

Anatomy of the Early Cretaceous bird *Eoenantiornis buhleri* (Aves: Enantiornithes) from China

Zhonghe Zhou, Luis M. Chiappe, and Fucheng Zhang

Abstract: A detailed description of the anatomy, in particular of the skull, of *Eoenantiornis* is provided. This description reveals many morphological characters previously unknown for enantiornithine birds, such as presence of a distinct facet for the intramandibular articulation between the dentary and postdentary bones. *Eoenantiornis* documents an intermediate stage in the abbreviation of the alular digit among Ornithothoraces, which paralleled a similar transformation within Ornithuromorpha. Our analysis also indicates that *Eoenantiornis* belongs to the Euenantiornithes.

Résumé : Une description détaillée de l'anatomie d'*Eoenantiornis* est présentée, plus particulièrement du crâne, qui révèle des caractères morphologiques jusqu'ici inconnus chez les oiseaux enantiornithines, tels que la présence d'une facette distincte de l'articulation intramandibulaire entre les os dentaire et post-dentaire. *Eoenantiornis* témoigne d'un stade intermédiaire de l'abréviation du doigt alulaire chez les Ornithothoraces qui s'inscrit parallèlement à une transformation semblable chez les ornithuromorphes. Notre analyse indique également qu'*Eoenantiornis* appartient aux Euenantiornithes.

[Traduit par la Rédaction]

Introduction

Remains of enantiornithine birds are rare in the Yixian Formation of northeastern China. Only a handful of enantiornithine fossils from this stratigraphic unit have been named: *Eoenantiornis buhleri* (Hou et al. 1999), *Protopteryx fengningensis* (Zhang and Zhou 2000), *Longirostravis hani* (Hou et al. 2004), and *Liaoxiornis delicatus* (Hou and Chen 1999). Because *Liaoxiornis delicatus* (a senior synonym of *Lingyuanornis parvus* Ji and Ji, 1999) was erected on a juvenile specimen that lacks characters discriminating it from other enantiornithines (Chiappe and Walker 2002), *Eoenantiornis*, *Protopteryx*, and *Longirostravis* are considered to be the only valid enantiornithines so far named from the Yixian Formation.

The holotype and only known specimen of *Eoenantiornis buhleri* was briefly described and illustrated by Hou et al. (1999). Despite sedimentary deposition, stratigraphic correlations of Yixian localities across northeastern China remain controversial, and *Eoenantiornis* is one of the oldest known enantiornithines (Chang et al. 2003). Thus, because of its age and the seemingly primitive condition of its skeleton among enantiornithines, this bird is important for clarifying the largely unknown interrelationships of Enantiornithes. In this paper, we offer a detailed description of this specimen with the aim of providing new morphological information (characters and coding) useful for better understanding character evolution across this diverse group of Cretaceous birds.

Systematic paleontology

Aves Linnaeus, 1758
Ornithothoraces Chiappe, 1995
Enantiornithes Walker, 1981
Euenantiornithes Chiappe, 2002
Eoenantiornis Hou et al., 1999
Eoenantiornis buhleri Hou et al., 1999

HOLOTYPE: IVPP V11537 (Institute of Vertebrate Paleontology and Paleoanthropology), a nearly complete and articulated skeleton with well-preserved feather impressions (Fig. 1, 2).

LOCALITY AND HORIZON: Heitizigou, Shangyuan, Beipiao, Chaoyang, Liaoning, China; Jianshangou bed, Lower Yixian Formation (Early Cretaceous, Aptian; approximately 125 Ma) (Zhou et al. 2003).

DIAGNOSIS: Moderate-sized enantiornithine with a short and deep rostrum, a broad skull, a dorsal process of the maxilla that forms virtually the entire caudal margin of the narial opening, upper dentition that decreases in size towards the back, a highly abbreviated mandibular symphysis, a sternum with laterocaudal processes shorter than the xiphoid process, an alular digit that extends to the distal end of the major metacarpal, a manus much shorter than ulna (carpometacarpus to ulna ratio is 47%), and an intermediate phalanx of the major manual digit that is significantly more slender than the proximal

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Fig. 1. Photo of the holotype of *Eoenantiornis buhleri*, IVPP V11537.



