle is considerably larger than the lateral one. A well-developed tibiofibular crest seems not to be present, although this part of the bone is too poorly preserved to allow a definite judgment (Figs. 9, 10).

The tibiotarsi are both exposed in medial view. They are straight and correspond in length to more than 125% of the femur. There is no anterior cnemial crest, unlike in extant birds. The proximal articulation appears to be round as in other enantiornithine birds. It is difficult to observe the morphology of the distal end of tibiotarsus due to the poor preservation. However, in the left tibia, a proximal tarsal is present at the distal end and seems not to be completely fused with the tibia. No fibulae are visible in the view the fossil is preserved (Figs. 9, 10).

The metatarsals are exposed in dorsal aspect. Metatarsals II to IV are about half the length of tibiotarsus. Metatarsal III is the most robust, and it reaches about equally far distally as metatarsal IV. Metatarsal II does not reach as far distally and curves laterally before its articulation with the first phalanx. This articulation is considerably broader than

Fig. 9. Left hind limb of *Vescornis hebeiensis.* D1, digit I; fe, femur; MtI–MtIV, metatarsals I–IV; ti, tibia; ta, tarsal.

Fig. 10. Right hind limb of *Vescornis hebeiensis.* D1–D4, digits I–IV; fe, femur; MtI–MtIV, metatarsals I–IV; pu, pubis; ti, tibia; ta, tarsal.
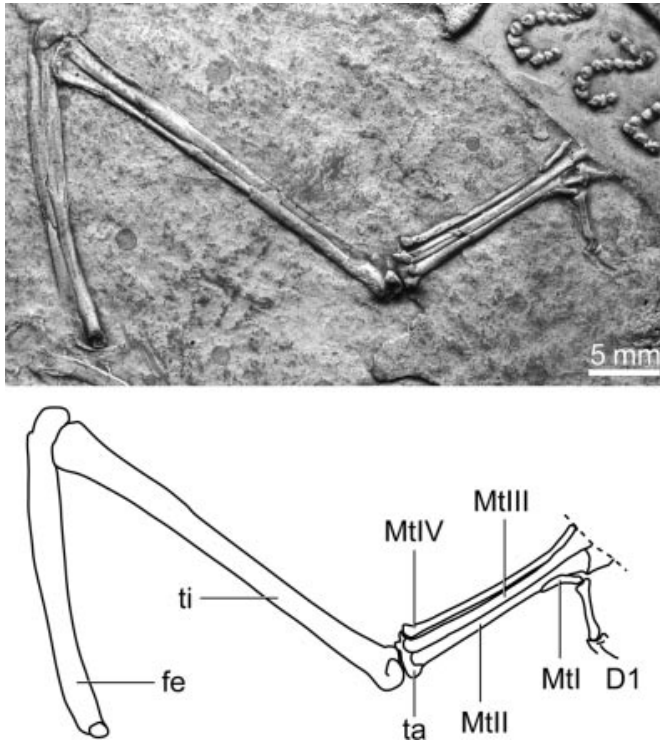

those of the third and fourth metatarsals. The first metatarsal is short and attaches to the distal part of the shaft of the metatarsal II. The twisted shape of metatarsal I causes the phalanx of this digit to articulate in a reversed position compared with all the other digits, and the foot is thus of the anisodactyl type. All the shafts of metatarsals II to IV are clearly distinguishable although they may be partly fused in their proximal ends. As observed in the right leg, the proximal ends of metatarsal II to IV are fused with the distal tarsals. There is no indication of a vascular foramen between metatarsals III and IV (Figs. 9, 10).

Similar to those of other birds, the phalangeal formula of the foot is 2–3–4–5. The second digit is the strongest toe, while the third is the longest. The hallux is long and strong. All phalanges have well-developed flexor tubercles. The claw phalanges (possibly with the exception of the small one in digit IV) are long and moderately recurved, resembling more that of a perching bird than one that lives on the ground (cf. Feduccia 1999; Figs. 9, 10).

PHYLOGENETIC POSITION: The inclusion of *Vescornis* in the Enantiornithes is based on its possession of the following characteristics used to define this taxon (Chiappe 2002): hypocleidum of the furcula well developed, ulna and humerus of equal lengths, metacarpal III projecting further distal than metacarpal II, and a round proximal articulation surface of tibiotarsus. As described by, for example, Chiappe and Walker (2002) and Chiappe (2002), the Enantiornithes of Walker (1981) was phylogenetically defined by Sereno (1998) to include all taxa that are closer to *Sinornis santensis* than to Neornithes. By this, the clade Enantiornithes came to include several taxa not previously thought of as enantiornithines,
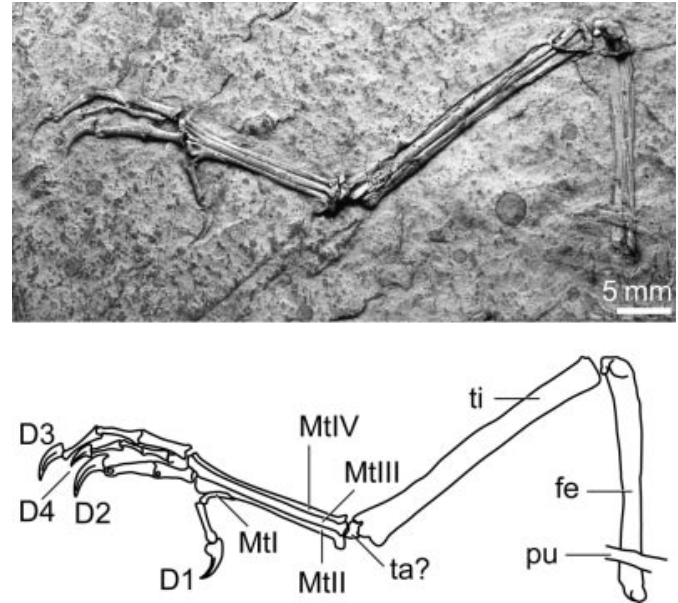
along with such taxa that possess a "classical" enantiornithine morphology. An analysis by Chiappe (2002) showed the latter group to be monophyletic; he named this clade Euenantiornithes. *Vescornis* belongs to the Euenantiornithes based on the possession of the following synapomorphies: sternum with a parabolic anterior margin, distinctly convex lateral margin of coracoid, concave humeral head, longitudinal groove on the ventrocaudal surface of radius, metatarsal II curves laterally before its articulation with the first phalanx, the articulation between metatarsal II and the first phalanx considerably broader than those of the third and fourth metatarsals, and metatarsal IV distinctly thinner than metatarsals II and III. It has not proven possible to establish general relationships among the euenantiornithines due to the fragmentary nature of many representatives of the group (Chiappe and Walker 2002; Chiappe 2002). Thus, the precise systematic position of *Vescornis* within this clade has not been possible to determine.

