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Juvenile Birds from the Early Cretaceous of China: Implications for Enantiornithine Ontogeny

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ABSTRACT

Mesozoic remains of embryonic and early juvenile birds are rare. To date, a handful of *in ovo* embryos and early juveniles of enantiornithines from the Early Cretaceous of China and Spain and the Late Cretaceous of Mongolia and Argentina have comprised the entire published record of perinatal ontogenetic stages of Mesozoic birds. We report on the skeletal morphology of three nearly complete early juvenile avians from the renowned Early Cretaceous Yixian Formation of Liaoning Province in northeastern China. Evidence of the immaturity of these specimens is expressed in the intense grooving and pitting of the periosteal surfaces, the disproportionately small size of the sterna, and the relative size of the skull and orbits. Size notwithstanding, anatomical differences between these three specimens are minimal, leaving no basis for discriminating them into separate taxa. Numerous osteological synapomorphies indicate that they are euenantiornithine birds, the most diverse clade of Enantiornithes, but their identification as members of a particular euenantiornithine taxon remains unclear. Their early ontogenetic stage, however, provides important information about the postnatal development of this specious clade of Cretaceous birds. The presence of pennaceous wing feathers suggests that fledging occurred very early in ontogeny, thus supporting a precocial or highly precocial strategy for enantiornithine hatchlings. The morphology of these new early-stage juveniles is also significant in that they allow a better understanding of the homologies of several avian compound bones because the components of these skeletal compounds are preserved prior to their coossification. The general morphology of the wrist and ankle of these juveniles highlights once again the striking similarity between nonavian theropods and early birds.

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INTRODUCTION

The avian skeleton is characterized by the ontogenetic fusion of numerous elements forming compound bones in adults (King and McLelland, 1984; Bellairs and Osmond, 1998). Individualization of these bones is visible only in the early phases of skeletal development, which among fossils represent rare occurrences. Indeed, among the hundreds of Mesozoic avian specimens now discovered only a few correspond to embryonic or early postnatal stages of ontogenetic development (table 1).

Despite the fact that the recent burst of exceptional discoveries of Early Cretaceous birds from China (e.g., Zhou, 1995a, 1995b; Hou, 1997; Chiappe et al., 1999; Zhang and Zhou, 2000; Chiappe and Witmer, 2002; Chiappe and Dyke, 2002, 2006; Zhou, 2002; Zhang et al., 2003; Hou et al., 2004; You et al., 2005, 2006; Zhou et al., 2005; Clarke et al., 2006; Chiappe, 2007) has brought to light an enormous body of new information on the diversity, morphological evolution, and lifestyles of basal avian lineages, little is known about the skeletal transformations and allometric patterns involved during the early ontogeny of these birds. Between 1998 and 2000, three small juvenile birds were recovered from the Early Cretaceous (~ 128–125 million years ago; see Swisher et al., 2002; Zhou et al., 2003; He et al., 2004) lacustrine deposits of the Yixian Formation in the northeastern Chinese Province of Liaoning. Two of them (GMV-2156/NIGP-130723 and GMV-2159), preserved mostly as natural molds, were unearthed from the village of Dawangzhangzi, not far from the town of Lingyuan (fig. 1). The third specimen (GMV-2158), a well-preserved and nearly complete skeleton, was recovered from the village of Jianshangou, a few kilometers from the renowned site of Sihetun, and some 150 km northeast of Dawangzhangzi (fig. 1).

In 1999, GMV-2156/NIGP-130723, split into two slabs, was briefly described and used as the holotype of both "*Liaoxiornis delicatus*" (Hou and Chen, 1999) and "*Lingyuamornis parvus*" (Ji and Ji, 1999) (here we recommend to abandon the use of these two synonyms; see Systematic Paleontology, below). The other two specimens, GMV-2158 and GMV-2159, remained unreported. Despite slight differ-

ences in size (table 2), the morphology of these three specimens is remarkably similar (see Taxonomic Identification, below). In this paper we provide a detailed description of the osteology of these juvenile enantiornithine specimens and discuss their significance for understanding the homology of several avian compound bones.

INSTITUTIONAL ABBREVIATIONS: GMV, National Geological Museum of China, Beijing; FMNH-UC, Field Museum, Chicago; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; NIGP Nanjing Institute of Paleontology and Geology, Nanjing, China; PVL, Instituto Miguel Lillo, Paleontología de Vertebrados, Tucumán, Argentina.

SYSTEMATIC PALEONTOLOGY

AVES LINNAEUS, 1758

PYGOSTYLIA CHIAPPE, 2002

ORNITHOTHORACES CHIAPPE, 1996

ENANTIORNITHES WALKER, 1981

EUENANTIORNITHES CHIAPPE, 2002

Euenantiornithes Indet.

MATERIAL: GMV-2158, a well-preserved and nearly complete skeleton (figs. 2, 3). This specimen was initially split into two slabs (fig. 2). These slabs were glued together and the specimen was then prepared from one side (fig. 3).

LOCALITY AND HORIZON: Jianshangou, Beipiao City, Western Liaoning Province; lower section of the Yixian Formation, Lower Cretaceous (Chang et al., 2003). These layers contain abundant fossil insects (Ren, 1998), plants, and conchostracans.

Euenantiornithes Indet.

MATERIAL: GMV-2159, a complete skeleton preserved in a single slab except for the skull (figs. 4, 5). By the time the specimen became part of the National Geological Museum of China, its bones were largely preserved as natural molds (fig. 4). The remaining bones were prepared and a positive mold of the entire slab was made using RTV

TABLE 1
Published Reports of Embryonic and Early Juveniles of Mesozoic Birds Excluding Those Described in this Study

Taxon	Material	Age/Provenance	Reference
Baptornithidae:			
<i>Baptornis advemus</i>	Juvenile	L. Cret./U.S.	Martin & Bonner, 1977
Enantiornithes:			
cf. <i>Gobipteryx minuta</i>	Embryos	L. Cret./Mongolia	Elzanowski, 1981
Taxon indet.	Juvenile	E. Cret./Spain	Sanz et al., 1997
Taxon indet.	Juveniles	E. Cret./Spain	Sanz et al., 2001
Taxon indet.	Embryo	E. Cret./China	Zhou & Zhang, 2004
Enantiornithes?:			
Taxon indet.	Embryo	E. Cret./Argentina	Schweitzer et al., 2002

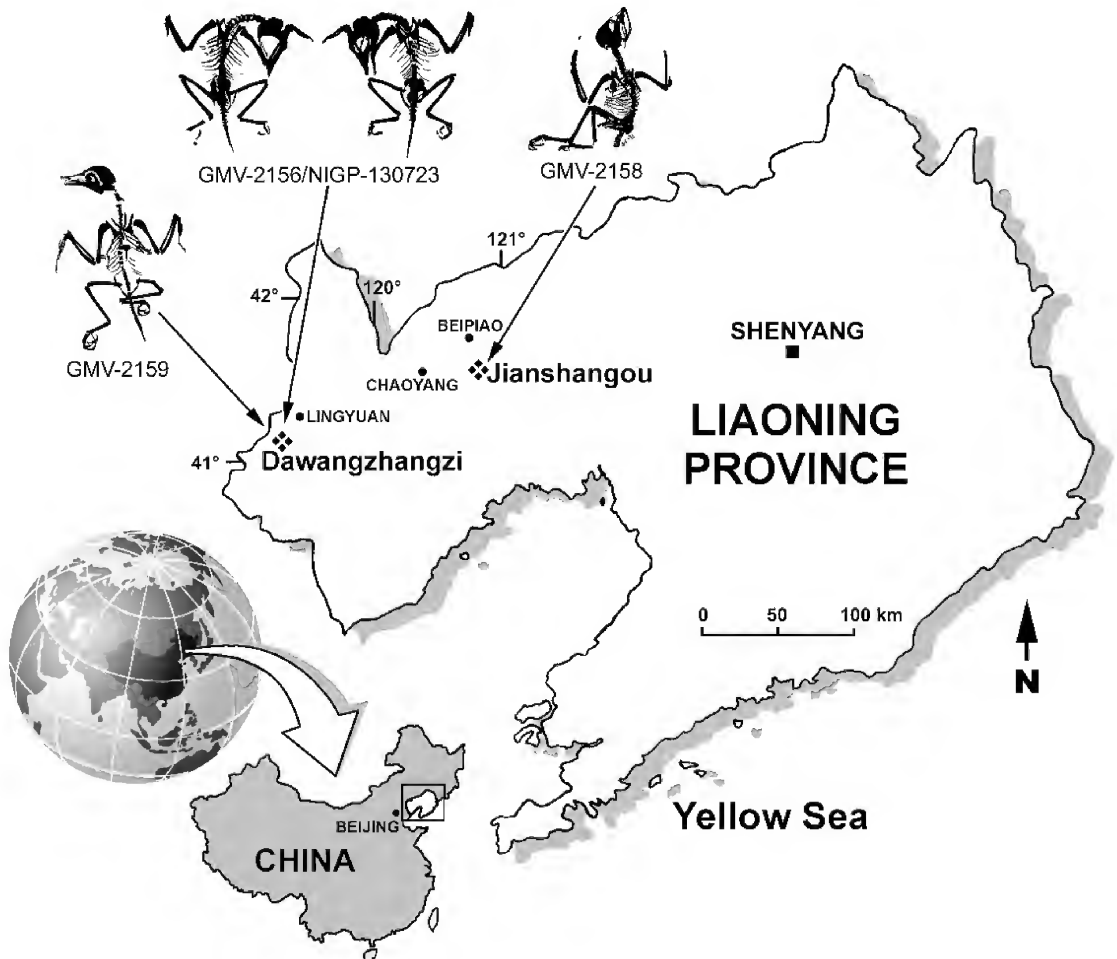


Fig. 1. Map of Liaoning Province (Northeastern China) showing the Early Cretaceous localities of GMV-2158 (Jianshangou) and NIGP-130723/GMV-2156 and GMV-2159 (Dawangzhangzi).

TABLE 2
Comparative Lengths (mm) of GMV-2158, GMV-2156/NIGP-130723, and GMV-2159

	GMV-2158		GMV-2156		NIGP-130723		GMV-2159	
	Left	Right	Left	Right	Left	Right	Left	Right
Scapula	9.9 e	10.2 e	10.1*	10.1*	10.7	—	—	—
Coracoid	7.0 e	—	—	—	7.4	7.6	9.7	9.8
Humerus	15.5	15.7	15.5*	15.4*	—	—	20.7	20.5
Ulna	15.6	—	15.6*	—	—	—	20.8	21.1
Radius	14.6	14.7	14.9*	—	—	—	19.4	19.6
Metacarpal I	1.4	—	—	—	—	1.3	—	—
Metacarpal II	6.9	—	—	—	—	6.5	9.0	8.8
Metacarpal III	7.2	—	7.4*	—	—	7.5	—	9.2
Pubis	9.5 e	—	—	—	—	—	—	12.5
Ischium	6.2	—	—	—	—	—	—	—
Femur	14.3	—	14.4*	14.5*	—	—	—	17.2
Tibia	18.0	—	16.5*	17.1*	—	—	20.1	21.6
Fibula	4.3	—	—	—	—	—	—	—
Metatarsal I	—	2.6	—	—	—	—	2.8	2.7
Metatarsal II	10.1	10.2	—	—	—	—	10.8	10.7
Metatarsals III-IV	11.0	11.2	10.4*	—	—	—	11.8	11.8

* Values taken from Ji and Ji (1999); e indicates estimated value.

(room temperature vulcanizing) silicon rubber (fig. 5).

LOCALITY AND HORIZON: Dawangzhangzi, Lingyuan City, Western Liaoning Province; lower section of the Yixian Formation, Lower Cretaceous (Chang et al., 2003). The fossil fauna of this site includes a variety of plants, insects, fish, salamanders, pterosaurs, and dinosaurs (Wang et al., 2000). Stratigraphically, the Dawangzhangzi beds are slightly higher than those at Jianshangou (GMV-2158 locality) (Wang et al., 2000; Chang et al., 2003).

Euenantiornithes Indet.

“*Liaoxiornis delicatus*” Hou and Chen, 1999

MATERIAL: A nearly complete specimen split into a slab (NIGP-130723) (fig. 6) and a counterslab (GMV-2156) (fig. 7). Most bones of this specimen are preserved as natural molds on both slabs.

LOCALITY AND HORIZON: Dawangzhangzi, Lingyuan City, Western Liaoning Province; lower section of the Yixian Formation, Lower Cretaceous (see locality of GMV-2159, above).

TAXONOMIC STATUS OF “*LIAOXIORNIS DELICATUS*”: Each of the slabs of this speci-

men was independently obtained by the Nanjing Institute of Paleontology and Geology and the National Geological Museum of China (Beijing). The Nanjing slab (NIGP-130723) was briefly described by Hou and Chen (1999), who used it as the holotype of a new taxon, “*Liaoxiornis delicatus*” (fig. 6). The Beijing slab (GMV-2156) was the focus of another short article in which Ji and Ji (1999) named the new taxon “*Lingyuanornis parvus*” (fig. 7). Because the latter article was published one month after Hou and Chen’s (1999) paper, “*Liaoxiornis delicatus*” took priority over its junior synonym, “*Lingyuanornis parvus*”. Although Hou and Chen (1999) interpreted NIGP-130723 as representing an adult bird, numerous features highlight the early juvenile condition of this individual (see Juvenile Characters, below). Given the lack of diagnostic characters that can distinguish this fossil as the holotype of a different species, as well as the problems associated with erecting new taxa on the basis of specimens of early ontogenetic age (Winston, 1999), we recommend that the taxon name “*Liaoxiornis delicatus*” should be abandoned. In this paper we refer to the Nanjing and Beijing slabs of “*Liaoxiornis delicatus*” by their collection numbers.



Fig. 2. Slab (A) and counterslab (B) of GMV-2158 prior to preparation. C. Details of the feather impressions preserved on the slab.

JUVENILE CHARACTERS

The three specimens here described show features that witness their early ontogenetic age. In GMV-2158, the surface of many bones is intensively scarred by small pits and

grooves. Although the pits are concentrated in the shafts of limb bones, the grooves are ubiquitous throughout the entire appendicular skeleton. Such a pattern of incomplete periosteal formation, previously reported for an Early Cretaceous enantiornithine neonate



Fig. 3. Photograph and interpretive drawing of GMV-2158 after complete preparation. The two slabs shown in figure 2 were glued and then prepared from one side. Abbreviations: alm, alular metacarpal; co, coracoid; cmm, claw of major manual digit; cv, caudal vertebrae; cve, cervical vertebrae; f, frontal; fem, femur; fib, fibula; fur, furcula; gas, gastralia; hum, humerus; hyo, hyoid; isc, ischium; ili, ilium; j, jugal; loj, lower jaw; mam, major metacarpal; mim, minor metacarpal; mtI-IV, metatarsals I-IV; o, orbit; p, parietal; pmx, premaxilla; pub, pubis; r, ribs; rad, radius; sc, scapula; st, sternum; syn, synsacrum; tib, tibia; tv, thoracic vertebrae; uln, ulna; vr, ventral ribs; (l) or (r), left or right element.

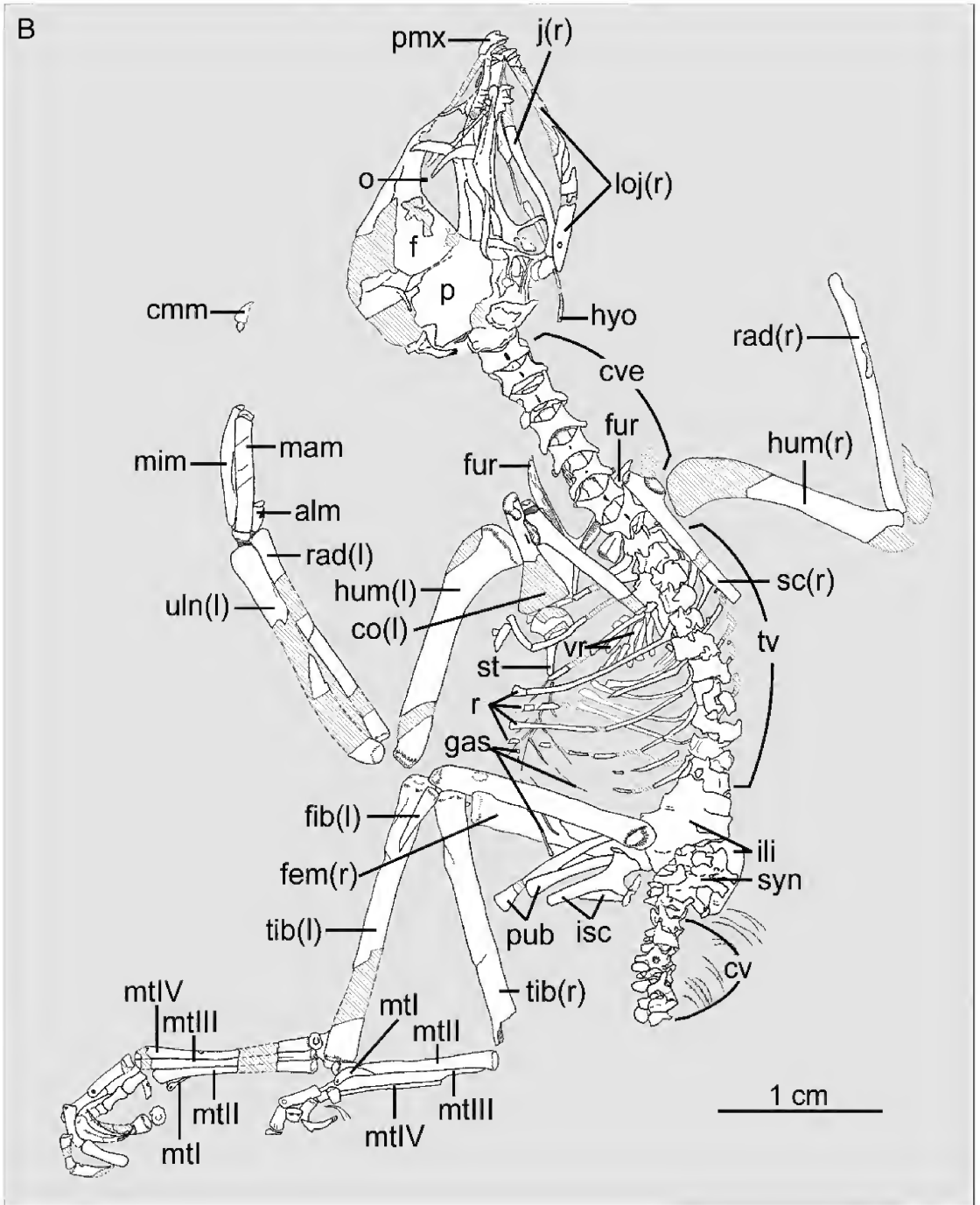


Fig. 3. Continued.



Fig. 4. Photograph of the natural mold of GMV-2159.