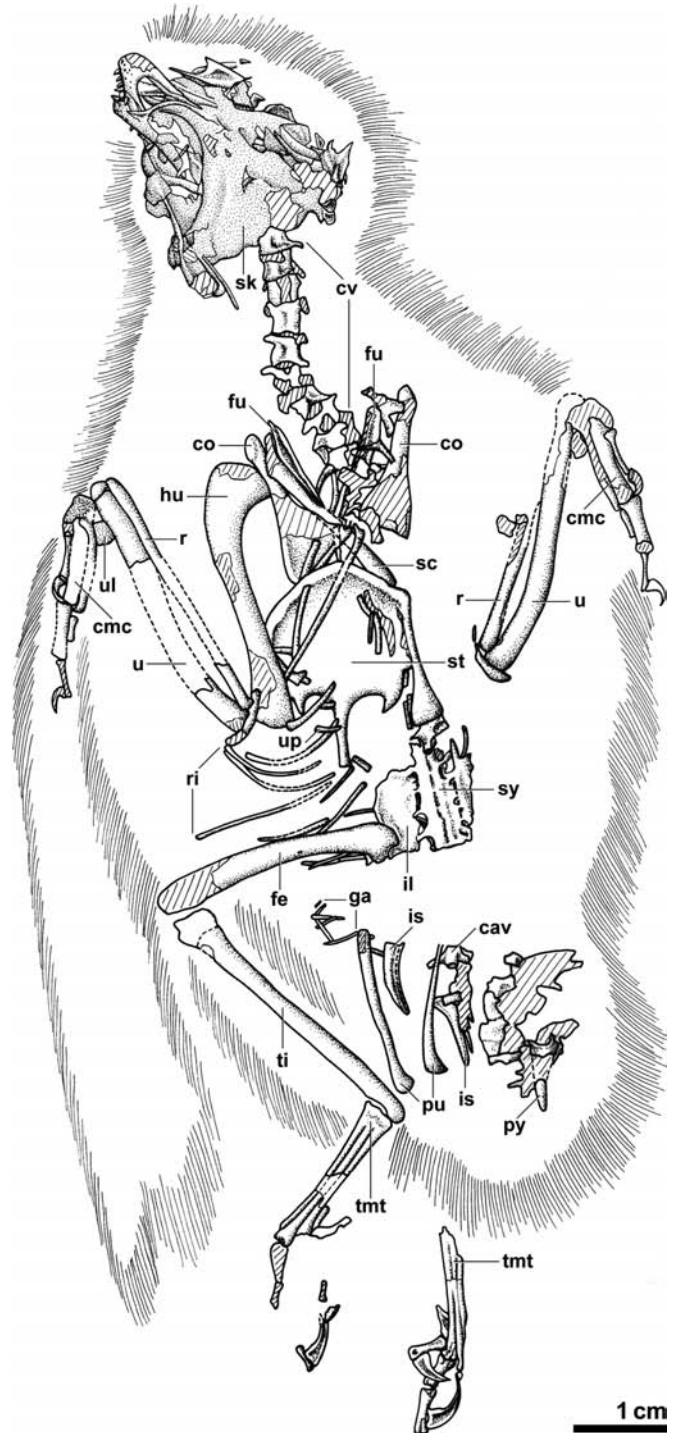
phalanx of this digit. The unique short and deep rostrum and the combination of many other characters set *Eoenantiornis* aside from all other enantiornithine birds.