Discussion

To have the sacral vertebrae fused together as a unit is a common indicator of adult individual in both birds and dinosaurs (Gauthier 1986). Although the eight sacral vertebrae of *Vescornis* are closely connected, they are not completed fused together suggesting that the holotype of *Vescornis* may not be fully adult. Further support for this comes from the observation that some elements in the skull, mandible, pelvic region, and hind limb are not fused as in adult birds. It thus seems to be clear that the holotype of *Vescornis* represents a nearly adult individual.

Several features characteristic of enantiornithine birds are present in *Vescornis*. These include a hypocleidum of furcula that is of the same length as the clavicular ramus, a metacarpal III that projects more distally than metacarpal II, and a sternum with a parabolic anterior margin. *Vescornis* also possesses

many autapomorphic characteristics, especially in the manus: The manual claws of *Vescornis* are weakly developed compared with other Mesozoic birds. Digits I and II all have minute claws that would provide less climbing or grasping abilities than those of their ancestors. Another observation that may also bear on this is that the four phalanges of the second and third digits of the left side were all in their correct anatomical positions relative to each other, even though they were not found in articulation with the rest of the manus. No obvious taphonomic explanation for this exists. The skeleton is otherwise almost completely articulated, but it suggests that the phalanges were kept together by ligaments or other soft tissue after they became separated from the manus. The occurrence of such ligaments between the digits II and III (present also in modern birds) would drastically minimize the ability of the digits to move independently and thus probably restrict their use for climbing or grasping.

The recurved claws on the anisodactyl foot of *Vescornis* are well suited for perching. The first (hallux) and second digits are proportionally more strongly built and the claws longer than in other enantiornithine birds (Zhang and Zhou 2000). This foot morphology enables the bird to perch steadily, and it is possible that this adaptation should be viewed in light of the occurrence of the rather weakly developed manus.

For a long time, it has been commonly viewed that a cursorial origin of avian flight is closely linked to a dinosaurian origin of birds. However, recent discoveries of dinosaurs, such as *Microraptor* and *Epidendrosaurus* (Xu et al. 2000; Zhang et al. 2002), provide fossil evidence that the origin of birds and the origin of avian flight are two different concepts. Increasingly, fossils not only provide evidence for a dinosaur origin of bird, but also for the hypothesis of an arboreal origin of avian flight. Both hind limb and forelimb anatomy of *Microraptor* and *Epidendrosaurus* suggest that these were tree-living. The long manus of *Epidendrosaurus* suggests that the forelimb plays an important role for their arboreal adaptation. As the adaptation towards flight increases in the forelimb, the climbing ability of birds gradually decreases.

Vescornis, with its powered flight, had lost many or most of the climbing adaptations that helped its ancestors to escape predators, search for food, and, maybe most importantly, reach high-level places from where it could start its flight. The relatively strong and powerful claws of the foot provided *Vescornis* with the ability to both perch in trees and launch flights. The anatomy of the manus of *Vescornis* suggests that it is well adapted to flying, but it has lost most of its climbing ability.

In size, as well as in some as morphological characteristics, *Vescornis* closely resembles *Jibeinia luanhera* (Hou 2000). *Jibeinia luanhera* first appeared in the book *Mesozoic Birds of China* (in Chinese, Hou 1997), but its scientific name is given only once in the legend of a schematic figure of the skeleton. In the text describing this specimen, only its Chinese name is used. The formal naming of this specimen instead occurred in the *Picture Book of Chinese Fossil Birds* (Hou 2000), where a short description of the age, etymology, locality, preservation and diagnosis was given. *Jibeinia luanhera* was collected from the same geological formation, not far from the locality of *Vescornis*. There is, thus, reason to closely examine the possibility that the two taxa are conspecific. Unfortunately, the holotype of *Jibeinia luanhera* (the only specimen known) is lost (L. Hou, personal communication, 2001). Furthermore, the casts of the holotype are of low quality and the available illustrations of *Jibeinia luanhera* add no information. The description of *Jibeinia luanhera* includes certain morphological characteristics that radically differ from the condition in *Vescornis*. For example, *Jibeinia luanhera* was found to have more maxillary teeth, no keel on the sternum, digit III in the manus with three phalanges, and astragalus and calcaneum unfused to the tibia. If correctly described, these characteristics unambiguously shows that *Jibeinia luanhera* is of a different taxon from *Vescornis*. However, the lack of the holotype of *Jibeinia luanhera* precludes an evaluation of these observations. Given the similar geological circumstances for the findings, their almost identical size, and the many shared morphological characteristics, it is clearly possible that a future reexamination of the holotype *Jibeinia luanhera* (if found) may result in the synonymization of this taxon and *Vescornis*.

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