(Sanz et al., 1997; referred to here as the “Montsec neonate”), is typical of the early phases of development (embryonic and post-natal) of birds and other archosaurs (Horner, 1997; Sanz et al., 1997; Chiappe et al., 1998; Codorniu and Chiappe, 2004). In GMV-2156/NIGP-130723 and GMV-2159, bones of which are mostly preserved as molds, these pits and grooves are clearly visible inside the molds. Evidence of immaturity is also present in the small size of the sternum of GMV-2158, GMV-2156/NIGP-130723, and GMV-2159 (figs. 3, 5–7). The sternum of these birds is disproportionately small relative to the size of their coracoids and to the size and number of their ventral ribs (figs. 13, 14). It is evident

that the coracoids and ventral ribs articulated with cartilaginous portions of the sternum that surrounded its already ossified portion. The relative size of the skulls and orbits—in particular GMV-2156/NIGP-130723—and the absence of compound bones (carpometacarpus, tibiotarsus, tarsometatarsus, synsacrum) provide additional evidence of the young ontogenetic age of these specimens.

ANATOMICAL DESCRIPTION

Although the material reported herein consists of nearly complete specimens, only in GMV-2158 is the actual bony skeleton preserved. GMV-2159 and NIGP-130723/GMV-2156 are mostly known from natural molds, and the anatomical information that can be confidently recovered from these specimens is significantly less than that available in GMV-2158. For this reason, the present description focuses largely on GMV-2158.

Anatomical nomenclature follows Baumel et al. (1993) except when the terms are not listed therein (e.g., dorsal maxillary process, maxillary fenestra, postorbital). The Latin terminology used by Baumel et al. (1993) is retained for muscles. Osteological structures are described with English equivalents of the Latin terms (although when these differ from one another, the Latin equivalents are given parenthetically the first time the anatomical term is used).

AXIAL SKELETON

SKULL: Due to the crushing, obliteration of sutures, and disarticulation of some bones, not much information can be retrieved from either the skull of GMV-2158 or the skulls of the other two juveniles (figs. 6–9). Like other juveniles, the orbits are large and the rostrum is relatively short (fig. 8), resembling the condition of a number of brevirostrine enantiornithines (e.g., *Eoenantiornis buhleri*, *Sinornis santensis*, *Eocathayornis walkeri*). In GMV-2158, the only preserved premaxilla (*Os premaxillare*), apparently the left one exposed in medial view, is incomplete. The length of the premaxilla is unknown because its precise boundary with the maxilla is unclear. This uncertainty cannot be solved by the other

specimens, in which the sutures between the premaxilla and maxilla (*Os maxillare*) are equally indistinguishable. At least two teeth are in place near the tip of the rostrum of GMV-2158 and another tooth, located just in front of the rostral margin of the external nares (*Apertura nasi ossea*) of this specimen, is likely another premaxillary tooth (fig. 8). Taking this into consideration, the premaxilla of GMV-2158 probably had four teeth, a condition typical of enantiornithines (Zhou et al., 1992; Sanz et al., 1997; Chiappe and Walker, 2002), *Archaeopteryx lithographica*, and other toothed theropods (Currie, 1997; Weishampel et al., 2004).

The premaxilla of GMV-2158 is relatively shallow. The ratio between the length of this bone rostral to the external nares and its height at the rostral margin of the latter is close to 2. This ratio is approximately 1.6 in an adult specimen of “*Cathayornis*” (IVPP-9169; we follow Sereno et al. [2002], who regarded “*Cathayornis yandica*” as a junior synonym of *Sinornis santensis* [Sereno and Rao, 1992]), 1.4 in *Eocathayornis* (Zhou, 2002), 1.1 in *Gobipteryx minuta* (Chiappe et al., 2001), and 0.75 in adults of *Boluochia zhengi* (Zhou, 1995b) and *Eoenantiornis* (Hou et al., 1999; Zhou et al., 2005). Not surprisingly, the ratio between the premaxillary length rostral to the external nares and the height of this bone at the nares’ rostral margin is much higher among longirostrine enantiornithines—approximately 3.1 in *Longipteryx chaoyangensis* (Zhang et al., 2001; L.M. Chiappe, personal obs.). Although the high ratio exhibited by the brevirostrine skull of GMV-2158 could be partially accounted for by crushing, this difference compared to other brevirostrines such as *Eoenantiornis* and *Boluochia* is doubtfully a result of postmortem deformation; unfortunately, this ratio cannot be calculated for either GMV-2159 or GMV-2156/NIGP-130723. The extension of the premaxillary frontal process (*Processus frontalis*) is unknown for GMV-2158 and the remaining early juveniles here reported, although it is clear that this process integrated the thin bar that forms the dorsal margin of the external nares (fig. 8).

Two teeth are preserved in place in the left maxilla of GMV-2158, exposed in medial view

(fig. 8). Small portions of the right maxilla of this specimen, apparently exposing its lateral side, are also preserved. Comparing the two maxillae and the space available for teeth, it seems unlikely that this bone carried more than five or six teeth. This low tooth count compares with that of the Montsec neonate (Sanz et al., 1997) as well as with estimates for *Eoenantiornis* (Zhou et al., 2005) where the maxillary tooththrow ends slightly caudal to the rostral margin of the antorbital cavity (*Fossa antorbitalis*). A thin, diagonal bar forms the caudal margin of the long and caudodorsally tapering external nares. A similar design is visible in the external nares of *Sinornis* (Martin and Zhou, 1997; Chiappe and Walker, 2002) and *Eoenantiornis* (Zhou et al., 2005). This subnarial bar, in place on the left side of GMV-2158 but with its right counterpart displaced and overlaying the left maxilla, probably received contributions of both the maxilla and the nasal (*Os nasale*), although the suture between these bones is not visible.

In GMV-2158, the region between the external nares and the orbit (*Orbita*) is difficult to interpret (fig. 8). Two curved bones that taper dorsally from the caudal ends of the maxillae are interpreted as lacrimals (*Os lacrimale*). If these bones are correctly interpreted, the opening between the orbit and the external nares corresponds to the antorbital cavity. Based on this interpretation, the antorbital cavity appears larger than the external nares, a primitive condition seen in most nonavian theropods, *Archaeopteryx*, and some other enantiornithines (Sanz et al., 1997; Chiappe et al., 2001). Using the crushed skull of the holotype of “*Cathayornis yandica*” (Zhou et al., 1992; here considered a synonym of *Sinornis santensis*) as representative of the enantiornithine condition, Chiappe (1996a) interpreted the presence of an antorbital cavity smaller than the external nares as a synapomorphy of Ornithothoraces (Enantiornithes + Ornithuromorpha). This hypothesis may need to be evaluated in light of new evidence indicating that some enantiornithines possessed the primitive condition of this character (antorbital cavity larger than external nares) and that other basal lineages (e.g., *Confuciusornis sanctus*) exhibit the derived one.



Fig. 5. Photograph and interpretive drawing of the positive cast of GMV-2159. The study of GMV-2159 was based on a positive cast of epoxy resin, which renders greater anatomical details. This positive cast was molded from a positive cast of RTV (room temperature vulcanizing) silicon rubber made from the natural mold (fig. 4). Abbreviations: d, dentary; mad, major digit; pyg, pygostyle; scl, sclerotic; I–IV, pedal digits I–IV; (l) or (r), left or right element. Other abbreviations as in figure 3.

B

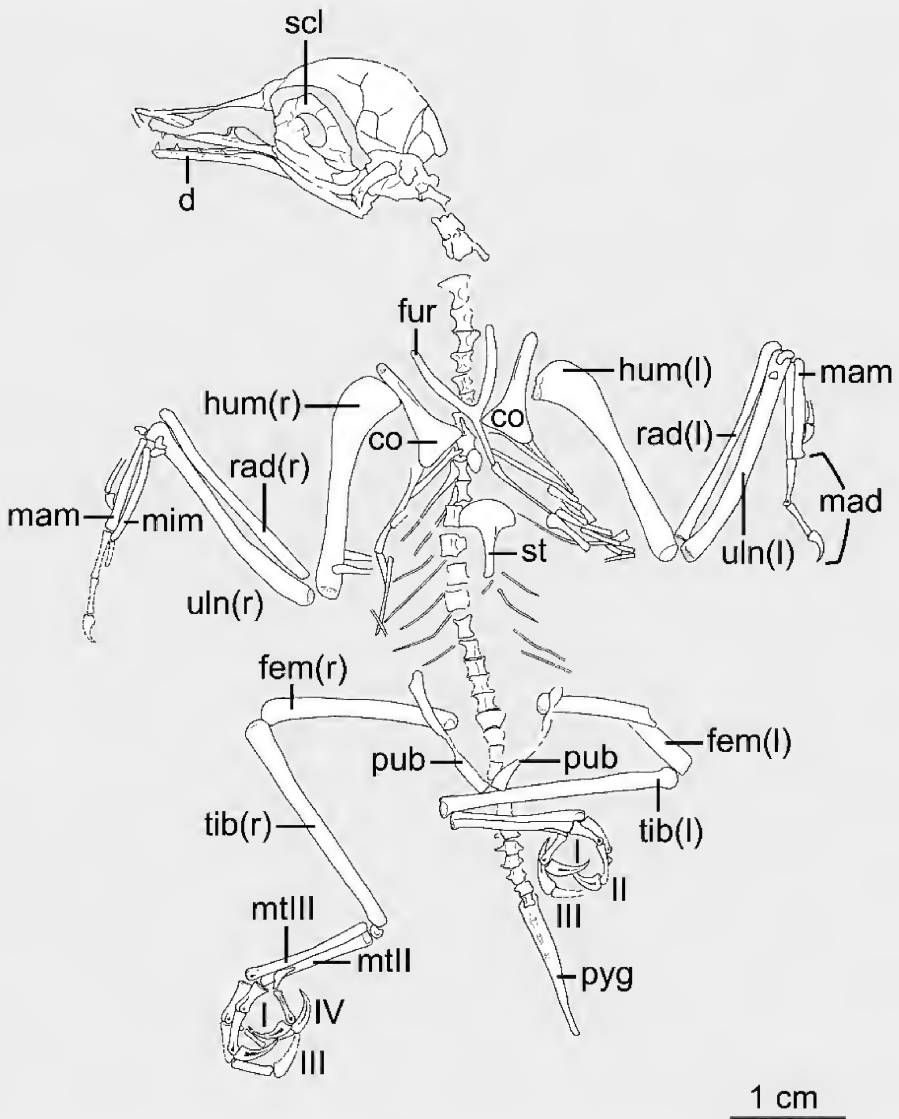


Fig. 5. Continued.

Although the poorly preserved antorbital cavity of GMV-2159 does not clarify the relative size of this structure (fig. 9), its rostral portion reveals a dorsal maxillary process subdividing an antorbital fenestra from a maxillary fenestra. The presence of accessory antorbital fenestrae, a primitive condition

known for other basal birds and nonavian theropods (Witmer, 1995), was also reported by Martin and Zhou (1997) in the enantiornithine “*Cathayornis*” (i.e., *Sinornis*).

A robust bony strut preserved between the two mandibular rami of GMV-2158 is interpreted to be the right jugal bar (*Arcus jugalis*).

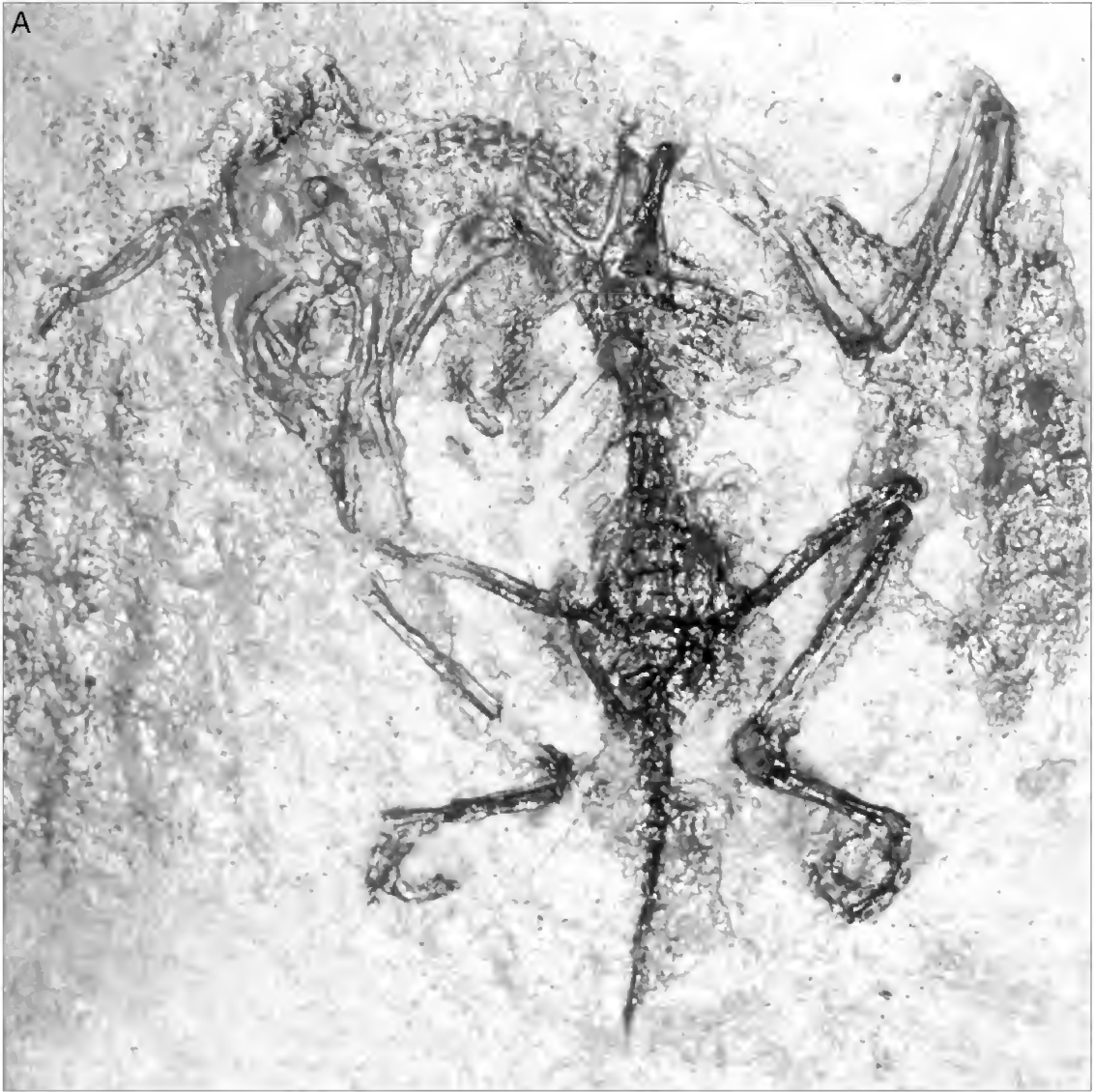


Fig. 6. Photograph and interpretive drawing of NIGP-130723. This slab, the counterpart of which is shown in figure 7, was used as the holotype of *Liaksiornis delicatus* by Hou and Chen (1999). Abbreviations: pyg, pygostyle; other abbreviations as in figures 3 and 5.

The rostral end of this slightly sigmoid bar approaches the right maxilla (fig. 8). Its caudal end connects to a vertical bar close to the caudal end of the right mandibular ramus (*Ramus mandibulae*). This vertical bar may be formed by overlapping portions of the quadrate and postorbital, although preservation prevents recovering any details about these elements. A larger portion of the left jugal bar

is visible within the orbit of GMV-2158 (fig. 8).

The large orbit is about one-fourth the length of the skull in GMV-2158 and GMV-2159 (figs. 8, 9). In GMV-2156 (figs. 6, 7), the orbit is even larger, with a diameter of about one-third the skull length (Ji and Ji, 1999). A ring of scleral ossicles (*Ossa sclerae*) is preserved inside the orbit of GMV-2159.

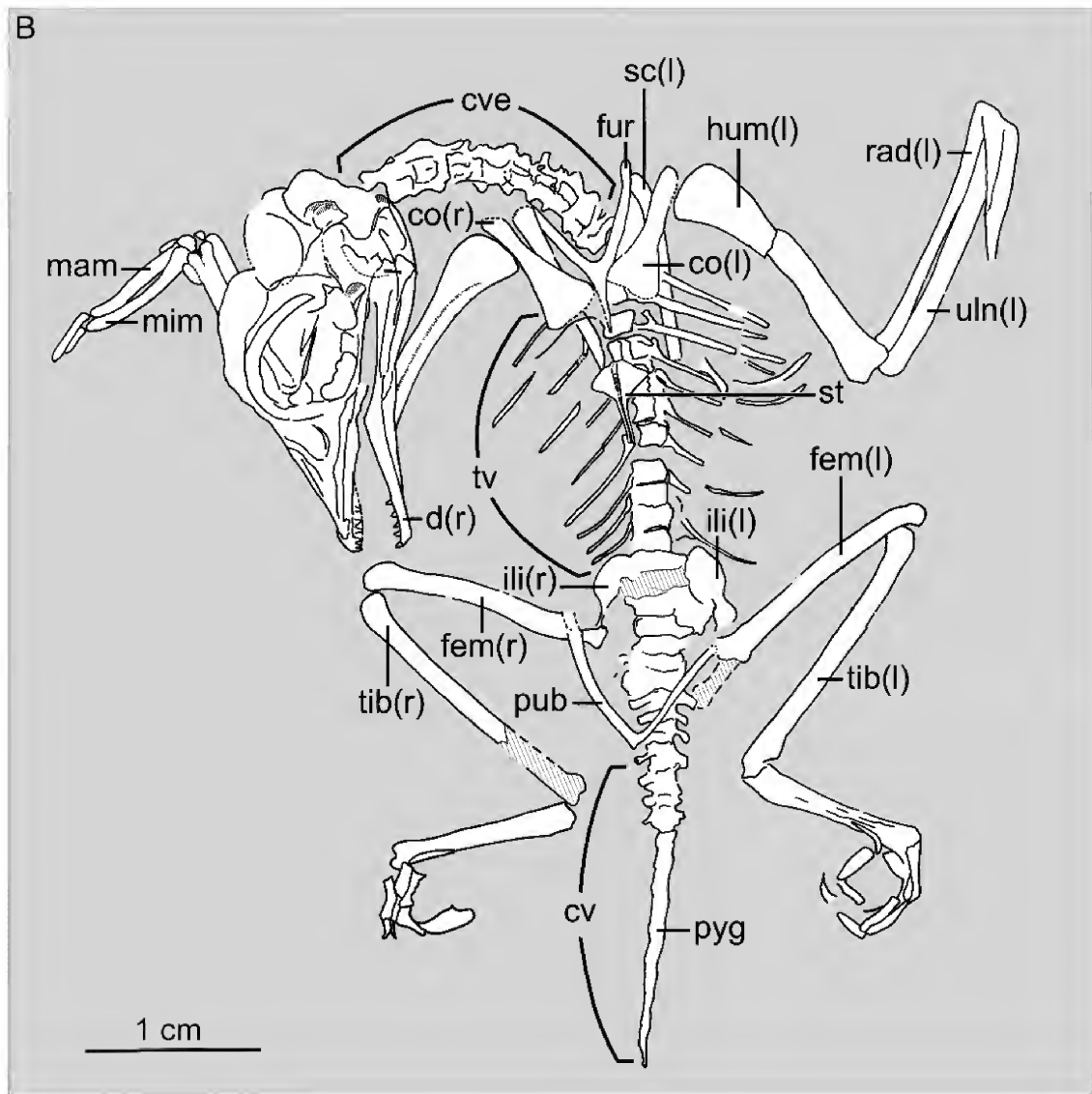


Fig. 6. Continued.