Anatomical description

Cranial bones

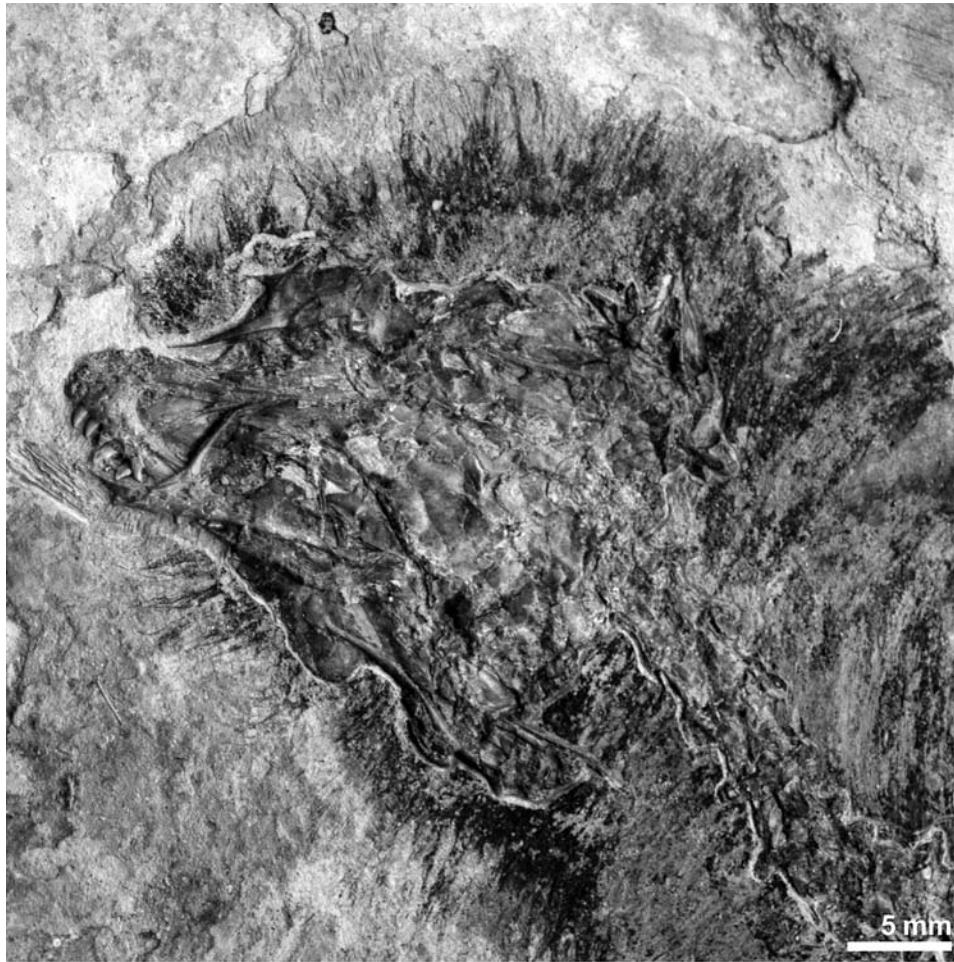
The skull is preserved in dorsal and lateral view (Fig. 3, 4). Compared to *Archaeopteryx* (Elzanowski 2002) and other euenantiornithine birds, such as *Cathayornis* (Martin and Zhou 1997; Chiappe and Walker 2002), it is short and deep. The premaxilla has a nearly vertical and slightly convex cranial margin. It has a caudally tapering nasal process that forms an angle of about 30° with the short maxillary process. The nasal process of the premaxilla approaches the cranial margin of the orbit, however it only reaches the cranial margin of

Fig. 2. Line drawing of the holotype of *Eoenantiornis buhleri*, IVPP V11537: cav, caudal vertebra; cmc, carpometacarpus; co, coracoid; cv, cervical vertebra; fe, femur; fu, furcula; ga, gastralia; hu, humerus; il, ilium; is, ischium; pu, pubis; py, pygostyle; r, radius; ri, rib; sc, scapula; sk, skull; st, sternum; sy, synsacrum; ti, tibiotarsus; tmt, tarsometatarsus; u, ulna; ul, ulnare; up, uncinat process.



the antorbital cavity in *Archaeopteryx* (Martin and Zhou 1997; Elzanowski 2002). It is unclear, however, whether the premaxillae fuse together rostrally, but the presence of a medial

Fig. 3. Close-up photo of the skull of the holotype of *Eoenantiornis buhleri*, in dorsolateral view, IVPP V11537.



facet in what appears to be the nasal process of the right premaxilla suggests that these bones remain unfused to one another caudally. Dorsal to the external nares, the lateral side of the nasal process of the premaxilla bears an indented, longitudinal facet for the articulation with the premaxillary process of the nasal. The dentigerous margin of the premaxilla is virtually straight; two rows of nutrient foramina occur parallel to the straight ventral margin of this bone. The rostralmost portion of this bone does not carry any teeth. Three teeth are preserved in situ, although a broken fallen tooth (overlapping the rostral end of the dentary) probably belongs to the premaxilla as well. Thus, *Eoenantiornis* has the typical four premaxillary teeth of most other early birds. The premaxillary teeth become progressively smaller caudally, which is a trend that is also congruent with the size of this latter fallen tooth. The teeth are subconical with their tips slightly curved backwards. As in most other Mesozoic birds (Martin and Stewart 1999), the root is somewhat inflated and separated from the crown by a slight constriction. Caudal to the last premaxillary tooth (the one that is broken and fallen from its place), this bone forms a narrow tapering maxillary process.

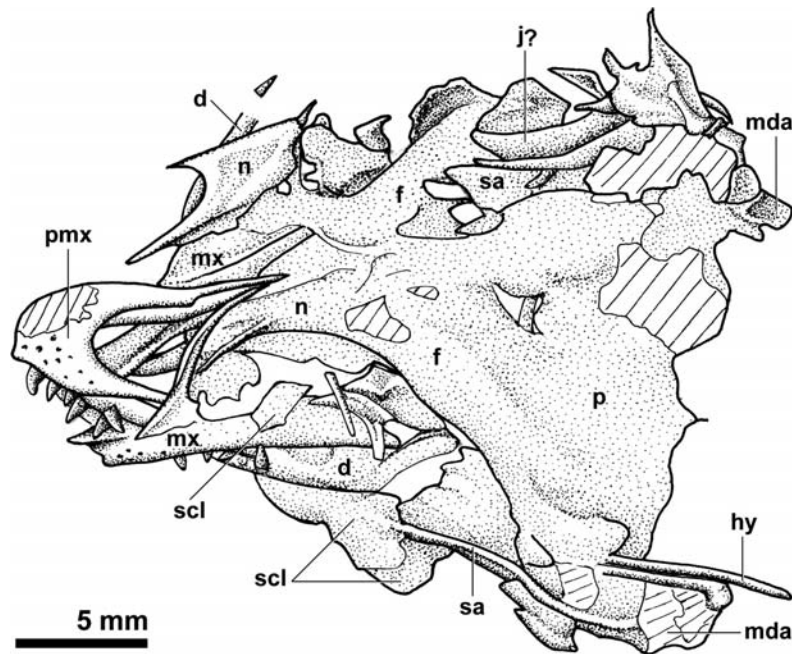
The maxilla is long and forms most of the upper jaw as in *Archaeopteryx* and other enantiornithines. It bears a tall, slender, and tapering dorsal process, which subdivides this bone into a short rostral portion and a long and tapering caudal portion.

Immediately caudal to the dorsal process, there is a recessed lamina pierced by a foramen on its ventral side. Although this lamina is poorly preserved, it likely represents the dorsal process of the maxilla closing the rostral portion of the antorbital cavity, and it is pierced by a subsidiary antorbital fenestra. The caudal extent of the dorsal process is unclear, but a similar configuration was reported for *Cathayornis* (Martin and Zhou 1997). The lateral surface of the maxilla bears a row of nutrient foramina parallel to the dentigerous margin. Two teeth are preserved in situ in the left maxilla, which is the only maxilla exposing the dentigerous margin. These are slightly smaller than the premaxillary teeth. It appears that the tooth row ends beyond the rostral portion of the antorbital cavity.

The nasals are large and broad, but they are relatively short compared to *Archaeopteryx* (Martin and Zhou 1997). Although disarticulated, it is clear that these bones form much of the dorsal surface of the rostrum. The rostral portion of the nasal forms a broad notched margin — the caudal border of the external nares. The long dorsal process, which is more than three times longer than the ventral process, articulates with the longitudinal facet of the lateral side of the nasal process of the premaxilla. This strong articulation extends caudally beyond the narial notch as evidenced by a broad articular facet on the medial surface of the right nasal.

The caudal portion of the antorbital cavity and cranial

Fig. 4. Line drawing of the skull of the holotype of *Eoenantiornis buhleri*, IVPP V11537: d, dentary; f, frontal; hy, hyoid bone; j?, ?jugal; mda, mandibular articulation; mx, maxilla; n, nasal; p, parietal; pmx, premaxilla; sa, surangular; scl, sclerotic plate.



margin of the orbit are less clear. Remnants of several scleral ossicles cover some of the bones of the left side. A large bone exposed on dorsal view bears a ventrolaterally projected process. This bone is interpreted as the lacrimal. If correctly identified, the lacrimal must have had a substantial dorsal exposure. The frontals are broad, defining an expanded skull roof together with the undifferentiated bones of the dorsal braincase. Virtually no information is available from the jugal bar and suspensorium. A long and robust bone on the right side is interpreted as the jugal, which bears some resemblance to that of *Archaeopteryx*. Remnants of the quadrate are also preserved on the right side, but these are anatomically uninformative.