Little can be said about the postorbital region of any of these juvenile specimens, which is badly crushed and poorly preserved. GMV-2159 best shows that the frontals (*Os frontale*) and parietals (*Os parietale*) were large ossifications forming inflated portions of the skull. Remnants of what appears to be the postorbital and quadrate (*Os quadratum*) are placed in their approximate position in GMV-2158, and a round, depressed area between them may be part of one of the temporal fenestrae (*Fossa temporalis*).

MANDIBLE: Portions of both mandibular rami are preserved in GMV-2158 and GMV-2159. The right dentary (*Os dentale*) of GMV-2158 is exposed in medial view with its dentigerous margin facing ventrally (fig. 8). Most of this bone is missing, however. The left dentary of GMV-2158 is crushed against several bones of the rostrum and exposed in medial view. Four teeth are preserved in this dentary (fig. 8), but the space available along the dentigerous margin suggests the existence of at least three more. Six teeth are preserved in



Fig. 7. Photograph and interpretive drawing of GMV-2156. This slab, the counterpart of which is shown in figure 6, was used as the holotype of *Lingyuangornis parvus* by Ji and Ji (1999) (drawing after Ji and Ji, 1999). Abbreviations as in figures 3 and 5.

the left dentary of GMV-2159 (fig. 9), exposed laterally. A large gap between the last two teeth suggests that the mandibular rami of this specimen probably bore one more tooth. Because the rostralmost end of the left dentary of GMV-2159 appears to be missing, it is possible that the dentary could have carried even one or two more teeth. Thus, our estimates of the number of number of teeth present in each mandibular rami of GMV-2158

and GMV-2159 range from 7 to 9, a number slightly larger than that estimated for other enantiornithines (e.g., Sanz et al., 1997; Zhang et al., 2004; Zhou et al., 2005). The dentary of GMV-2158 and GMV-2159 gradually narrows rostrally, although like in *Simornis* (IVPP-V-9769) its ventral and dorsal margins are subparallel throughout the dentigerous portion. GMV-2159 shows a few slitlike nutrient foramina on the lateral surface of the dentary,

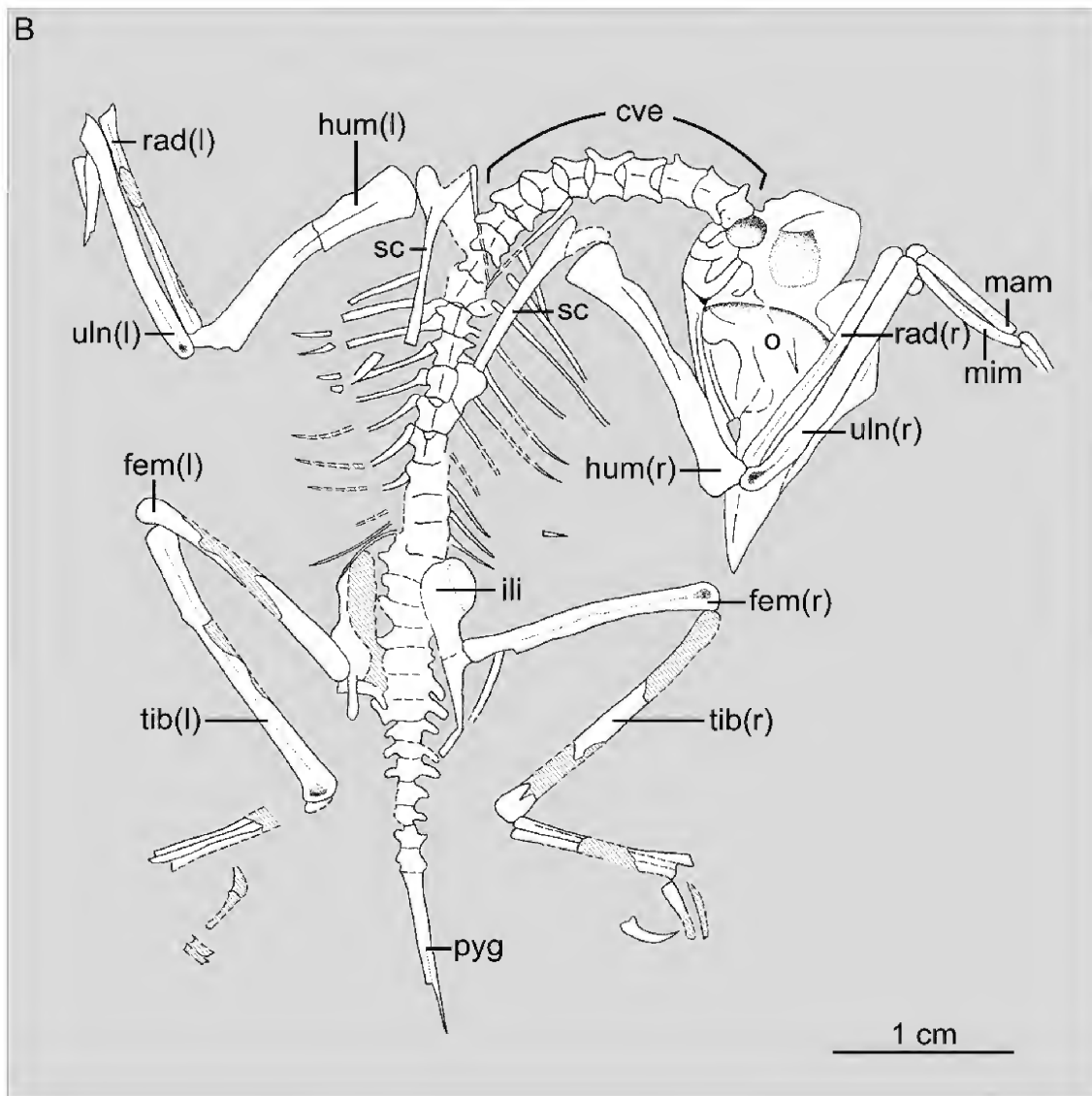


Fig. 7. Continued.

just below the toothrow (fig. 9). The caudal end of the dentary of these two specimens slants caudoventrally, forming a distinct articulation with the postdentary bones (figs. 8, 9). The postdentary portion of the right ramus of GMV-2158 is exposed in lateral view. Only a small round opening near the caudal end perforates its mandible (fig. 8). This opening is clearly homologous to the surangular foramen of nonavian theropods (Weishampel et al., 2004). Although the lower jaw of the Chinese Early Cretaceous enantiornithine early juve-

niles resembles that of their Montsec counterpart in most respects (see Sanz et al., 1997), it differs from the latter in the absence of a greatly fenestrated postdentary region.

TEETH: The dental morphology of these juveniles is clearest in GMV-2158. These teeth have wide bases and sharp crowns that are separated from their bases by a slight waist. As in all other toothed birds (Chiappe and Witmer, 2002) and some nonavian theropods (Ji et al., 1998; Norell et al., 2000), tooth crowns lack serrations, although their enamel

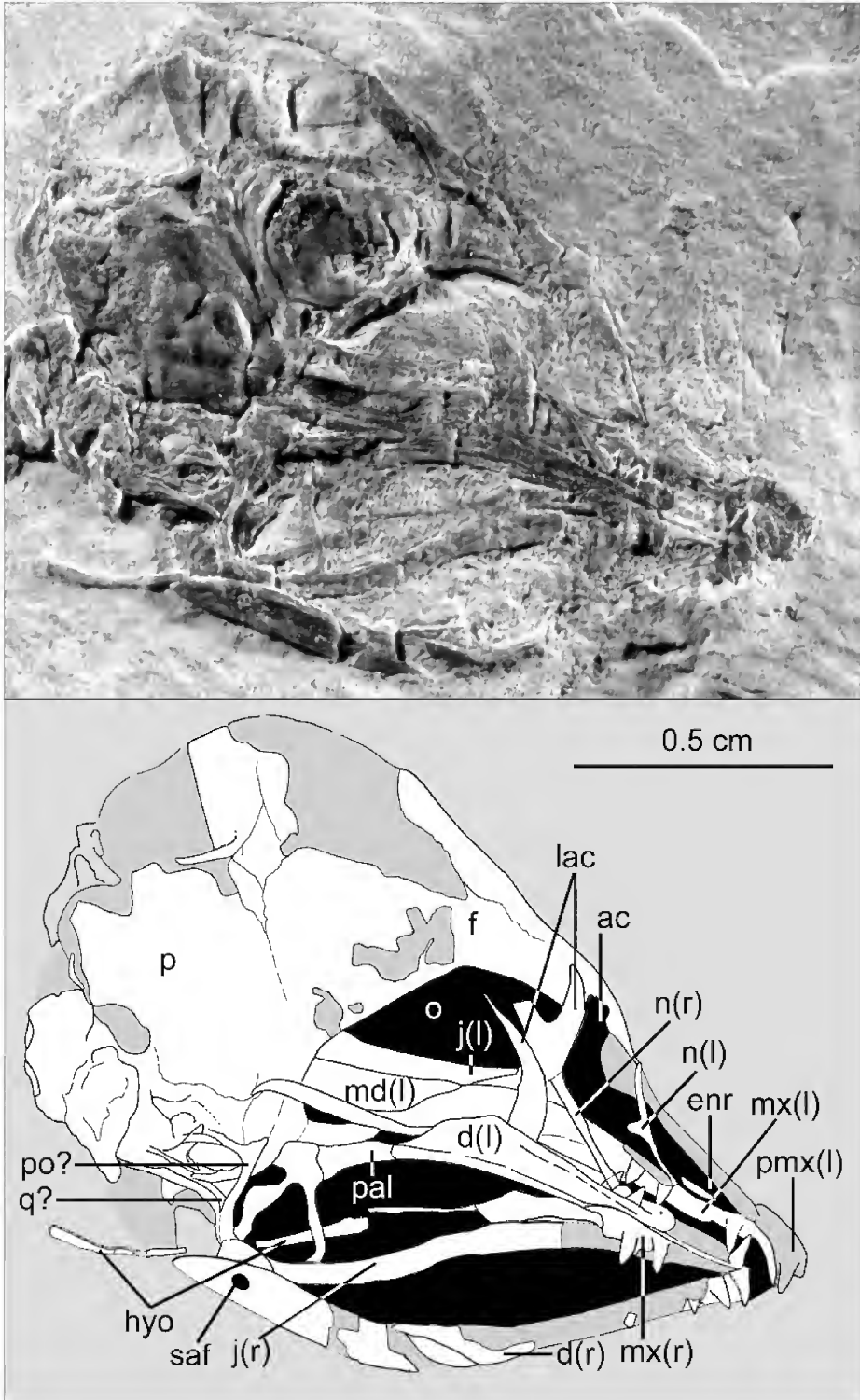


Fig. 8. Photograph and interpretive drawing of the skull of GMV-2158. Abbreviations: ac, antorbital cavity; enr, external nares; lac, lacrimal; md, mandible; mx, maxilla; n, nasal; p, parietal; pal, palatine; po, postorbital; q, quadrate; saf, surangular fenestra. Other abbreviations as in figures 3 and 5.

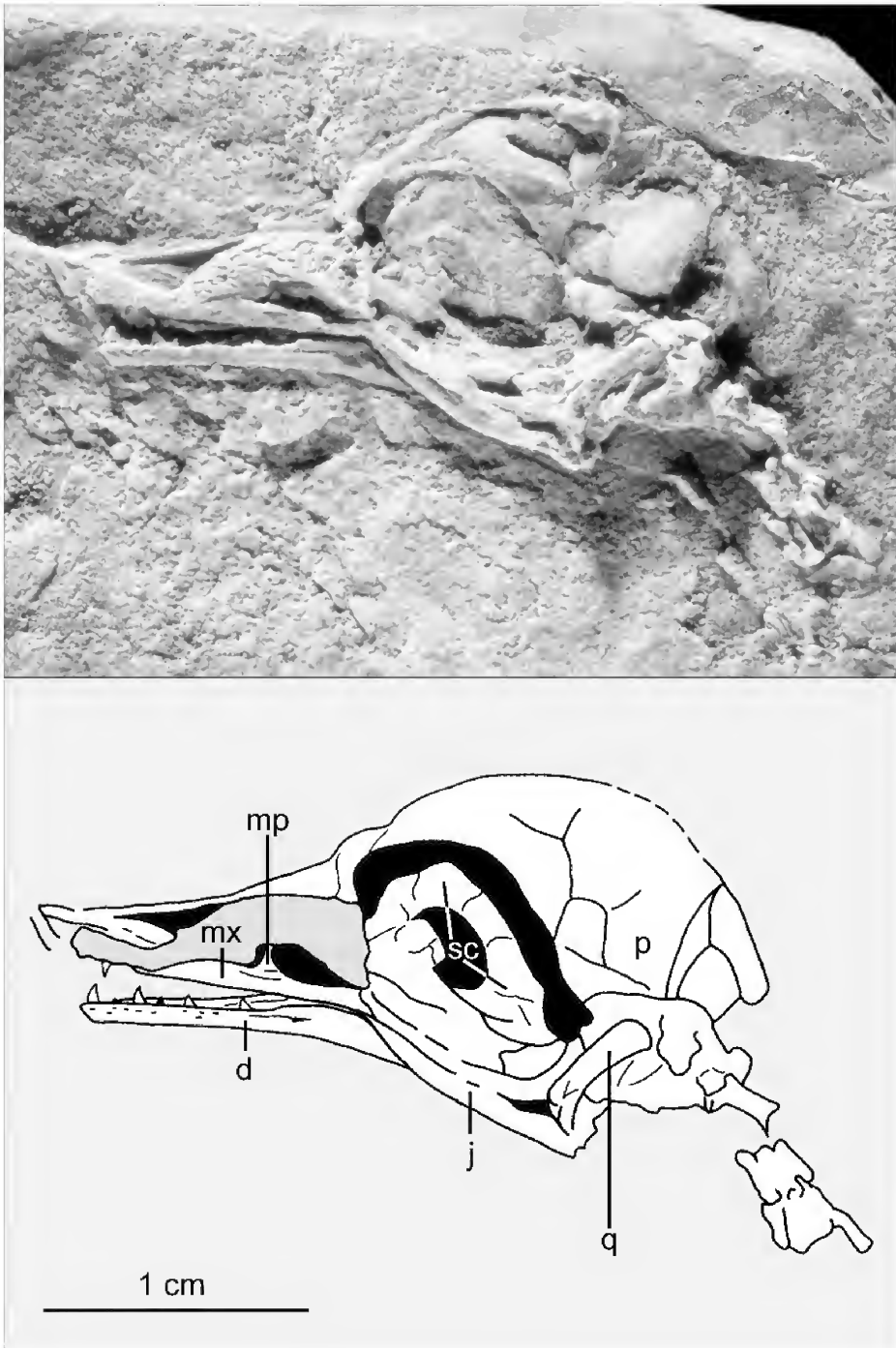


Fig. 9. Photograph and interpretive drawing of the skull of GMV-2159. Abbreviations: mp, dorsal maxillary process. Other abbreviations as in figures 3 and 5.

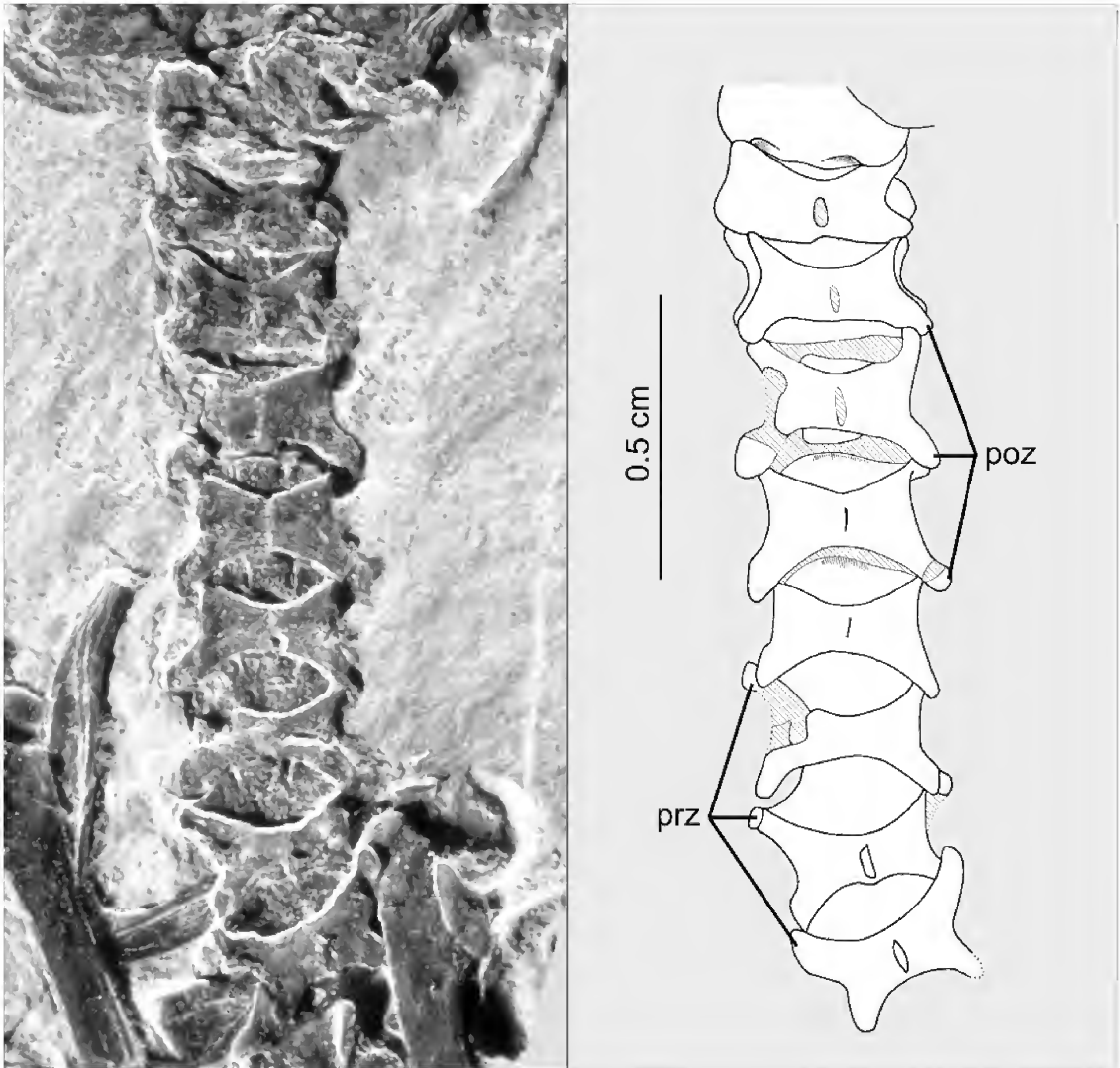


Fig. 10. Detail of the cervical series of GMV-2158 (photo and interpretive drawing). Abbreviations: poz, postzygapophysis; prz, prezygapophysis.

is thicker along the rostral and caudal edges. In most teeth, the rostral edge is somewhat convex and the caudal one is slightly concave. This condition is best seen in the dentary teeth. The center of the teeth is somewhat translucent, suggesting the presence of the pulp cavity typical of most archosaurian teeth (Edmund, 1969). No resorption pits are visible in any of the preserved teeth. The alternation of large and small teeth in the dentary of GMV-2159, however, attests to the existence of this primitive pattern of dental replacement,

which like in other archosaurs must have followed cranially advancing waves of tooth shedding (Edmund, 1969).