Much of the left mandible and portions of the caudal end of the right one are preserved. The toothed dentary is slender and approximately half the length of the lower jaw as in *Archaeopteryx* and other enantiornithines. Four teeth placed in well-defined alveoli are preserved on the left dentary. The middle portion of this bone is overlaid by the maxilla, thus preventing us from ascertaining the total number of teeth borne by the mandible. Nonetheless, the space between the rostralmost teeth and the caudalmost teeth does not permit more than three teeth. Thus, the dentary of *Eoenantiornis* probably had six, if not seven, teeth, which is a number comparable to that of a juvenile euenantiornithines from the Early Cretaceous of Spain (Sanz et al. 1997). The rostralmost two teeth are large — slightly larger than the largest premaxillary tooth — but the caudalmost teeth are significantly smaller. The morphology of these teeth is similar to those of the upper jaw. Much of the left dentary is exposed on medial view. No evidence of interdental plates can be found; these ossifications have been reported in the lower jaw of *Archaeopteryx* (Wellnhofer 1993). Although the rostralmost portion of the left dentary is covered by the premaxilla, its exposed parts suggest the mandibular symphysis

must have been very short and probably limited to the level of the first tooth. Caudally, the ventral margin of the dentary extends beyond the extension of its dorsal margin. The caudal border of this bone is therefore caudoventrally slanted. This border bears a well-developed trough-like facet for the articulation of the postdentary bones. The existence of this facet suggests the presence of a highly movable intramandibular articulation. The surangular is a robust bone of sigmoid appearance; the caudal half defines the dorsal margin of a large medial mandibular fossa. Similarly large fossae have been described for other euenantiornithines (Chiappe and Walker 2002). The articular defines a transversally broad cotyle, without projecting onto a medial process. As in other euenantiornithines (Chiappe and Walker 2002), the retroarticular process is relatively short and stout.

Cranial fenestrae

The narial opening is large and tear-shaped, with its rostral margin nearly vertical. It is bordered dorsally by the nasal, caudally by the nasal and maxilla, and ventrally and rostrally by the premaxilla. The antorbital cavity is poorly preserved. Nonetheless, it appears to be more vertically elongated than in *Archaeopteryx* and other enantiornithines (Martin and Zhou 1997). The rostral portion of this cavity is bordered by the dorsal process of the maxilla, which is perforated by at least one subsidiary antorbital fenestra. The size and dimensions of the antorbital fenestra are unclear. The nasal clearly forms much, if not the entire, dorsal margin of the antorbital cavity. The orbit is large, although its shape is obscured by the dorsoventral crushing of the entire skull. No evidence is available of the presence, shape, and dimensions of the temporal fenestrae.

Axial skeleton

The vertebral column is poorly preserved. The neck is

relatively long, comprising 11 cervical vertebrae. The cervical vertebrae are exposed on dorsal view but their poor preservation prevents recovering any information with confidence. The thoracic vertebrae appear to be narrow; their number is unknown. Five or six synsacral vertebrae are preserved in dorsal view but the synsacrum is largely incomplete. The synsacral vertebrae are completely fused to one another and their transverse processes are tightly attached to the ilia. Dorsally, these vertebrae appear to form a low and undifferentiated neural crest. Remnants of several caudal vertebrae are preserved in disarticulation. The best-preserved one has a cylindrical and amphiplatyan centrum with long, distally expanding, and laterocaudally oriented transverse processes. The caudal half of the pygostyle is preserved, probably in dorsal view. This element shows the forked proximal end characteristic of other euenantiornithines (e.g., *Halimornis*, Chiappe et al. 2002).

Several thoracic ribs are preserved in various degrees of completeness. At least two uncinat processes are discernable, based on their curved and acuminate shape. These short processes are not fused to the ribs (Fig. 2). Uncinac processes are also known in other euenantiornithines (e.g., *Longirostravis*, *Longipteryx*, Zhang et al. 2001). Several rod-like gastralia are also present. These are long, slightly sigmoid, and medially tapering bones that articulate with their counterparts along the sagittal plane. The proportion of overlapping is unclear for most of the preserved elements, but it is about one-fourth the length of the gastralium in the cranialmost row. Although incomplete, the gastralia seem to extend from the caudal end of the sternum to behind the acetabulum. The caudalmost elements are substantially smaller than those preserved in front of the acetabulum. A basket of gastralia is also preserved in other enantiornithines (e.g., *Longipteryx*, *Protopteryx*) as well as in more basal birds (Chiappe et al. 1999; Chiappe and Witmer 2002; Zhou and Zhang 2002).

Appendicular skeleton

The scapula has a straight blade and a prominent acromion. The tip of the acromion appears rounded, but it is impossible to tell whether it is expanded costolaterally as in other euenantiornithines (Chiappe and Walker 2002). The scapular blade is incomplete — its distal end missing — but if a fragment preserved near the sternum is considered to be in place, the bone was at least a third longer than the coracoid. The latter is a strut-like bone, with the proximal half slender and rod-shaped, and the distal half expanded and triangle-shaped. The proximal end is poorly preserved but it appears to be laterally compressed, with the humeral articular facet, the scapular facet, and the acrocoracoid more or less aligned and slanting caudodorsally. As in other euenantiornithines (e.g., Chiappe 1996; Chiappe and Walker 2002; Sanz et al. 2002; Zhou 2002), the dorsal surface of the sternal part was excavated by a fossa. Also in common with other members of this group is the presence of a convex lateral margin and large supracoracoid nerve foramen that is separated from the medial margin by a robust bar. The medial margin of the coracoid is concave and its sternal border is straight (Fig. 2).

The furcula is Y-shaped and it bears a slender hypocleideum. The medial margins of the clavicular rami join at a sharper angle than in *Cathayornis*, where the internal angle between the rami is more U-shaped (Zhou et al. 1992). The clavicular

rami are L-shaped in cross-section; as in other euenantiornithines (e.g., Chiappe and Calvo 1994; Zhang et al. 2001; Sanz et al. 2002), the ventral margin is wider than the dorsal one. Also in common with other euenantiornithines is the presence of a dorsal crest on the hypocleideum.

The sternum is cranially rounded with a short mediocaudal process on each side and a longer, sagittal xiphoid process. The sternum is preserved in ventral view, thus the shape of the keel is unknown. However, the mediocaudal processes are tapered and slightly curved medially. This morphology approaches that of the mediocaudal sternal processes of other euenantiornithines (e.g., *Longirostravis*). Faint impressions of the distal end of the laterocaudal processes of the sternum are also preserved (Fig. 5). These extend caudally less than the xiphoid process, and, as in other euenantiornithines (e.g., Chiappe and Calvo 1994; Zhou 1995; Sanz et al. 1995), they have their caudal end expanded. The xiphoid process is laterally compressed and slightly expanded distally. Although crushed, the raised edges of the sternum suggest that this bone was dorsally concave. The anterior edge is grooved by coracoid sulci along the entire width but evidence of costal facets is missing.

Both forelimbs are in articulation, although the right humerus is missing. The left humerus, exposed in caudal view, exhibits some degree of shaft torsion and a dorsally projected deltopectoral crest (not cranially deflected). The superior (proximal) margin of the humeral head is flat, apparently less concave centrally than typical euenantiornithines (Chiappe and Walker 2002), but the poor preservation of this area prevents being definitive about this condition. Proximally, the ventral tubercle is well-developed and the capital groove is deep. The distal end is poorly preserved and no details are appreciable.

The ulna is slightly longer than the humerus and about twice as wide as the radius. It is gently curved over the proximal two-thirds. The straight radius exhibits the longitudinal groove characteristic of some other euenantiornithine birds (e.g., *Neuquenornis*, Chiappe and Calvo 1994; *Eoalulavis*, Sanz et al. 1996). A small projection of the proximal end of the radius, just distal to the articular surface, is probably the bicipital tubercle. The ulnare is large and it appears to be square-shaped.