CERVICAL VERTEBRAE: The cervical series is in articulation in the three studied early juveniles. Nine vertebrae of cervical morphology are preserved in GMV-2158, although the most cranial one does not appear to be the atlas (fig. 10). This number falls within the range estimated for the cervical series of other enantiornithines: 9 in *Longipteryx* (Zhang et al., 2001) and the Montsec neonate (Sanz et

al., 1997), 11 in *Eoenantiornis* (Hou et al., 1999; Zhou et al., 2005) and *Eocathayornis* (Zhou, 2002), and at least 10 in *Sinornis* (Zhou, 1995a) and *Vescornis hebeiensis* (Zhang et al., 2004). It also agrees with the 9 or 10 cervicals described by Ji and Ji (1999) and Hou and Chen (1999) for GMV-2156 and NIGP-130723, respectively. As in other enantiornithines, the spinal processes (*Processus spinosus*) of these vertebrae are much reduced, forming no more than faint ridges in some of them (fig. 10). The vertebral arches (*Arcus vertebrae*)—and vertebrae as a whole—are very wide. Although there may be some degree of exaggeration due to their compression, the transversal width of the vertebrae appears to be almost twice their craniocaudal length, thus suggesting that the cervical vertebrae were rather short. The vertebral arches are shortest along the sagittal plane—this condition is in general more pronounced in the last cervicals. The craniocaudal width of the vertebral arch along this plane is less than half the distance between the prezygapophysis (*Processus articularis cranialis*) and postzygapophysis (*Processus articularis caudalis*) (fig. 10). This condition is more accentuated than that of the Montsec neonate, the midcervicals of which have a ratio between the craniocaudal width of the vertebral arch along its sagittal plane and the distance from prezygapophyses to postzygapophyses of approximately 0.6. Little information is available about the cervical morphology of enantiornithines; however, much longer vertebral arches are also present in *Sinornis*, although the examined specimen (IVPP-V-9769) is not a juvenile.

The articular facets of the pre- and postzygapophyses of GMV-2158 are separated by subequal distances until the penultimate cervical (fig. 10). From this vertebra on, the distance between postzygapophyses narrows gradually—a trend that continues onto the thoracic series. Wide and round epipophyses that project beyond the postzygapophyses are present on the second preserved cervical and apparently on the third as well. Although the condition in the fourth cervical is unclear, by the fifth preserved element the epipophyses have disappeared. In this respect, MGV-2158 contrasts the morphology of the Montsec neonate, in which prominent epipophyses are

present farther down the cervical series (Sanz et al., 1997). No details are available for the morphology of the cranial and caudal articular surfaces (*Facies articularis cranialis et caudalis*) of the studied juveniles as well as for their centra (*Corpus vertebrae*).

THORACIC VERTEBRAE: At least 10 and possibly 11 vertebrae compose the thoracic series of MGV-2158 (fig. 11). This condition compares well with the 11 thoracic vertebrae that are typical for adult Enantiornithes and other basal ornithothoracines (e.g., *Patagopteryx deferrariisi*) (Sanz and Bonaparte, 1992; Chiappe, 1996a, 2002; Chiappe and Walker, 2002). It also agrees with the 11 thoracic vertebrae and ribs identified by Ji and Ji (1999) for GMV-2156. Comparable number of vertebrae and ribs are visible in NIGP-130723.

The first three vertebrae of GMV-2158 are essentially exposed in dorsal view; the remaining ones are exposed in lateral view. Although the spinal process of the first thoracic vertebra is relatively short, it represents an abrupt difference from the condition in the last cervical vertebra. By the fourth thoracic element, the vertebral arch (and spinal process) is as high as the centrum. The dorsal exposure of the first three thoracic vertebrae prevents determination of a ventral process (*Processus ventralis*). Such a process, however, is absent in the subsequent thoracic vertebrae. Even though the transverse processes (*Processus transversus*) are not well preserved, they appear to be short. Some of the thoracic centra seem to be excavated by a large lateral fossa, a condition widespread among enantiornithines (Chiappe and Calvo, 1994; Chiappe, 1996a; Sanz et al., 1995, 1996; Chiappe et al., 2002) and other basal birds (Marsh, 1880; Chiappe et al., 1999; Clarke et al., 2006), although preservation prevents being conclusive in this respect.

SYNSACRAL VERTEBRAE: The synsacrum of GMV-2158 appears to be composed of six vertebrae. Seven (Ji and Ji, 1999) or eight (Hou and Chen, 1999) synsacrals were reported for GMV-2156 and NIGP-130723, respectively. Although this number compares better with the eight synsacrals that are typical of Enantiornithes (Chiappe, 1996a; Chiappe and Walker, 2002), the precise number of



Fig. 11. Photograph of the thoracic series of GMV-2158.

synsacral vertebrae of GMV-2156/NIGP-130723 is difficult to determine in the poorly preserved sacra of the two slabs; our examination suggests that only six vertebrae may form the synsacrum of this specimen (fig. 7). The degree of fusion of the centra of GMV-2158 is also difficult to ascertain, but at least the spinal processes of the first four elements are not fused to one another. Long and strong transverse processes are preserved in the last

three synsacral vertebrae; the last one points slightly more caudal than the others. These processes are not fused to the medial surface of the ilium. Their length suggests that the synsacrum completely separated the two ilia, at least over its caudal half. Such a condition is comparable to those known for *Sinornis*, *Confuciusornis*, and other basal avians.

CAUDAL VERTEBRAE: The caudals of GMV-2158 are poorly preserved, although eight vertebral segments are distinguishable in the portion of tail preserved in this specimen (fig. 12). A minimum of seven free caudals can be seen but it is unclear whether the last vertebral segment formed the most proximal part of a pygostyle. Seven free caudals were described for GMV-2156 (Ji and Ji, 1999) and four for NIGP-130723 (Hou and Chen, 1999). This notable difference highlights the poor preservation of this region in these two slabs. Our observations of GMV-2156/NIGP-130723 suggest that some seven free caudals separated the synsacrum from the pygostyle of this specimen (figs. 6, 7), although we admit that the boundary between synsacrum and proximal caudal vertebrae is difficult to ascertain. Eight free caudals appear to have preceded the pygostyle of *Iberomesornis romerali* (Sanz et al., 2002) and six to seven those of *Sinornis* (Serenio et al., 2002) and *Protopteryx fengningensis* (Zhang and Zhou, 2000); thus, the numbers of free caudal vertebrae of GMV-2158 and GMV-2156/NIGP-130723 fall within the range known for other enantiornithines. However, GMV-2156/NIGP-130723 differs from most other enantiornithines in that its pygostyle is much longer than the tarsometatarsus. Although the pygostyle of GMV-2156/NIGP-130723 and *Boluochia* (Zhou, 1995b) is close to 25% longer than the tarsometatarsus, it is minimally longer (e.g., *Iberomesornis*) or even shorter (e.g., *Sinornis*, *Vescornis*) in other enantiornithines.

The caudal vertebrae of GMV-2158 are exposed dorsally. As in other enantiornithines (e.g., *Iberomesornis*, *Halimornis thompsoni*), the caudals of GMV-2158 bear strong prezygapophyses and short transverse processes. Some exposed caudal surfaces show that the intercentral articulations (*Facies articularis*) were flat. At least four, and possibly five, subrectangular chevrons (*Processus haemalis*)

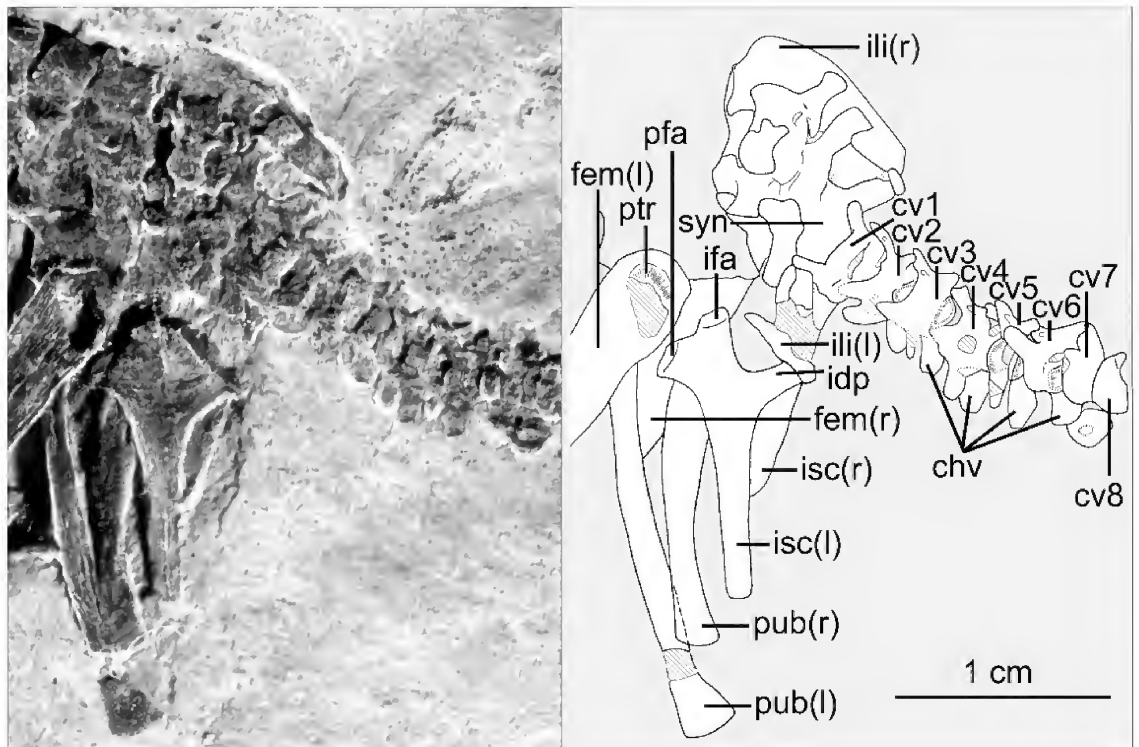


Fig. 12. Photograph and interpretive drawing of the caudal series and pelvis of GMV-2158. Abbreviations: cv1–8, caudal vertebrae 1–8; idp, ischiadic proximal dorsal process; ifa, iliac articular facet of ischium; pfa, pubic articular facet of ischium; ptr, posterior trochanter. Other abbreviations as in figure 3.

are preserved in the distal half of the tail (fig. 12).

THORACIC AND VENTRAL RIBS: Most ribs (*Costa sternalis*) of GMV-2158 are preserved in near articulation with their respective thoracic vertebrae, and remnants of the ribcage are also present in the other studied juveniles. These bones are long and slightly expanded at their distal ends (figs. 3, 11). They show no evidence of ossified uncinat processes (*Processus uncinatus*). The presence of these processes has often been regarded as a synapomorphy of Ornithurae (Martin, 1983; Cracraft, 1986; Sanz and Bonaparte, 1992; Chiappe, 1996a; Hou et al., 1996), but ossified uncinat processes have now been reported for a variety of nonavian theropods (Clark et al., 1999; Norell and Makovicky, 1999; Zhou and Wang, 2000) and nonornithurine birds (Chiappe et al., 1999). Although most enantiornithine taxa show no evidence of these processes, evidence of them is at least preserved in *Eoenantiornis* (Zhou et al., 2005) and

Longipteryx (Zhang et al., 2001) from the Early Cretaceous of China. The lack of evidence of these processes in most enantiornithine taxa may not be taken as evidence of absence. Some well-preserved and articulated specimens of *Confuciusornis* lack uncinat processes, even though these ossifications are clearly present in this taxon (Chiappe et al., 1999). Consequently, the absence of uncinat processes in GMV-2158 should not be considered as a definitive attribute of this bird's anatomy—it could well be a preservational artifact or a consequence of its early ontogenetic age. The matrix surrounding the caudal two-thirds of the ribcage of GMV-2158 is somewhat darker than that surrounding the rest of the skeleton—this darker area appears to define the visceral cavity (fig. 3).

Several ventral (sternal) ribs (*Extremitas ventralis costae*) are also preserved in GMV-2158 and GMV-2159 (figs. 3, 5, 11). They are approximately one-third the length of the thoracic ribs, with slight expansions both

proximally and distally. Scattered ventral ribs of the left side lay close to the sternum; one of them is articulated to the third thoracic rib (*Extremitas dorsalis costae*). At least six, and perhaps seven, ventral ribs from the right side can be seen between the fourth and fifth left thoracic ribs. These are clustered as if they had retained their articular relation to the sternum, although they are not joined to the ossified portion of the latter. The number of ossified ventral ribs of GMV-2158 is significantly greater than that of nonavian maniraptoriforms (Clark et al., 1999; Norell and Makovicky, 1999), also exceeding the five elements known for *Confuciusornis* (Chiappe et al., 1999). The number of ventral ribs of GMV-2158 appears to approach more that of *Iberomesornis* in which the number of ventral ribs seems greater than five.

GASTRALIA: A minimum of six rows of gastralialia follow the caudal end of the sternum of GMV-2158 (fig. 3), with the distal end of the last one reaching the left pubis. Among birds, definitive evidence of a gastralial system is known for nonornithothoracine birds (e.g., *Archaeopteryx*, *Confuciusornis*, *Sapeornis chaoyangensis*, and others; Chiappe and Dyke, 2006) and Enantiornithes (e.g., *Eoenantiornis*, *Longipteryx*, *Vescornis*)—these abdominal ossifications were clearly widespread among early avians. In GMV-2158, the rows of gastralialia are arranged in zigzag, a primitive pattern common to nonavian reptiles and basal birds (Claessens, 2004). Although the gastralial system is poorly preserved, it appears that the first row is formed by a single element, while some of the subsequent rows are formed by pair elements on each side, a condition best seen in the right third row. The presence of a gastralial system with a first row formed by one element on each side is comparable to the condition reported for nonavian theropods (Claessens, 2004) and *Confuciusornis* (Chiappe et al., 1999). Even though we may be underestimating the number of rows of gastralialia due to preservational factors, the real number of rows in the gastralial system of GMV-2158 must have been significantly smaller than the 12 to 15 rows of nonavian coelurosaur theropods (Norell and Makovicky, 1997; Claessens, 2004) because there is little space for them between the sternum and pelvis. This number must have

been even smaller than the maximum 10 rows estimated for *confuciusornithids* (Chiappe et al., 1999).

APPENDICULAR SKELETON

Thoracic Girdle

CORACOID: Although impressions of the coracoid (*Os coracoideum*) are preserved in GMV-2156/NIGP-130723, details are visible only in GMV-2158 and GMV-2159. This bone is robust and pillar-shaped, with a length somewhat smaller than 70% of the length of the scapula (figs. 13, 14). The sternal end (*Extremitas sternalis coracoidei*) is expanded and with a straight end. The existence of a prominent, triangular fossa excavating the dorsal surface of the coracoid is evidenced in the right element of GMV-2158, which is exposed in dorsal view (fig. 13). A similar ventral fossa is known for a variety of enantiornithine taxa (Chiappe and Calvo, 1994; Chiappe and Walker, 2002; Zhou, 2002). Although the upper margin of this fossa is not preserved in any of the two coracoids of GMV-2158, it is clear that this fossa was restricted to the sternal half of the bone. A slitlike foramen for the passage of the supracoracoid nerve (*Foramen nervus supracoracoidei*) pierces the left coracoid of GMV-2158. This foramen is separated from the medial margin of the bone by a robust bony bar. A similar configuration is known for other enantiornithine taxa (Chiappe and Calvo, 1994; Chiappe and Walker, 2002). Unlike some of them (e.g., *Neuquenornis volans*), however, the supracoracoid nerve foramen of GMV-2158 does not open inside its dorsal coracoidal fossa. In fact, GMV-2158 differs from many other enantiornithines (e.g., *Eoalulavis hoyasi*, *Enantiornis leali*, *Sinornis*) in that this foramen is not even close to where the upper margin of this fossa would have been placed.

The shoulder end of the coracoid (*Extremitas omalis coracoidei*) is well preserved on the left element of GMV-2158. The kidney-shaped glenoid facet (*Facies articularis humeralis*) reaches the end of the bone. This extension of the glenoid facet results in the apparent absence of a differentiated acrocoracoid (*Processus acrocoracoideus*). To some

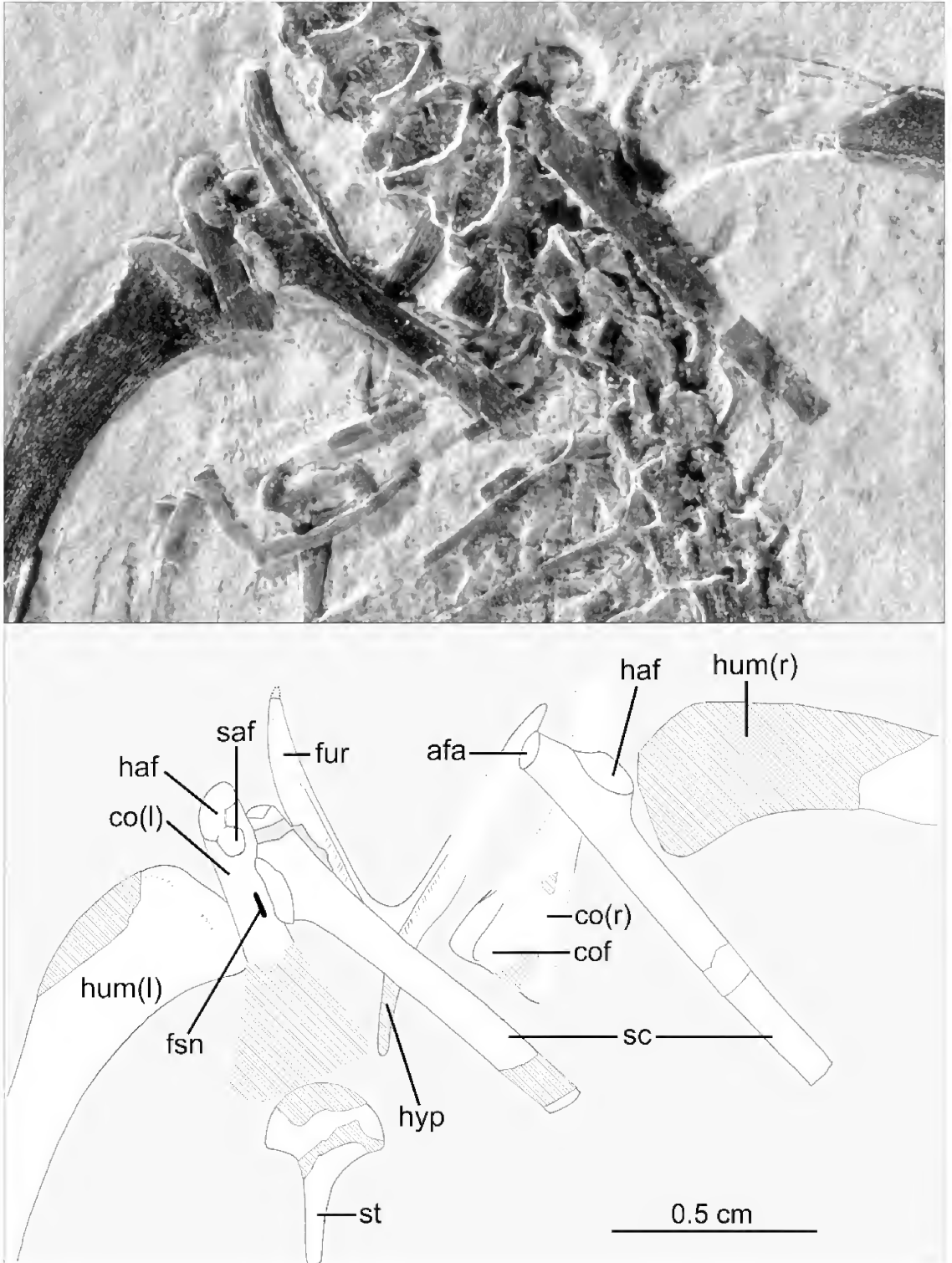


Fig. 13. Photograph and interpretive drawing of the thoracic girdle of GMV-2158. Abbreviations: afa, articular facet of acromion; cof, dorsal coracoidal fossa; fsn, supracoracoid nerve foramen; haf, humeral articular facet; hyp, hypocone; saf, scapular articular facet. Other abbreviations as in figure 3.

extent, this unusual condition may be the result of the obvious compaction suffered by this bone; however, even if this were the case, the acroracoid would be significantly shorter than that of *Enantiornis*, *Gobipteryx*, *Alexornis antecedens*, and other enantiornithines. Distally and medially, the glenoid facet of GMV-2158 connects to a subcircular facet (*Facies articularis scapularis*) for the articulation with the scapula (fig. 13). These two facets are co-planar, although it is clear that this is due to their compaction. That the glenoid facet faces somewhat more laterally and the scapular facet faces slightly more medially suggest a condition similar to that of the Late Cretaceous euenantiornithine *Enantiornis* and *Gobipteryx*, in which the two surfaces are at an angle of approximately 90 degrees. As in most other enantiornithines and more basal birds, the coracoid of these juveniles lacks a procoracoid process (*Processus procoracoideus*) (figs. 13, 14). The coracoid of GMV-2158 shares with other enantiornithine coracoids (e.g., *Alexornis*, *Gobipteryx*, *Eoalulavis*) the absence of a distinct tubercle medial to the glenoid facet characteristic of *Enantiornis* and certain other enantiornithines (Chiappe, 1996b; Buffetaut, 1998).

SCAPULA: As in most other skeletal elements, nearly all the anatomical information on the scapula derives from GMV-2158, the scapulae of which are exposed in lateral view (fig. 13). The shoulder end bears a robust and long acromion, roughly two-thirds the length of the glenoid facet (*Facies articularis humeralis*). Although Ji and Ji (1999) described an elongate acromion for GMV-2156, this feature is likely the impression of the coracoid shoulder end (fig. 7). A great deal of morphological variation exists in the acromion of Enantiornithes. However, the scapula of many of these birds, if not of all, bears an elongate and robust acromion (e.g., *Sinornis*, *Eoenantiornis*, *Eoalulavis*, *Enantiornis*, *Halimornis*, *Gobipteryx*) (Chiappe and Walker, 2002). In these taxa, the acromial length is subequal to longer than the length of the glenoid facet. This condition, however, is likely to be primitive since a well-developed acromion is also present in the scapula of other basal birds (e.g., *Archaeopteryx* [best observed in the

London specimen], *Patagopteryx* [Chiappe, 1996a]) and to some extent in dromaeosaurids (Norell and Makovicky, 1999). A smooth, oval facet occupies the entire tip of the acromion of GMV-2158. This facet, also present in *Enantiornis* and *Halimornis* among enantiornithines, likely received ligaments that connected the scapula to the furcula. The glenoid facet of the scapula is suboval and slightly depressed in its center. It faces lateroventrally. The scapular blade (*Corpus scapulae* and *Extremitas caudalis*) is straight with subparallel margins (figs. 13, 14), a condition also visible in GMV-2156/NIGP-130723 (figs. 6, 7). The distal end is missing in both elements so it is not possible to ascertain whether it narrowed into a point or expanded as did the scapulae of *Archaeopteryx* and *Rahonavis ostromi*.

FURCULA: The furcula of the enantiornithine early juveniles is V-shaped, possessing a long hypocleideum (*Apophysis furculae*) (figs. 13, 14). The furcular rami (*Scapus clavicularae*) are essentially straight, forming an interclavicular angle of approximately 60° in GMV-2158, GMV-2159, and GMV-2156 (contra Ji and Ji, 1999). The furcula is caudally exposed in GMV-2158. This specimen shows that the medial margin of the rami is cranio-caudally thicker than the lateral margin (fig. 13), although this difference decreases as the rami taper toward their proximal end (*Extremitas omalis clavicularae*). This morphology gives the midshaft of the rami an L-shaped section in which the caudal surface is concave. This condition is typical of a variety of other euenantiornithines (Chiappe and Calvo, 1994; Chiappe and Walker, 2002) including *Neuquenornis*, *Eoalulavis*, *Concornis lacustris*, *Gobipteryx*, and *Eoenantiornis*. In GMV-2159, the length of the hypocleideum, apparently complete, is nearly two-thirds the length of the furcular rami (fig. 14). In GMV-2158, this proportion is close to one-third, although the fact that the hypocleideum of this specimen is preserved as an impression and partially covered by ribs makes it difficult to rule out that it was not longer (fig. 13). A short hypocleideum was described for NIGP-130723 by Hou and Chen (1999). However, our examination of this specimen (fig. 6) revealed that the hypocleideum is much longer than that illustrated by these authors. Indeed, the hypocleideum of the

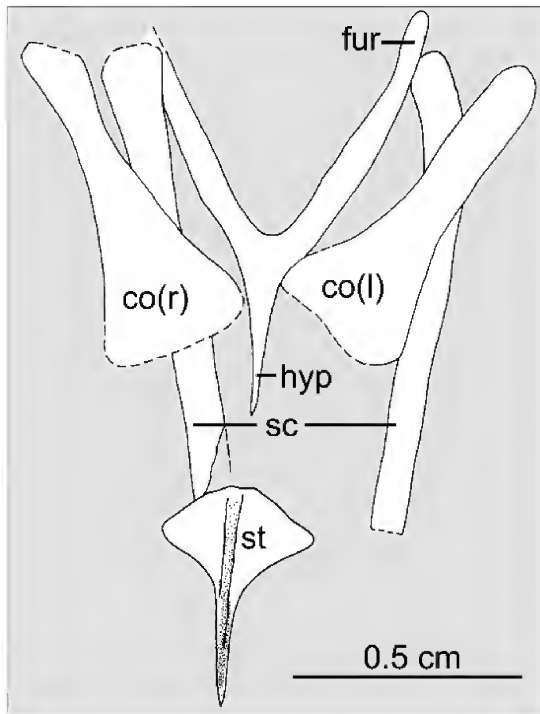


Fig. 14. Interpretive drawing of the thoracic girdle of NIGP-130723. Abbreviations as in figure 13.

furcula of NIGP-130723 is approximately two-thirds the length of the rami.

STERNUM: The sterna of the Chinese early juveniles are small and fan-shaped (figs. 6, 13, 14). The overall morphology of the sternum is reminiscent of that which Hou et al. (1999) described for *Eoenantiornis*. Nonetheless, new studies of this species (Zhou et al., 2005) have documented a sternum that, like that of most other enantiornithine species, has paired lateral (*Trabecula lateralis*) and medial processes (*Trabecula intermedia*). The main portion of the sternum of the juveniles is roughly semicircular, with a rounded cranial margin (*Margo cranialis sterni*). Caudally, this bone narrows into a slender process (figs. 13, 14). In GMV-2158 and GMV-2159, this process extends nearly 60% of the sternal length; this process is slightly shorter in NIGP-130723 (contra Hou and Chen, 1999). The sternum is ventrally exposed in GMV-2159, revealing that this bone lacks a carina. Hou and Chen (1999) regarded the presence of a central groove in the impression of the sternum of

NIGP-130723 as evidence of a sternal keel. However, because the sternum of this specimen imprinted its dorsal side (fig. 6) (the whole skeleton is in ventral view), Hou and Chen's (1999) statement cannot be verified. A sternal keel could have been present in NIGP-130723, although the early ontogenetic age of this individual makes it highly unlikely. In extant birds, the sternum is largely cartilaginous at the time of hatching (Starck and Ricklefs, 1998; Bellairs and Osmond, 1998), and sternal carina is the last portion of the sternum to ossify, an event that often occurs weeks after hatching (Hogg, 1980). The groove observed in the central portion of the sternum of NIGP-130723 most likely indicates a central thickening of the sternal body, a condition that is clear in GMV-2159 (fig. 14).

The disproportion between the size of this bone and that of the coracoids (figs. 6, 13, 14) suggests that the preserved sterna of GMV-2158, GMV-2159, and NIGP-130723 are only ossified portions of largely cartilaginous sterna—the ossified center is perhaps homologous to the single median center of ossification or lophosteon of many modern birds (Parker, 1868). This interpretation is consistent with the large number of ventral ribs of GMV-2158 and the absence of costal articular facets (*Processus costalis*) on its sternum; the ventral ribs probably joined the cartilaginous portion of the developing sternum. Likewise, this interpretation is consistent with the sternal morphology and proportions of the sternum of another early juvenile enantiornithine, a specimen contained within a bone aggregate from the Early Cretaceous of Las Hoyas, in Spain, that was interpreted as a pellet (Sanz et al., 2001).

Thoracic Limb

HUMERUS: In the three studied specimens, the length of the humerus is subequal to slightly shorter than that of the ulna (figs. 3–7). GMV-2158 and GMV-2159 show that the humeral head (*Caput humeri*) is convex caudally and concave cranially, respectively. The deltopectoral crest (*Crista deltopectoralis*) is weakly developed, with a slightly rounded border. Both the pneumotricipital fossa (*Fossa*

pneumotricipitalis) and foramen (*Foramen pneumaticum*) are absent, at least in GMV-2158, the only specimen with the humeri exposed caudally (fig. 13). A pneumotricipital fossa excavates the caudoproximal surface of the humerus in most adult specimens of enantiornithines—an exception is a new fragmentary specimen from the Early Cretaceous of Gansu Province in China (You et al., 2005). This specimen notwithstanding, the absence of this structure in GMV-2158 and presumably the other two juveniles suggests that this structure likely formed later in development. In the chicken, humeral pneumatization begins approximately 2 weeks after hatching (Bremer, 1940). A caudally projected ventral tubercle (*Tuberculum ventrale*) is also absent (fig. 13). As in the case of the pneumotricipital fossa, a well-developed, caudally projected ventral tubercle is typical of adult enantiornithines (e.g., *Eoalulavis*, *Neuquenornis*, *Eo-enantiornis*, *Enantiornis*, *Halimornis*). Its absence in the Chinese juveniles may also be linked to their immaturity. A round, somewhat prominent bicipital crest (*Crista bicipitalis*) is present on the cranioventral corner of the humerus, adjacent to the humeral head. Although the presence of an expanded bicipital crest is typical of all of enantiornithines (Chiappe and Calvo, 1994; Chiappe and Walker, 2002), the elevated position of this expansion in the Chinese juveniles approaches the condition seen in *Halimornis* (Chiappe et al., 2002).

Distally, the ventral margin of the humeral extremity (area of the *Processus flexorius*) projects beyond the dorsal one, much like in most other enantiornithines. The distal condyles (*Condylus dorsalis/ventralis*) are poorly developed, presumably an ontogenetic feature. The olecranal fossa (*Fossa olecrani*) is at best weak.

ULNA AND RADIUS: The ulna of the Chinese juveniles is slightly longer than the radius (fig. 3). This bone is essentially straight although its proximal half is somewhat bowed. The olecranon is not developed and quill knobs (*Papillae remigales caudales*) are not visible in any of the specimens here reported. The radius is straight. In GMV-2156, a longitudinal ridge runs throughout the length of the molds of the radii. This ridge appears to be the

negative expression of the longitudinal groove that scars the ventral surface of the shaft of the radius of enantiornithines (Chiappe and Calvo, 1994; Chiappe and Walker, 2002). In GMV-2158, the ratio between the widths of the radius and ulna at midshaft is approximately 0.6. This proportion is comparable to that of other enantiornithines (Chiappe, 1996a) and smaller than the one exhibited by more primitive birds such as *Archaeopteryx*, *Rahonavis*, and *Confuciusornis* (Chiappe et al., 1999).

CARPUS: All of the Chinese early juveniles preserve evidence of both proximal and distal carpals (figs. 15–17). In GMV-2159, two distinct ossifications overlap the distal ends of the ulnae (fig. 17). One of these is heart-shaped, thus suggesting its identification as the ulnare (*Os carpi ulnare*). The other element, more elongated and rounded, is likely the radiale (*Os carpi radiale*). A heart-shaped ulnare has been reported for several other enantiornithines (e.g., Sereno and Rao, 1992; You et al., 2005). In GMV-2158, a large semilunate carpal caps the proximal ends of the major metacarpal (*Os metacarpale majus*) and to some extent the minor metacarpal (*Os metacarpale minus*) (fig. 15). An individualized semilunate carpal is also present in GMV-2156/ NIGP-130723 (fig. 16) (this distal carpal was mislabeled as the radiale by Ji and Ji, 1999). In the latter specimen, the impression of the semilunate carpal also caps the major and minor metacarpals. Although the proximal ends of these metacarpals remain unfused in GMV-2159, a semilunate carpal is not visible in its original position (fig. 17). The morphology of the semilunate carpal of GMV-2158 and GMV-2156/ NIGP-130723 is essentially the same as that of *Archaeopteryx* and nonavian maniraptorans (Ostrom, 1976; Norell and Makovicky, 1999). Nevertheless, the topographic relationship between the semilunates of these juvenile enantiornithines and their metacarpals approach more that of *Archaeopteryx* in which the semilunate has a minor participation capping the alular metacarpal (*Os metacarpale alulare*) (Zhou and Martin, 1999) (see Implications for Ontogenetic Change in Basal Birds, below).

In GMV-2158, a small distal carpal appears to be wedged between the proximal end of the

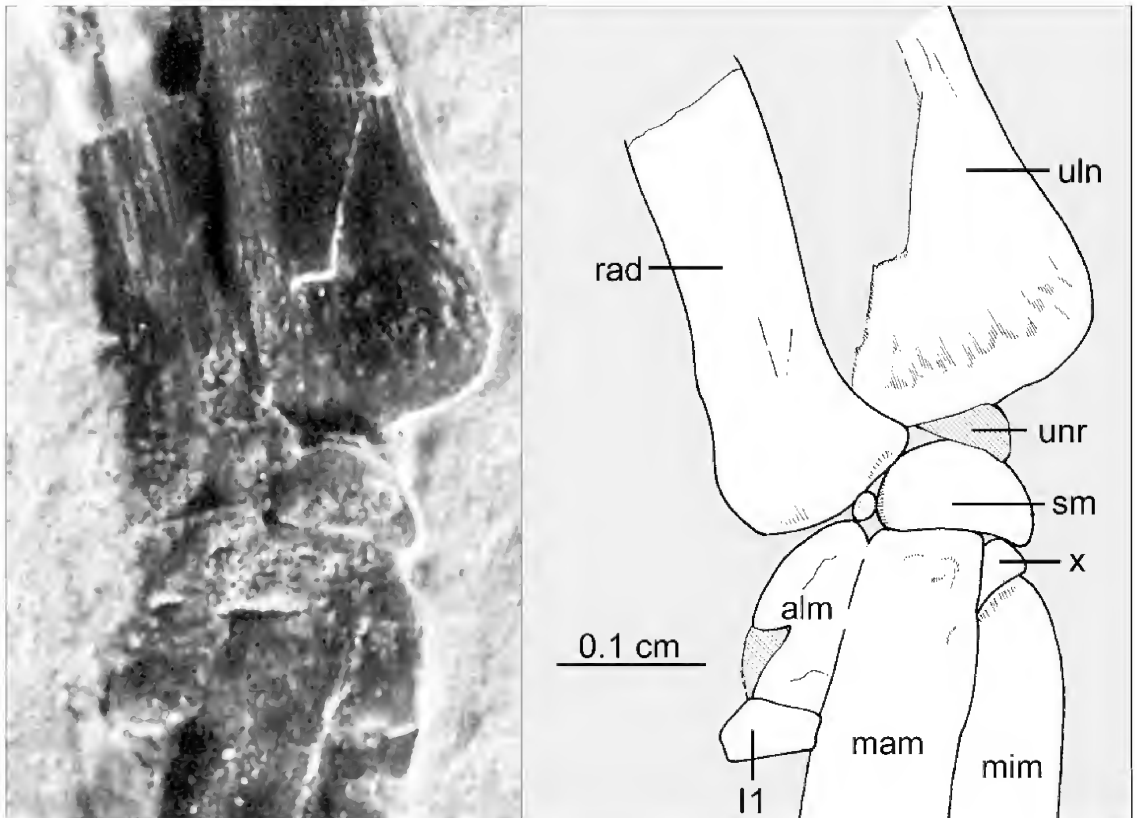


Fig. 15. Photograph and interpretive drawing of the carpus and manus of GMV-2158. Abbreviations: sm, semilunate carpal; unr, ulnare; x, carpal X; II, proximal phalanx of alular digit. Other abbreviations as in figure 3.

minor metacarpal and the semilunate carpal (fig. 15). This area is obscured by the ulna in NIGP-130723, and no extra carpal has left an impression in GMV-2159. This carpal is in a comparable position to the carpal X of *Archaeopteryx* and modern birds, a distal carpal of unclear homology (Hinchliffe, 1985; see Hogg [1980] for the identification of a similarly placed ossification of modern birds as distal carpal IV). Another small carpal may be present at the proximal junction of the alular and major metacarpals of GMV-2158 (fig. 15), although this one is less obvious than the other carpals.

MANUS: The hand, including fingers, is best preserved in GMV-2159, whose hand is slightly shorter than both the humerus and the ulna (fig. 5). In all these juveniles, the metacarpals and carpals are not fused to one another, although there may be an incipient

fusion between the proximal ends of the major and alular metacarpals in GMV-2158 (fig. 15). Hou and Chen (1999) reported a complete fusion between carpals and metacarpals in NIGP-130723. Our examination of GMV-2156/NIGP-130723, however, indicates that the metacarpals and carpals of this specimen remain unfused (figs. 6, 16).