The manus is much shorter than the ulna and radius (Fig. 6). The carpometacarpus is very short — less than half the length of the ulna. The ratio of the carpometacarpus to ulna length is 47% in *Eoenantiornis* and is about 63% in *Confuciusornis* (Chiappe et al. 1999). The same ratio is 89%, 98%, and 104% in the euenantiornithines *Cathayornis* (Zhou 1995), *Eocathayornis* (Zhou 2002), and *Longipteryx* (Zhang et al. 2001), respectively. The carpometacarpus is well fused proximally. The major metacarpal is straight and significantly thicker than the minor metacarpal. No apparent intermetacarpal space separates these two bones. The minor metacarpal is slightly curved and it extends distally well past the distal end of the major metacarpal, as in other euenantiornithines (Zhou 1995; Chiappe and Walker 2002). Metacarpal I is short and subrectangular in shape; it bears no extensor process. The manual digits are also short. The phalangeal formula is 2–3–1. The longest digit (major digit) is only slightly longer than the carpometacarpus. The alular digit extends distally to the distal end of the major metacarpal. The proximal phalanx of

Fig. 5. Close-up photo of the sternum of the holotype of *Eoenantiornis buhleri*, in dorsal view, IVPP V11537.



this digit is the longest; the claw is curved and sharp. In *Propteryx* and *Longipteryx*, the alular digit extends distally beyond the distal end of the major metacarpal whereas for most other enantiornithines, which have the hand preserved, the alular digit does not extend distally past the major metacarpal. The proximal phalanx of the major digit of *Eoenantiornis* is much more robust than its remaining two phalanges; it appears to taper slightly towards its distal end. This proximal phalanx is slightly longer than the intermediate phalanx, thus exhibiting the condition typical of euenantiornithines, where the proximal phalanx of the major digit is longer than the intermediate phalanx (Chiappe and Walker 2002). The unguis phalanx of this digit is as large and curved as the unguis of the alular digit. The minor digit is greatly abbreviated. Distally, it approaches the distal end of the proximal phalanx of the major digit; its only phalanx is slender and slightly curved, and tightly appressed against the proximal phalanx of the major digit.

Some portions of the pelvis are also relatively well preserved. The ilium articulates with, and appears to be fused to, the transverse processes of the sacral vertebrae. The ilium has an ample preacetabular portion. The pubis is strongly opisthopubic, although the degree at which this bone is directed caudally could be exaggerated by dislocation. It is a slender bone with a craniocaudally compressed shaft and an

expanded boot-like distal end. This distal expansion is rather small compared to that of euenantiornithines, such as *Sinornis* (Serenio et al. 2002). Although the two ends of the pubes are not fused to one another, it is likely that in life these bones formed a ligamental symphysis. The small size of the distal expansion and the lack of symphyseal fusion may well be owing to the fact that the individual was not completely grown up. Although the ischium is incomplete, it is clear that this bone was substantially shorter than the pubis. The distal half of the ischium exhibits the dagger-like appearance of some other euenantiornithines (Serenio et al. 2002). Its dorsal (caudal) margin is concave and its ventral (cranial) border is convex. The shaft of the ischium tapers distally, although the end is rather blunt. Laterally, it bears a distinctive ridge that gives the ischium a sub-triangular appearance.

Despite the preservation of most bones of the hind limb, they do not provide a great deal of anatomical information. The femur is distinctly curved. Its proximal third exhibits a slight compression that is likely the result of post-mortem deformation. Proximally, on its lateral surface, the femur has a prominent posterior trochanter, a condition typical in other euenantiornithines (Chiappe and Calvo 1994; Chiappe and Walker 2002). The tibiotarsus is straight and slender, and longer than the femur. The tarsometatarsus is only fused proximally as in enantiornithines and other basal birds (Chiappe and

Fig. 6. Close-up photo of the right manus of the holotype of *Eoenantiornis buhleri*, IVPP V11537.