In GMV-2158, the subrectangular alular metacarpal is short (ca. 20% of metacarpal II) and lacks an extensor process (*Processus extensorius*) (fig. 15). This shape and proportion are comparable to those of GMV-2156/NIGP-130723 (fig. 16); the alular metacarpal is missing from both hands of GMV-2159 (fig. 5). The morphology of the alular metacarpal of enantiornithines is diverse. Those of these juveniles differ from the semi-circular appearance of the alular metacarpal of some other enantiornithines (e.g., *Neuquen-*

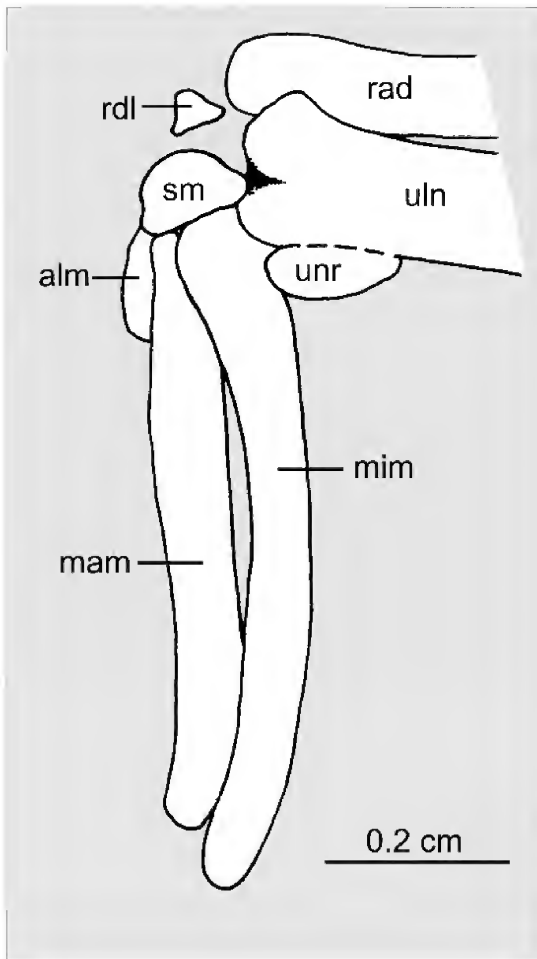


Fig. 16. Interpretive drawing of the carpus and manus of NIGP-130723. Abbreviations: rdl, radiale. Other abbreviations as in figure 15.

ornis, *Enantiornis*) but resemble more the subrectangular-shaped bone of certain members of the group (Zhang et al., 2004; You et al., 2005; Zhou et al., 2005). In the Chinese juveniles here studied, the major metacarpal is straight, slightly wider and more robust than the minor metacarpal (figs. 15–17). As in other enantiornithines (e.g., *Eoenantiornis*, *Neuquenornis*, *Enantiornis*, *Eoalulavis*, *Vescornis*, *Sinornis*, *Longipteryx*, *Longirostravis hani*) (Chiappe and Walker, 2002), the distal end of the major metacarpal extends less than that of the minor metacarpal. The minor metacarpal is somewhat bowed, with a convex caudal margin. In GMV-2158 there is no

intermetacarpal space (*Spatium intermetacarpale*) between the major and minor metacarpals (figs. 3, 15); in the right hand of GMV-2156/NIGP-130723 and GMV-2159, the intermetacarpal space is very narrow (figs. 16, 17). This difference may well be due to preservational factors, as it is suggested by the fact that the left hand of these two specimens completely lacks such a space (figs. 5, 6). A narrow intermetacarpal space is typical of most other basal birds (Chiappe et al., 1999), including enantiornithines (Chiappe and Walker, 2002). The manual phalanges (*Ossa digitorum manus*) are best seen in GMV-2159 (fig. 5). The alular digit is formed by two phalanges, with the last one being a claw. This digit ends proximal to the distal end of the major metacarpal. The major digit bears three phalanges. The proximal one is the longest, lacking the cranio-caudal expansion of most ornithuromorph birds (Clarke and Chiappe, 2001; Clarke and Norell, 2002; Zhou and Zhang, 2005; Clarke et al., 2006). This phalanx is followed by a slightly shorter intermediate phalanx and a curved claw. Evidence of the proximal phalanx of the minor digit can be seen in GMV-2159 (figs. 5, 17) and NIGP-130723 (fig. 6). It is likely that this finger was much more reduced than the other two, lacking an unguis, a condition typical of Enantiornithes (Chiappe and Walker, 2002). In GMV-2158, fragments of the proximal phalanges of the alular and major digits are preserved in articulation to their respective metacarpals. A small unguis located 4.65 mm from the distal end of the two main metacarpals is interpreted as the claw of the major digit (fig. 3). Based on this interpretation, the relative length of this digit is approximately the same as that of GMV-2159.

Pelvic Girdle

The pelvis is best preserved in GVM-2158. It is preserved in articulation with both the synsacrum and the hindlimbs (fig. 3). The three pelvic elements are not fused to one another. Due to the dorsolateral crushing of this pelvis, the pubis and ischium of the left side are more distally placed than are those of the right side. The orientation of the pubis and ischium with respect to the ilium, however,

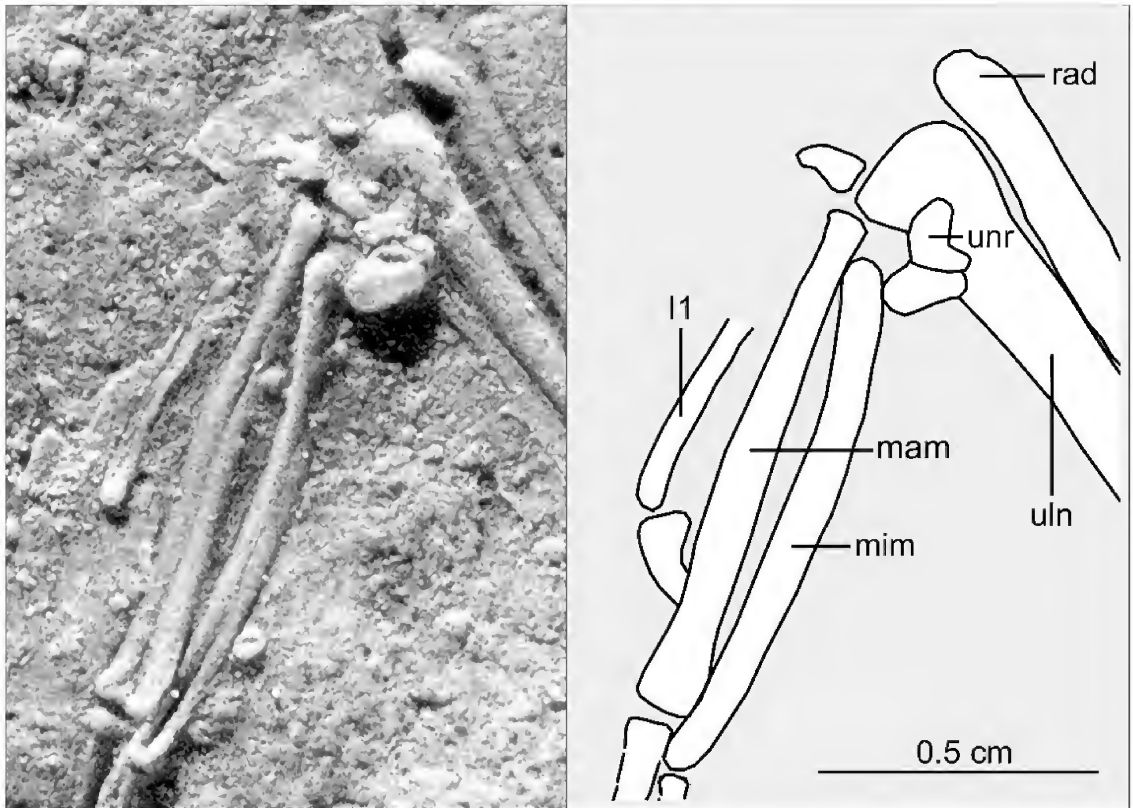


Fig. 17. Photograph and interpretive drawing of the carpus and manus of GMV-2159. Abbreviations as in figure 15.

shows no sign of any significant displacement. Portions of the pelvic bones are also preserved in GMV-2156/NIGP-130723 and GMV-2159 (figs. 3, 5–7).

ILIUM: Little can be said about the ilium of GMV-2158 (fig. 12). A portion of the left preacetabular wing is crushed against the ventral margin of the cranial synsacral vertebrae. The acetabular region (*Acetabulum*) of the left element is also preserved, although it is partially covered by the femur. The postacetabular wing (*Ala postacetabularis ilii*) of the right ilium underlies the transverse processes of the synsacral vertebrae, and what appears to be a fragment of the left postacetabular wing is attached to the left ischium. The postacetabular wing is about 20–25% shorter than the preacetabular wing (*Ala preacetabularis ilii*), a proportion similar to that observed in GMV-2156 (fig. 7). The postacetabular wing of the ilium is also shorter than its

preacetabular counterpart in other basal birds including enantiornithines (Sanz et al., 1996; Zhang and Zhou, 2000; Chiappe and Walker, 2002). In GMV-2158, the postacetabular wing narrows caudally to a blunt end (fig. 12); this end appears more pointed in GMV-2156 (fig. 7) but this could well be an artifact of the poor preservation of this specimen. The caudal end of the ilium of GMV-2158 is not as narrow as in other enantiornithines (Walker, 1981; Zhou, 1995a; Hou, 1997), *Confuciusornis* (Chiappe et al., 1999), *Archaeopteryx* (Wellnhofer, 1984, 1993), and certain non-avian maniraptoriforms (Burnham et al., 2000).

PUBIS: The shafts of the left and right pubes of GMV-2158 are preserved in the lateral and medial views, respectively. The pelvis is opisthopubic. The pubic shaft is slightly bowed cranially and oriented roughly 50° with respect to the longitudinal axis of the

synsacrum (fig. 12). The position of the pubes of GMV-2159 and GMV-2156/NIGP-130723 confirms the existence of an opisthopubic pelvis, but the dorsoventral postmortem compression of these specimens prevents any estimation of the angle of pubic orientation (figs. 5–7). Although it is difficult to determine the precise shape of the pubic section, the shaft of GMV-2158 is not as laterally compressed as the distal end. In none of these Chinese early juveniles is there evidence of a pubic apron—the distal portion of the pubic shaft (*Scapus pubis*) is laterally flat. Although the distal ends of the pubes of GMV-2158 and GMV-2159 bear a slight expansion, the pubes do not form the bootlike end like that some other enantiornithines (e.g., *Simornis*, *Eoenantiornis*). Likewise, there is no indication that the pubes formed a distal symphysis (fig. 12), which is present in most (e.g., *Concornis*, *Propteryx*) but not all enantiornithines (Chiappe and Walker, 2002). The two pubes of GMV-2158 and GMV-2159 are not fused to one another. The condition in GMV-2156/NIGP-130723 cannot be ascertained from the impression of these bones.

ISCHIUM: The left ischium is almost completely preserved in GMV-2158, although it appears to be slightly dislocated caudoventrally (fig. 12). Portions of the caudal margin of the right element can be seen lying under the main body of its left counterpart and the synsacrum. The ischium is roughly 65% the length of the pubis, a proportion that falls within the range known for other enantiornithines (Chiappe and Walker, 2002). A short iliac process and a slightly longer pubic process outline the ischiadic contribution (*Corpus ischii*) to the acetabulum (fig. 12). The relative lengths of these processes are comparable to those of other basal birds and nonavian maniraptoriforms (Norell and Makovicky, 1997; Burnham et al., 2000). Each of these processes bears a terminal facet for their respective articulations with the pubis and the ischiadic peduncle of the ilium. The ischiadic shaft (*Ala ischii*) is straight, becoming slightly narrower toward its distal end (*Processus terminalis ischii*). Although the end of the left ischium of GMV-2158 appears to be missing, the tapering caudal margin of the right element suggests that the ischium tapered

distally (fig. 12). As in other basal birds (Chiappe et al., 1999), the cranial margin of the shaft shows no evidence of a well-developed obturator process (*Processus obturatorius*), a condition contrasting that of most nonavian maniraptorans (Hutchinson, 2001). However, the caudal margin of the left ischium of GMV-2158 bears a prominent process centered on the proximal half. This proximal dorsal process has been recognized in a variety of basal birds (Forster et al., 1998; Chiappe et al., 1999; Zhou and Zhang, 2003) including enantiornithines (Chiappe and Walker, 2002) and some nonavian theropods (Novas and Puerta, 1997; Burnham et al., 2000). This structure has been interpreted as the attachment area for an ilio-ischiadic membrane, which in modern birds closes caudally the ilio-ischiadic fenestra and partially supports the origin of the *M. ischiofemoralis* (Hutchinson, 2001).

Pelvic Limb

FEMUR: The femur is nearly straight in all the studied juveniles (figs. 3–7). In lateral view, the greater trochanter has a round contour. The trochanteric crest (*Crista trochanteris*) is continuous with the greater trochanter (*Trochanter femoris*), without any notch separating the latter from a primitive lesser trochanter—the absence of an individualized lesser trochanter appears to be a synapomorphy of all birds except *Archaeopteryx*. On the left femur of GMV-2158, immediately distal to the greater trochanter, the proximolateral surface grades into a wide depression that occupies most of the proximal lateral end of this bone (fig. 12). Although most of this depression is broken, its proximal margin is clearly visible. We interpret this as the proximal margin of the posterior trochanter, presumably the attachment of the *M. iliofemoralis* (Hutchinson, 2001). The development of this structure approaches the strong development seen in other enantiornithines (Chiappe and Walker, 2002).

The distal end of the right femur (*Extremitas distalis femoris*) of GMV-2158 and the left element of GMV-2159 are exposed caudally. These femora lack a distinct popliteal fossa (*Fossa poplitea*). This area, however, is

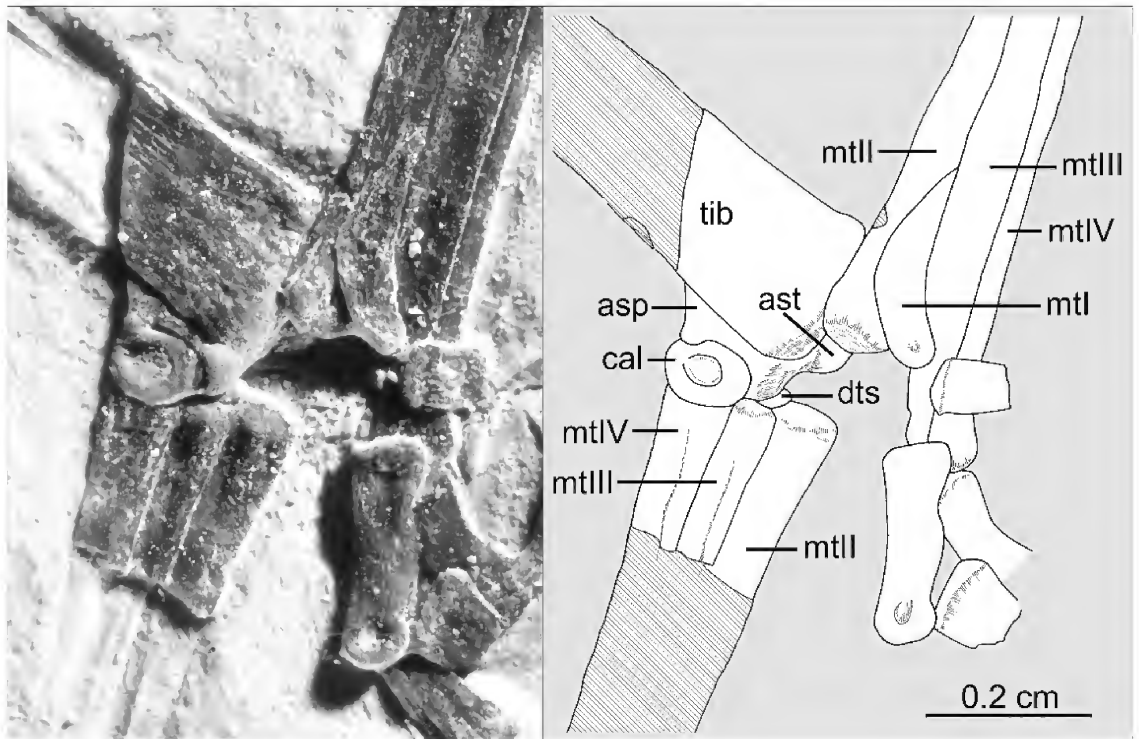


Fig. 18. Photograph and interpretive drawing of the tarsus of GMV-2158. Abbreviations: asp, ascending process of astragalus; ast, astragalus; cal, calcaneum; dts, distal tarsal. Other abbreviations as in figure 3.

depressed with respect to the condylar region. In contrast to the ridge that bounds distally the popliteal fossa and connects both condyles in adult enantiornithines and more advanced birds (Chiappe, 1996a), only a low rim joins both condyles below the popliteal area. The right femur of GMV-2159 lacks a patellar groove (*Sulcus patellaris*), a primitive condition shared by Enantiornithes and several other basal birds (Chiappe, 1996a, 2002). The distal ends of the femora of GMV-2158 show no evidence of a lateral ridge projecting caudally, a feature present in certain enantiornithines (e.g., *Neuquenornis*; Chiappe and Calvo, 1994; Chiappe and Walker, 2002). The laterodistal end of the femur appears to lack a tibiofibular crest (*Crista tibiofibularis*). This division between the articulations of the tibia and fibula with the lateral condyle (*Condylus lateralis*) is also minimally developed in enantiornithines and more basal taxa (Chiappe, 1996a).

TIBIA: The straight tibia is roughly 20–25% longer than the femur in all the Chinese

juveniles here studied (figs. 3–7). As in other skeletal elements, this bone is best preserved in GMV-2158. Its proximal articular surface (*Caput tibiae*) is flat. The cnemial crests (*Crista cnemialis cranialislateralis*) are not developed; the proximal end does not show any significant expansion with respect to the width of the shaft (*Corpus tibiotarsi*). Tibiotarsi with minimal development of cnemial crests are characteristic of enantiornithines (Molnar, 1986; Chiappe, 1993, 1996a; Chiappe and Walker, 2002) and some other basal birds (e.g., *Confuciusornis*, *Sapeornis*). A fibular crest (*Crista fibularis*) is also not apparent. Distally, the tibia is not fused to the proximal tarsals (*Ossa proximalia tarsi*), a condition clearly visible in GMV-2158 (fig. 18) and GMV-2159. The proximal tarsals, however, fuse to the tibia in the adults of confuciusornithids, enantiornithines, and more advanced birds; the complete fusion of proximal tarsals and tibia appears to be a synapomorphy of Pygostylia (the common ancestor of *Confuciusornis* and Neornithes

plus all its descendants [Chiappe, 2002]), although it may be synapomorphic of a more inclusive clade depending on the phylogenetic placement of *Sapeornis* (Zhou and Zhang, 2002; Chiappe, 2007).

FIBULA: Only the proximal end of the left fibula of GMV-2158 is preserved. This bone is exposed in lateral view. The proximal end of the fibula is much smaller than that of the tibia. Although the preserved portion comprises the entire segment proximal to the splintlike spine, no tubercle for the *Musculus iliofibularis* (*Tuberculum musculus iliofibularis*) can be seen.

TARSUS: The left tarsal bones (*Ossa tarsi*) are preserved in GMV-2158 (fig. 18), and the medial surface of the right astragalus (*Tibiale*) is present in GMV-2159. The calcaneum (*Fibulare*) is not fused to the astragalus. These two proximal tarsals fuse, at least partially, to one another in the adults of most Mesozoic birds, although the nature of their articulation remains unclear in *Archaeopteryx*. The tibia of GMV-2158 covers most of the astragalus. However, it can be seen that the astragalus is much larger than the calcaneum (fig. 18). Although viewed in laterocaudal view, a prominent ascending process is visible crushed against the lateral side of the tibia of GMV-2158. The medial edge of this tall process is also visible in GMV-2159. Although the ascending process of the astragalus is fused to the tibia in the adults of most basal birds, it is individualized in *Archaeopteryx* (Mayr et al., 2005), *Rahonavis* (Forster et al., 1998), *Jeholornis* (Zhou and Zhang, 2002), and *Vorona* (Forster et al., 1996). This ossification is clearly homologous to the ascending process of nonavian theropods (see Implications for Ontogenetic Change in Basal Birds, below). The calcaneum is round and its lateral surface is excavated by a circular fossa. A small central fossa also excavates the medial surface of the astragalus of GMV-2159.

Only one distal tarsal (*Os tarsi distale*) is preserved in GMV-2158 (fig. 18). This small, round bone can be seen between the astragalus and the proximal end of metatarsals (*Os metatarsale*) II and III. Among Mesozoic birds, free distal tarsals have been preserved in very few instances. These bones remain unfused to the metatarsals in adult specimens

of *Archaeopteryx* (Wellnhofer, 1992) and *Rahonavis* (Forster et al., 1998). Free tarsals were also reported for the Spanish Early Cretaceous *Iberomesornis* (Sanz and Bonaparte, 1992), although this claim was refuted by Sereno (2000), who argued that the proximal ends of the metatarsals of this bird were fused to one another and to the distal tarsals. While the presence of these individual ossifications in *Iberomesornis* is inconclusive, Sereno's (2000) assertion that the metatarsals of this taxon were proximally fused is undoubtedly mistaken.

METATARSUS: Although much of the metatarsus (*Ossa metatarsalia*) is preserved in all studied early juveniles, there is no evidence of metatarsal V. We do not regard this as evidence for the loss of this ossification, however, as the feet of these fossils are not favorably exposed.

The metatarsals are not proximally fused to one another, a condition best observed in GMV-2158 (figs. 18, 19). The lack of proximal metatarsal fusion of GMV-2158 contrasts with Hou and Chen's (1999) description of the foot of NIGP-130723. Our observations of this slab (fig. 6), however, failed to confirm the fusion proposed by Hou and Chen (1999). In fact, the impression of the metatarsus of NIGP-130723 seems to indicate that metatarsals II–IV were unfused throughout their length. The proximal width of the metatarsus of GMV-2158 is approximately the same as the distal one (fig. 19). Metatarsals II–IV of GMV-2158 have roughly the same width. The apparent thinness of metatarsal IV in the right foot of this specimen is misleading (figs. 18, 19); much of this bone is clearly underlying metatarsal III. The subequal sections of these metatarsals differ from the condition typical of many other enantiornithines, in which the cross section of metatarsal IV is distinctly thinner than those of other metatarsals (Chiappe, 1992, 1993, 1996a). This feature is often difficult to interpret in specimens preserved in two dimensions, however, because this character refers to the cross-section of each of these bones, not necessarily to their width in dorsal or plantar view. Thus, Ji and Ji's (1999) claim of a metatarsal IV thinner than the remaining metatarsals of GMV-2156 is hard to evaluate by the impressions of these

bones. Unfortunately, the preservation of the feet of NIGP-130723 does not provide any help in determining the presence or absence of this condition, and metatarsal IV is not exposed in MGV-2159.

A distinct feature of GMV-2158 is the different distal extension of metatarsals III and IV, on the one hand, and metatarsal II on the other hand (fig. 19). Although the distal ends of metatarsals IV and III reach approximately the same level, that of metatarsal II falls substantially more proximal; that is, metatarsal II is nearly 10% shorter. Unfortunately, this peculiar condition, otherwise known for the contemporaneous *Vescornis* from Hebei Province (China; Zhang et al., 2004) and the bizarre Late Cretaceous *Lectavis* of northwestern Argentina (Chiappe, 1993) cannot be ascertained in the remaining Chinese Early Cretaceous juveniles. The trochleae (*Trochlea metatarsi*) of metatarsals III and II are formed by well-developed ginglymus. The latter trochlea is kidney-shaped in palmar view, with a concavity at its center.

A short metatarsal I is preserved in both feet of GMV-2158 and GMV-2159. In GMV-2158, the distal end of the right metatarsal I lies at the same level as the trochlea of metatarsal II. This location, however, is likely displaced from its original articulation on the medial surface of metatarsal II, visible in the left foot of this specimen (fig. 19) as well as in both feet of GMV-2159. In the feet of the latter, the distal end of metatarsal I is slightly proximal to the trochlea of metatarsal II (fig. 5). Metatarsal I is laterally compressed and somewhat J-shaped in medial view, with a rounded distal facet, projected medially (fig. 19). This morphology approaches that of enantiornithine avisaurs such as *Neuquenornis* and *Soroavisaurus australis* (Chiappe, 1993). This condition should not be confused with the J-like appearance of the metatarsal I of some other Mesozoic birds (e.g., *Confuciusornis*, *Changchengornis*), which is only apparent when the metatarsal is viewed in dorsal or palmar view.

PEDAL PHALANGES: With the exception of the hallux (digit I), digital identification of GMV-2158 is complicated by the fact that not all phalanges remained in articulation. Our interpretation is presented in figure 19.

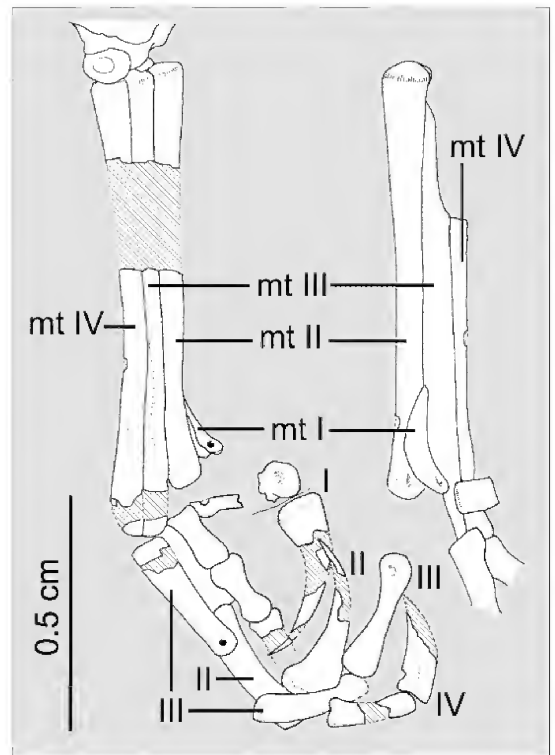


Fig. 19. Interpretive drawings of the pes of GMV-2158 and GMV-2159. Abbreviations as in figures 3 and 5.

According to this interpretation, the three phalanges (*Phalanges proximales et intermediae*) of digit II are preserved in the left foot. The intermediate phalanx is roughly 25% longer than the proximal phalanx. Digit II bears a large claw (*Phalanx unguialis*). The three pre-ungual phalanges of digit III are also preserved in the left foot. The proximal phalanx is the longest of this digit, and the second phalanx is somewhat shorter than the third. The first two phalanges of digit IV are short and subequal in length. The third phalanx is very incomplete, but the fourth is approximately 20% longer than the proximal ones. The hallux is opposable. Its unguinal phalanx is as large as that of digit II. None of the unguinal phalanges bears distinct flexor tubercles (*Tuberculum flexorium*); collateral fossae (*Fovea ligamentum collateralis*) can be seen in some of the nonungual phalanges. Phalangeal identification is clearer in GMV-2159 (fig. 5). In general, the shape and relative

proportions of these phalanges agree with those of GMV-2158. Nothing can be confidently stated about the foot of either GMV-2156/NIGP-130723 beyond the fact that its hallux was also opposable (Ji and Ji, 1999) (figs. 6, 7).

PLUMAGE

Faint impressions of a few primary feathers (*Remiges primarii*) can be seen attached to the hand of GMV-2158 and along the sides of its caudal vertebrae (figs. 2, 3). Feather impressions are also visible in both GMV-2159 and GMV-2156/NIGP-130723 (Hou and Chen, 1999; Ji and Ji, 1999), in which the vanes of these feathers are tinted with a darker color (figs. 4, 6, 7). It seems apparent that to some extent the coloring of these feathers has been artificially added, presumably by the farmers who discovered the specimen. However, natural impressions of pennaceous primary and secondary remiges (*Remiges secundarii*) attached to the hand and ulna, respectively, are distinguishable in both GMV-2159 and GMV-2156/NIGP-130723. Although no other details can be seen in the flight feathers of the three juveniles, the extensive pitting/grooving of the periosteum combined with the presence of pennaceous distal remiges suggests that these birds fledged their wing feathers very early during postnatal development, a fact that hints at precocial or highly precocial strategies of hatchling development (Chinsamy and Elzanowski, 2001; Chiappe and Dyke, 2002). The fact that fledging substantially predated skeletal maturation also suggests that these juveniles continued to grow in size for a prolonged period after fledging, an inference that is concordant with the available histological evidence on enantiornithines (Chinsamy et al., 1995; Chinsamy, 2002). It is more difficult to determine, however, whether they were capable of flying and, if so, to what degree. The skeletal structure of the Chinese juveniles—in particular, the small bony sternum—indicates that despite being fledged, they probably did not have the flying capabilities of the adults. A pair of long tail feathers (*Rectrices*) projects from the pygostyle of GMV-2159 (fig. 4). However, the authenticity of these feathers cannot be confidently established.

TAXONOMIC IDENTIFICATION

Beyond slight differences in size (table 2), the morphology of GMV-2158, GMV-2156/NIGP-130723, and GMV-2159 is remarkably similar. The only apparent morphological difference between these specimens is in the shape of the main body of the sternum, which in GMV-2156/NIGP-130723 has a rhomboid appearance and in GMV-2158 and GMV-2159 is more semicircular (figs. 3, 5–7). Given the overall similarity of these specimens and the fact that such a minor difference in sternal morphology may be either a preservational artifact or a result in differences in their degree of ossification, we find no basis for discriminating these roughly coeval specimens into separate taxa.

The juvenile nature of GMV-2158, GMV-2156/NIGP-130723, and GMV-2159 makes their inclusion in a phylogenetic analysis problematic—previous phylogenetic work on early birds has been largely based on fossils representing adult ontogenetic stages. Nonetheless, the presence of several derived characters supports the identification of these immature specimens as Enantiornithes (all taxa closer to *Sinornis* than to Neornithes) and Euenantiornithes (all taxa closer to *Sinornis* than to *Iberomesornis*), the most diverse clade of the Cretaceous Enantiornithes (Chiappe, 2002). Although the monophyly of Enantiornithes has been consistently supported (Chiappe, 1991, 1995, 1996a, 2002; Chiappe and Calvo, 1994; Zhou, 1995a, b; Kurochkin, 1996; Chiappe and Walker, 2002; Zhou and Zhang, 2002; Clarke et al., 2006; You et al., 2006), the interrelationships of the group remain largely unresolved. Consequently, synapomorphies diagnosing either the entire clade or its subsets substantially vary from one phylogenetic analysis to another. On the basis of the phylogenetic analyses of Chiappe (2002) and Chiappe and Walker (2002), the synapomorphies of Enantiornithes recognizable in the juveniles include the presence of a furcula with a well-developed hypocleideum, an ulna nearly equivalent to or longer than the humerus, and a metacarpal III projecting distally more than metacarpal II. The juveniles also exhibit several other synapomorphies that the phylogenetic studies of Chiappe (2002) and Chiappe and Walker

(2002) have regarded as diagnostic of Euenantiornithes: a broad and deep fossa on the dorsal surface of the coracoid, the ventral margin of the furcula distinctly wider than its dorsal margin, the presence of a prominent and cranioventrally projecting bicipital crest of the humerus, a radius with an extensive longitudinal groove on the ventrocaudal surface of the shaft, and a hypertrophied posterior trochanter on the lateral surface of the proximal end of the femur. If the specimens here described can be safely placed within Euenantiornithes, their identification as members of a particular euenantiornithine taxon is complicated by the fact that (1) all valid euenantiornithine species are based on adult holotypes, (2) growth series of these birds are unknown, and (3) the new juveniles do not show any autapomorphy that could support their placement within any enantiornithine species.

At least nine valid enantiornithine species—all from Early Cretaceous age—have been described from China: *Protopteryx fengningensis* (Zhang and Zhou, 2000), *Longirostravis hani* (Hou et al., 2004), and *Vescornis hebeiensis* (Zhang et al., 2004) from Hebei Province; *Boluochia zhengi* (Zhou, 1995b), *Longipteryx chaoyangensis* (Zhang et al., 2001), *Eoenantiornis buheleri* (Hou et al., 1999), *Sinornis santensis* (Sereno and Rao, 1992), and *Eocathayornis walkeri* (Zhou, 2002) from Liaoning Province; and *Otogornis genghisi* (Hou, 1994) from Inner Mongolia. The known specimens of all these species are substantially larger than the juveniles here reported. The juveniles can be easily discriminated from *Protopteryx*, which exhibits the primitive conditions of having a manual digit I projecting distally more than metacarpal II and the intermediate phalanx of manual digit II longer than its proximal phalanx. In fact, these and other primitive characters suggest that the enantiornithine *Protopteryx* may fall phylogenetically outside Euenantiornithes (Zhang and Zhou, 2000), although such a statement will have to be tested against robust and well-resolved hypotheses of enantiornithine interrelationships. The new juvenile specimens can also be differentiated from the long-snouted *Longipteryx* (Zhang et al., 2001) and *Longirostravis* (Hou et al., 2004) in which the teeth are

restricted to the tip of the rostrum and their upper dentition is limited to the premaxilla. *Longipteryx* also exhibits the primitive condition of having a manual digit I projecting more distally than metacarpal II and a much more elongated wing (the humerus/femur ratio of *Longipteryx* is 30–45% larger than those of the juveniles). Although known from a single incomplete specimen, *Boluochia* (Zhou, 1995b) possesses a hooked premaxilla that makes this species another unlikely candidate for the juveniles.

The new juveniles are more difficult to discriminate from *Eoenantiornis*, *Vescornis*, *Sinornis*, *Eocathayornis*, or the poorly known *Otogornis*, for which only elements of the thoracic limb and girdle are available. Just like the early juveniles here described, *Eoenantiornis* is from the Yixian Formation of Liaoning Province. Morphologically, however, this taxon differs from the juveniles in having a much higher premaxilla and a knife-like ischium with a concave caudal margin. *Vescornis* also comes from sediments interpreted as part of the Yixian Formation, although located within Hebei Province (the stratigraphic correlation is therefore more tenuous; Zhang et al., 2004). This taxon resembles GMV-2158 in the subequal distal extension of metatarsals III and IV but it differs markedly by its vestigial manual claws and proportionally shorter pygostyle (Zhang et al., 2004), even if it is unclear how the length of the pygostyle is affected by allometry. *Sinornis* and *Eocathayornis* are known from the Jiufotang Formation (ca.120 mya; He et al., 2004), a stratigraphic unit estimated to be five million years younger than the Yixian Formation. As for *Vescornis*, the ratio between the pygostyle and the tarsometatarsus of *Sinornis* appears to be much smaller than that of the juveniles, but this comparison cannot be established with *Eocathayornis* for which the legs and tail are missing. Although *Sinornis* and *Eocathayornis* occur in substantially younger deposits than those containing the early juveniles here described, the problem of discriminating them on the basis of age alone becomes more critical when considering that several other vertebrate taxa (genus or species level) have been recorded in both the Yixian and Jiufotang Formations (Chang et

al., 2003; Zhou et al., 2003). The age of the Ejinholo Formation, from which *Otogornis* originates, is poorly known, although it has been regarded as early–middle Early Cretaceous (Bureau of Geology and Mineral Resources of Nei Mongol Autonomous Region, 1991), something that suggests an age closer to the Yixian Formation than to the Jiufotang Formation. Regardless of its age, the incompleteness of the only known specimen of *Otogornis* makes difficult comparisons with the juveniles.

IMPLICATIONS FOR ONTOGENETIC CHANGE IN BASAL BIRDS

Ontogenetic studies provide important evidence for understanding organismal character evolution and phylogeny. Information on early developmental stages often helps the formulation of homology statements, in particular those involving structures for which topographical relationships are drastically modified through ontogeny (Witmer, 1995). GMV-2158, GMV-2156/NIGP-130723, and GMV-2159 differ from adult euanantiornithines in several features, most notably in the absence of a pneumotricipital fossa of the humerus, the small size of the sternum, and the unfused condition of the carpus and tarsus (i.e., distal carpals and tarsals not fused to metacarpals and metatarsals, respectively)—these differences are here interpreted as ontogenetic variation. The information provided by these juvenile specimens clarifies important aspects of basal avian ontogenetic development. These are discussed separately below.

CARPAL DEVELOPMENT: Ostrom's (1969) seminal study of the Early Cretaceous theropod *Deinonychus antirrhopus* recognized a large distal carpal (misinterpreted in his study as a proximal carpal, the radiale) of semicircular aspect as a fundamental element of the dromaeosaurid wrist. In subsequent studies, Ostrom (1973, 1975, 1976) proposed the homology between this “semilunate” carpal and a similar element of the wrist of *Archaeopteryx* (Wellnhofer, 1974; 1992, 1993; Wellnhofer and Röper, 2005), a hypothesis that has been frequently highlighted by studies favoring the origin of birds from manirapto-

ran theropod dinosaurs (e.g., Gauthier, 1986; Witmer, 1991; Padian and Chiappe, 1998; Chiappe, 2004, 2007; Weishampel et al., 2004). Although acknowledging the striking similarity between the semilunate carpal of *Deinonychus* and *Archaeopteryx* (fig. 20), Martin (1983) dismissed Ostrom's proposed homology simply on the basis of the misinterpretation of this element as the radiale, a rather circumventing argument since it was obvious that Ostrom was comparing the same element (regardless of the name he used) of the carpus of these taxa. In the following years, Ostrom's terminological mistake was rectified (see Padian and Chiappe, 1998) and a similar semilunate carpal (often considered to be derived from the fusion of distal carpals 1 and 2; Chure, 2001) was documented in a great variety of nonavian maniraptoran theropods (see Chure [2001] for its possible presence in other nonavian theropods) including other dromaeosaurids (Gauthier, 1986; Currie and Peng, 1993; Norell and Makovicky, 1999; Xu et al., 1999a; Burnham et al., 2000), oviraptorosaurs (Barsbold et al., 1990; Ji et al., 1998; Zhou et al., 2000), troodontids (Russell and Dong, 1993), and therizinosaurids (Xu et al., 1999b).