Witmer 2002). It is slender and about half the length of the tibiotarsus; its midshaft is slightly more compressed. Metatarsal IV is more slender than metatarsals II and III, as is typical of many euenantiornithines (Chiappe 1993). Distally, the trochleae for metatarsal II and IV are higher than that of metatarsal III. The medial rim of the trochlea of the latter metatarsal lacks the strong plantar projection seen in some other euenantiornithines (e.g., *Soroavisaurus*, Chiappe 1993). However, as seen in many other euenantiornithines (Chiappe and Walker 2002), this trochlea is narrower than that of metatarsal II. Metatarsal I is small and dorsally pointed. It is uncertain whether this bone had the J-like shape of the metatarsal I of some other euenantiornithines when viewed in medial or lateral aspect.

The pedal digits are not completely preserved. The hallux is reversed as in most other birds. The unguis phalanx of this digit is approximately the size of its proximal phalanx. The second digit is robust; its intermediate phalanx is longer than the proximal phalanx. The unguis of the second digit is preserved with the horny sheath. The maximum length of this claw is approximately the same as that of its intermediate phalanx; the unguis is longer when the horny sheath is con-

sidered. The proximal phalanx of the third digit is robust and probably larger than any other pedal phalanges, although this phalanx is poorly preserved. The fourth digit is not preserved. Overall, the unguis of *Eoenantiornis* are less curved than those of other euenantiornithines, such as *Cathayornis* (Zhou 1995) and *Sinornis* (Sereno et al. 2002).

Plumage

The plumage is preserved as a dark halo surrounding much of the skeleton. The rectrices are long and extend to the level of the feet. The alula is also visible — an occurrence that confirms the presence of this important aerodynamic structure in enantiornithine birds (Sanz et al. 1996). No long, vaned feathers are visible on the hind limbs. As in most other birds, the feet were not covered with plumage.

Discussion

The taxon Euenantiornithes was erected by Chiappe and Walker in 2002 as a monophyletic group comprising the majority of the known enantiornithines that exclude *Iberomesornis* and *Noguerornis* (Chiappe 2002). Many derived characters support the identification of *Eoenantiornis buhleri* as an euenantiornithine bird (Chiappe and Walker 2002). Among these are the presence of (1) a coracoid with a convex lateral margin, (2) a broad dorsal fossa on its sternal half, and (3) a large supracoracoidal foramen that is separated from the medial margin of the coracoid by a robust bar, (4) a Y-shaped furcula with a long hypocleideum, (5) clavicular rami that are L-shaped in cross-section, (6) distally expanded caudolateral processes of the sternum, (7) a radius scarred by a distinct longitudinal groove, (8) a minor metacarpal that extends distally beyond the major metacarpal, (9) a proximal phalanx of the major digit of the manus that is longer than the intermediate phalanx, (10) a prominent posterior trochanter on the proximolateral side of the femur, and (11) a slender metatarsal IV when compared with metatarsals II and III.

Eoenantiornis adds to our knowledge of the earliest phases of enantiornithine evolution — one of the most important chapters of the Mesozoic history of birds. Its anatomy, in particular that from its well-preserved skull, provides evidence of morphologies previously unknown for enantiornithine birds. Most notable among these is the presence of a distinct facet for the intramandibular articulation between the dentary and postdentary bones, which may have helped both to augment the size of the gap and to absorb the stresses of struggling prey.

Eoenantiornis also ratifies the presence of an alula (bastard wing) among early enantiornithines. In fact, *Eoenantiornis* may well document one of the earliest occurrences of this important aerodynamic structure (Sanz et al. 1996). Furthermore, although the correlation between the sizes of the alular digit, the size of the alula, and the aerodynamic performance of this structure is not well understood, *Eoenantiornis* provides information concerning the evolution of the alular digit in enantiornithines. With an alular digit distally on same level with the major metacarpal, *Eoenantiornis* documents an intermediate stage in the abbreviation of this digit — from the presumably more basal *Protopteryx* whose alular digit extends distally beyond the end of the major metacar-

pal to most other enantiornithines whose much shorter alular digit does not extend beyond this metacarpal. Because the presence of an alula is considered to be a synapomorphy of Ornithothoraces — the clade that originated from the common ancestor of Enantiornithes and Ornithuromorpha (Chiappe 2002) — the abbreviation of the alular digit of *Eoenantiornis* (and other euenantiornithines), when compared to *Protopteryx*, suggests that such a transformation could have paralleled a similar transformation within Ornithuromorpha, which comprises the Ornithurae and some more basal forms, such as *Patagopteryx* and *Vorona* (Chiappe 2002).

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