Until the present study, comparisons between the semilunate carpal of nonavian theropods and those of birds were restricted to *Archaeopteryx* (Wellnhofer, 1974; 1992, 1993; Wellnhofer and Röper, 2005) and to embryonic stages of its extant counterparts (Hinchliffe, 1985). Limitations in evidence coupled with minor topological differences and the apparent mismatch in the number of centers of ossification of the semilunate carpal (two in nonavian theropods and one in birds) have led to additional questioning of the homology initially proposed by Ostrom (Zhou and Martin, 1999; Martin, 2004). The unfused metacarpus of GMV-2158 and other early juveniles here reported offer an additional source of evidence for assessing the homology of the semilunate carpal of nonavian theropods and birds. Although the position of the semilunate carpal in these juveniles echoes the topological difference highlighted by Zhou and Martin (1999), namely that in *Archaeopteryx* and modern birds the semilunate caps the proximal end of

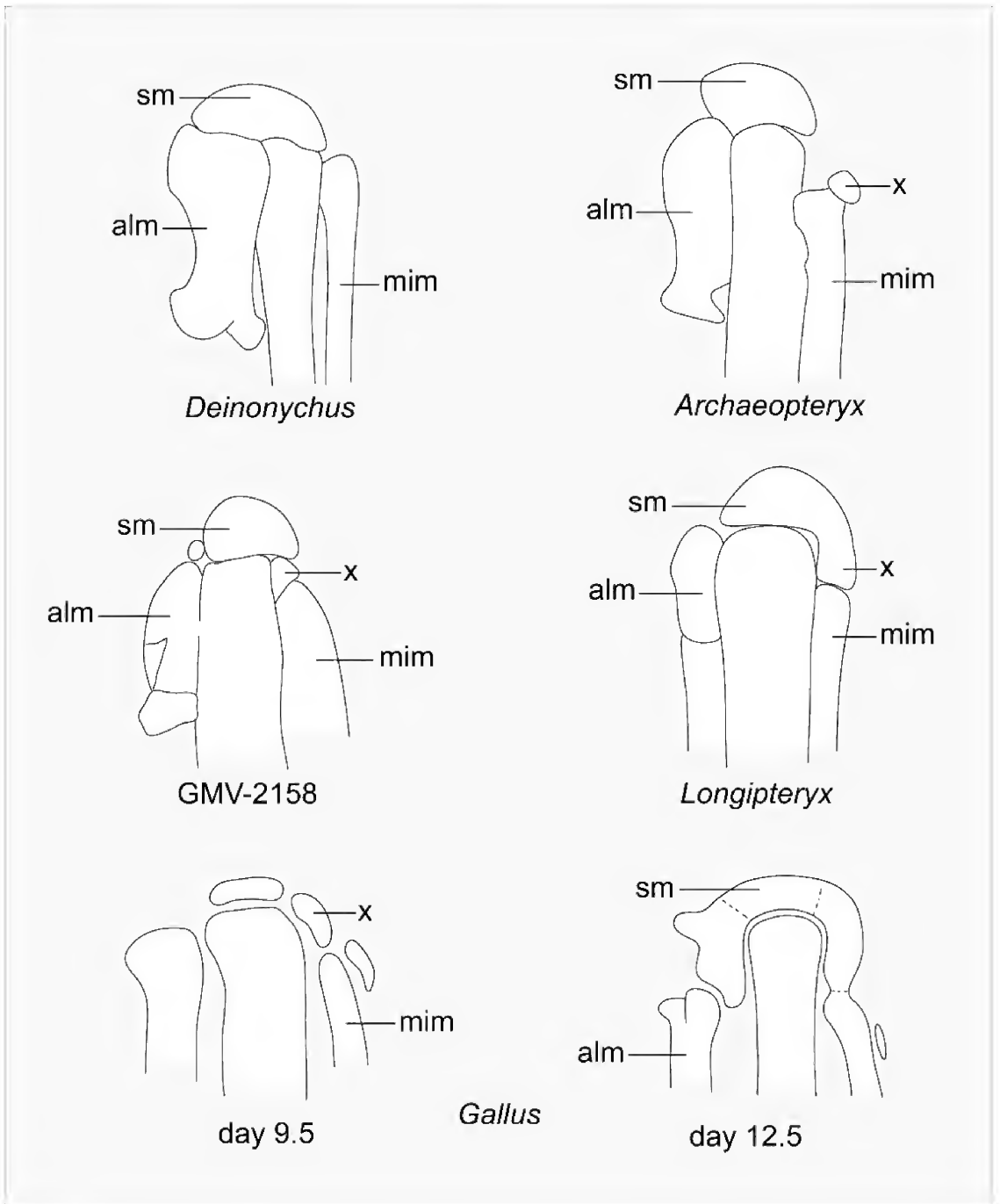


Fig. 20. Comparisons of the carpus of a nonavian theropod (*Deinonychus antirhopus*), *Archaeopteryx lithographica*, GMV-2158, the enantiornithine *Longipteryx chaoyangensis*, and the embryo of a modern bird (*Gallus gallus*). Abbreviations as in figure 15.

the alular metacarpal in lesser degree than it does the major metacarpal (fig. 20), the remarkable similarity between these enantiornithine semilunates and those of nonavian maniraptorans supports the homologous nature of this structure—the reduced articulation between the semilunate and the alular metacarpal may be a derived condition of birds. Likewise, the use of variation in the number of ossification centers for assessing the homologies of adult endochondral bones has been seriously questioned (Rieppel, 1996).

The morphology of GMV-2158 and the other early juveniles here reported also highlights the conservatism of the developmental pathway of the wrist of birds. The morphology of these juveniles not only resembles that of *Archaeopteryx* in that it consists of four carpals—the proximal ulnare and radiale, and the distal semilunate and carpal X (see Hinchliffe, 1985; Zhou and Martin, 1999)—but also in that the proximal end of the minor metacarpal lays more distally than the proximal end of the major metacarpal (fig. 20). Further evidence of this developmental conservatism comes from comparisons between GMV-2158 and the Early Cretaceous enantiornithine *Longipteryx* (Zhang et al., 2001). In *Longipteryx*, the semilunate carpal—unfused to the proximal ends of the alular, major, and minor metacarpals—bears a latero-distal projection that likely abutted the lateral side of the major metacarpal and articulated with the minor metacarpal, which proximally ends distal to the proximal end of the major metacarpal (fig. 20). The condition in *Longipteryx* is therefore intermediate between the design of GMV-2158 and that of other adult enantiornithines, in which the semilunate carpal and proximal metacarpal ends are fused to one another, thus presumably incorporating the “carpal X” into the proximal end of the carpometacarpus. This evidence suggests that the carpometacarpus of enantiornithines followed the same developmental trajectory—the semilunate incorporated the carpal X prior to these bones becoming fused to the proximal ends of the metacarpals—characteristic of modern birds (fig. 20).

TARSAL DEVELOPMENT: Although the postnatal fusion of the proximal tarsals and distal

tibia to form the avian tibiotarsus has long been known, some of the specific homologies of this compound bone have remained contentious (Baumel and Witmer, 1993). One of these controversies involves the homology of the cranioproximal projection of the proximal tarsals known as the ascending process. Huxley (1870) pioneered the comparisons between the ascending processes of birds with those of nonavian theropods during his quest for the origin of birds (Witmer, 1991; Padian and Chiappe, 1998). Huxley (1870) was confident that the ascending process of the avian tarsus was, like that of nonavian theropods, part of the astragalus. Following this observation, the similarity of the proximal tarsals of nonavian theropods and birds (fig. 21) led other researchers to regard the ascending process as part of the astragalus and to support the homology proposed by Huxley (e.g., Baur, 1883; Wells and Long, 1974; Ostrom, 1976; Gauthier, 1986; Forster et al., 1996, 1998; Zhou and Zhang, 2002; Mayr et al., 2005). Indeed, the similarities between the ascending process of the astragalus of nonavian theropods and birds are striking. The enlarged astragalus of many of these dinosaurs (e.g., ornithomimids, oviraptorids, dromaeosaurids) is characterized by the presence of a tall and laminar ascending process that covers much of the cranial surface of the distal end of the tibia and extends laterally to the border of the latter. In spite of this, the homology between the ascending process of the astragalus of nonavian theropods and birds has continued to be rejected by those contesting the theropod origin of the latter (e.g., Heilmann, 1926; Martin et al., 1980; Martin, 1991, 2004; Feduccia, 1999). Current arguments against this homology have been centered around the nature of the ascending process of birds, namely whether it is a proximal extension of the body of the astragalus (e.g., Ostrom, 1976; Forster et al., 1996; Mayr et al., 2005) or an alleged independent ossification—termed “pretibial bone”—associated primarily with the calcaneum (Martin et al., 1980; Martin, 1983, 2004).

McGowan's (1984) study of X-rayed and double-stained embryos and neonates documented independent ossifications fusing during postnatal phases to the calcaneum and

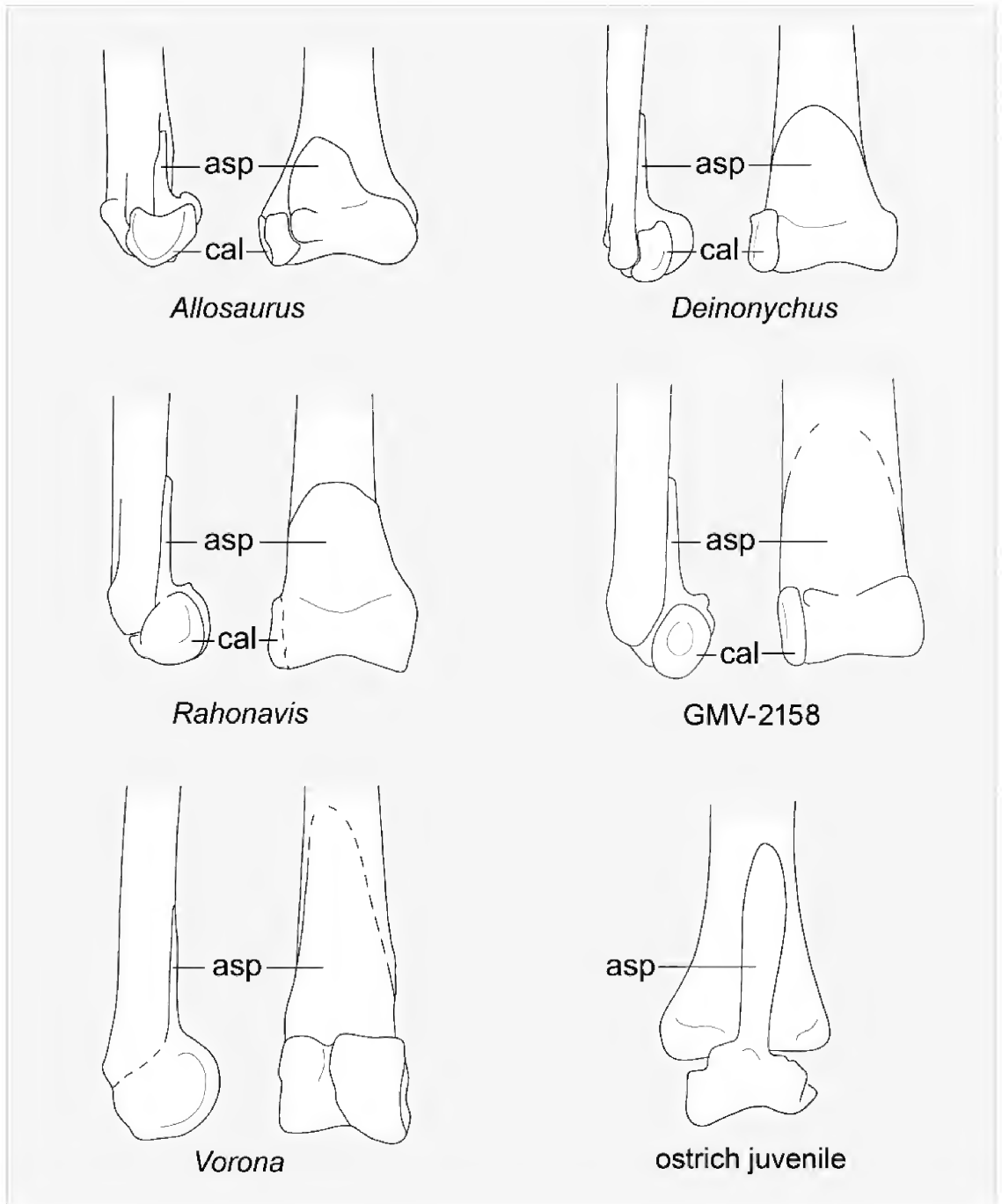


Fig. 21. Comparisons of the tarsus of nonavian theropods (*Allosaurus fragilis* and *Deinonychus antirhopus*), basal birds (*Rahonavis ostromi* and *Vorona berivotrensis*), GMV-2158, and a juvenile modern bird (*Struthio camelus*). Abbreviations as in figure 18.

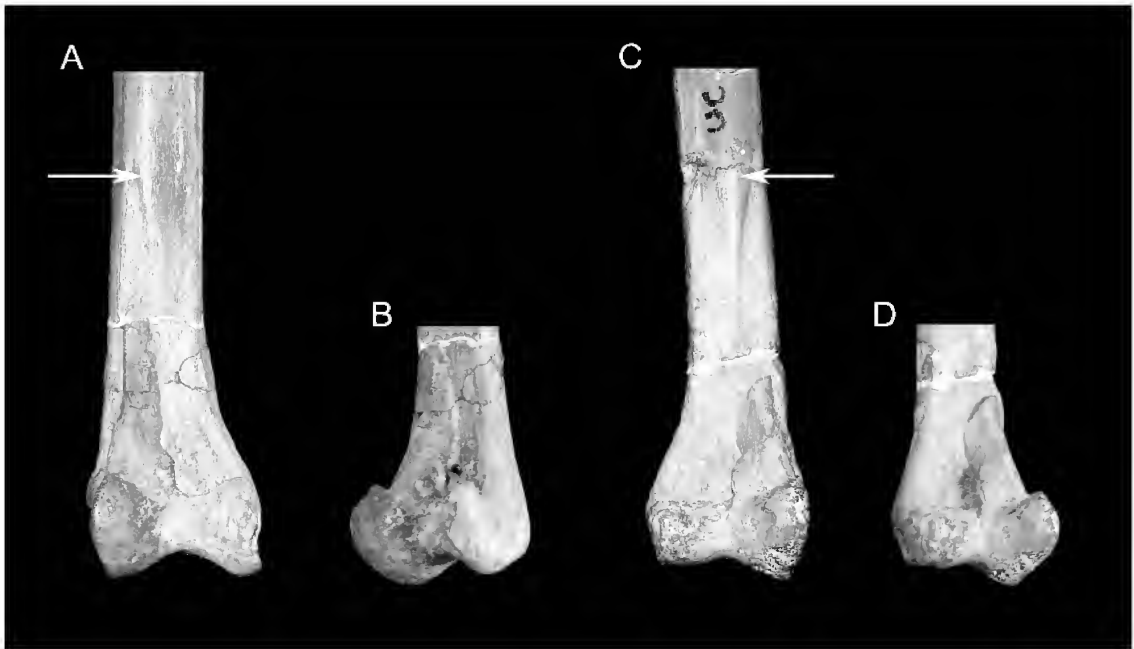


Fig. 22. Right (A, B) and left (C, D) distal tibiotarsi of a juvenile specimen of *Baptornis advenus* (FMNH-UC-395) in cranial (A, C) and mediocranial (B, D) views. Note the absence of a suture separating the tall ascending process (mostproximal extension marked by arrows) from the astragalus' body.

astragalus in neognath and paleognath birds, respectively, thus demonstrating the existence of an ossified ascending process of the astragalus and a pretibial bone. Additional studies revealed that the pretibial bone ossifies from a cartilaginous process that originates in the astragalus (McGowan, 1985) and that the center of ossification of the astragalus process and the pretibial bone is the same one. On the basis of these observations, McGowan (1985) regarded the association of this ossification to the calcaneum of neognaths as a derived condition of these birds and defended the homology between the ascending process of nonavian theropods and birds. Subsequent discoveries documented the presence of an ascending process with a broad connection to the main body of the astragalus in a number of adult individuals of basal birds (e.g., Forster et al., 1996, 1998; Zhou and Zhang, 2002; Mayr et al., 2005), but some (e.g., Martin, 1991; 2004; Feduccia, 1999) have continued to reject the proposed homology of the ascending process of the astragalus of nonavian theropods and birds. One fossil seemingly supporting such dismissal was a juvenile specimen

of the hesperornithiform *Baptornis advenus* (FMNH-UC-395) in which the proximal tarsals are only partially coossified to the tibia. Martin and Bonner (1977) reported the existence of a pretibial bone, separated from the astragalus, in this specimen. Nonetheless, our examination of FMNH-UC-395 questions Martin and Bonner's (1977) interpretation of this structure as a pretibial bone. Although much of the tall and slender ascending process is separated from the tibia by a distinct suture in FMNH-UC-395 (fig. 22), in neither the left or right element of this specimen is there evidence of a suture between this process and the main body of the astragalus. The process simply exhibits a basal, transversal constriction and a groove separating it from the condylar region of the astragalus, a plesiomorphic condition typical of nonavian maniraptoran theropods (P. Makovicky, personal comm.). Continuity between the process and the main body of the astragalus is best shown on the mediobasal border of the process (fig. 22). Because the process is evidently fused to the main body of the astragalus, we find no reason to think that it corresponds to a differ-

ent bone or to assume that it is a pretibial bone.

The structure of the ankle of GMV-2158 sheds additional light on the homology of the ascending process of the avian tarsus. As described earlier, the left proximal tarsals of this specimen are not fused between them or to the tibia (fig. 18). Although somewhat compressed and exposed in laterocaudal view, the main body of the astragalus projects proximally into a process that clearly braced the cranial surface of the tibia. While a distinct suture completely separates the calcaneum from the main body of the astragalus, no suture is visible between the latter and its proximal process. Undoubtedly, this proximal process is the ascending process of GMV-2158, which was already fused to the astragalus. Therefore, the evidence provided by the early postnatal development of the tarsus of GMV-2158 documents the complete disassociation between the ascending process and the calcaneum of enantiornithine birds and, once again, it lends support to the hypothesis that the avian astragalus is characterized by a proximal projection homologous to the ascending process of the astragalus of nonavian theropods.

CONCLUSIONS

This study provides the first detailed characterization of the morphology of early juvenile enantiornithines and describes morphologies previously unrecorded for this group of Cretaceous birds. Taxonomically, this study recognizes the holotype of "*Liaoxiornis delicatus*" as an early juvenile that cannot be discriminated from all other enantiornithines and it recommends that this species is considered as a *nomen vanum*.

The morphological evidence here presented clarifies aspects of the development and character evolution of enantiornithines. In particular, it provides new evidence for comparing the highly modified carpus and manus of birds, which components are fused into compound bones, and those of nonavian theropods. The anatomy of the juveniles here studied supports the homology of the semilunate carpal and ascending process of the astragalus of these animals, and it highlights the evolutionary conservatism that has char-

acterized the development of the skeleton of the wrist and ankle of theropod dinosaurs (including birds).

The early juveniles here described document that among enantiornithines, fledging may have substantially predated skeletal maturation. The presence of fledged wings in these juveniles also suggests a highly precocial developmental strategy (Elzanowski, 1981; Chinsamy and Elzanowski, 2001)—although not necessarily the superprecocial strategy of living megapods (see Chiappe and Dyke, 2006; Chiappe, 2007)—for the hatchlings of these and other basal birds.

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