AMERICAN MUSEUM
*Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3420, 19 pp., 12 figures, 1 table October 29, 2003

# An Early Ostrich Dinosaur and Implications for Ornithomimosaur Phylogeny

QIANG JI,[1] MARK A. NORELL,[2] PETER J. MAKOVICKY,[3] KE-QIN GAO,[4]
SHU'AN JI,[4] AND CHONGXI YUAN[5]

## ABSTRACT

A new ornithomimosaur from the Yixian Formation of Liaoning Province People's Republic of China is described. These beds are near the Jurassic-Cretaceous boundary. This specimen is interesting because it has several primitive characters for ornithomimosaurs such as teeth and a short first metacarpal. This taxon is placed in a phylogenetic analysis of Coelurosauria and shown to be near the base of the ornithomimosaur clade. Using this phylogeny we comment on the biogeographic history of this group.

## INTRODUCTION

Spectacular fossils from China's Liaoning Province have become commonplace in the last few years (Ji and Ji, 1996; Ji et al., 1999; Hou, 1997; Gao et al., 2000). However, most of these are nearly two-dimensional fossils found in paper shales that represent ancient pond and lake deposits. Although beautiful and often preserving soft-part anatomy, these fossils can be frustrating because of a lack of three-dimensional preservation. Furthermore, theropod remains from Liaoning only include the maniraptoran groups Dromaeosauridae (Xu et al., 1999b, 2000), Oviraptorosauria (Ji et al., 1998, Xu et al., 2002a), Troodontidae (Xu et al., 2002b), and Segnosauridae (Xu et al., 1999a) and the more

[1] Department of Earth Sciences, Nanjing University, 22 Hankou Road, Nanjing 210093, and Institute of Geology, Chinese Academy of Geological Sciences, 26 Baiwanzhuang Road, Beijing 100037 China. e-mail: jirod@cags.net.cn
[2] Division of Paleontology, American Museum of Natural History. e-mail: norell@amnh.org
[3] The Field Museum, 1400 S. Lake Shore Drive, Chicago IL, 60660. e-mail: pmakovicky@fieldmuseum.org
[4] School of Earth and Space Sciences, Peking University, Beijing 100871, China. e-mail: kqgao@geoms.geo.pku.edu.cn
[5] China University of Geosciences, Beijing 100083, China.

 ISSN 0003-0082

primitive compsognathid *Sinosauropteryx* (Chen et al., 1998). Here we describe a new ornithomimid dinosaur, the first from the Liaoning beds, and comment on its relationships to other ornithomimids.

Ornithomimid dinosaurs were the first toothless nonavian dinosaurs to be described (Marsh, 1890). Consequently, much has been written concerning their relationships and diet (Gauthier, 1986; Holtz, 1994; Sereno, 1997, Kobayashi et al., 1999; Norell et al., 2001b). Although toothed forms have been recovered (Pérez-Moreno et al., 1994; Barsbold and Perle, 1984), these are either difficult to place phylogenetically or are extremely fragmentary.

Local farmers collected the specimen, and some of the elements were clearly lost during the excavation process. It is apparent that both the tail and the forelimbs were present in adjoining blocks (fig. 1). When the specimen was collected it was cracked into two blocks, shattering many bones and leaving parts of the skeleton in each block. During the preparation process parts of the counter block were glued to the main slab, and the sediment surrounding the bones was removed. In other cases individual elements were prepared completely free of the counter slab and affixed to the main slab. This preparation process resulted in a single block with the specimen preserved in bas-relief (fig. 2).

### Institutional Abbreviations

| | |
|---|---|
| AMNH | American Museum of Natural History |
| IGM | Institute of Geology Mongolia |
| NGMC | National Geological Museum of China |
| ROM | Royal Ontario Museum |

## SYSTEMATIC PALEONTOLOGY

### THEROPODA MARSH, 1881

### COELUROSAURIA VON HUENE, 1914

### ORNITHOMIMOSAURIA BARSBOLD, 1976

### ORNITHOMIMINAE SERENO, 1998

### *Shenzhousaurus orientalis*, new taxon

Type Specimen: NGMC (National Geological Museum of China) 97-4-002.

Material: A partial skeleton preserved on a sandstone block in a death pose with its head above the torso. The distal hindlimbs, distal tail, and the forelimbs (except for part of the right hand) and the pectoral girdle are missing. The head is crushed, exposing the left side obliquely.

Etymology: *Shenzhou* is the ancient name of China, *orientalis* refers to the east.

Type Locality: Sihetun fossil site, Beipiao, Western Liaoning, China (fig. 3).

Geological Occurrence: The holotype comes from the lowermost, fluvial part of the Early Cretaceous Yixian Formation. These rocks are older than 128 mybp and younger than 139 mybp (Swisher et al., 2002); older dates have been reported (Lo et al., 1999).

Diagnosis: an ornithomimosaur distinguishable from all others except *Harpymimus* in having teeth restricted to the anterior dentary. *Shenzhousaurus orientalis* shows primitive characters not found in advanced ornithomimosaurs, like a straight ischium and a postacetabular process that is gently curved rather than truncated. *Shenzhousaurus orientalis* is distinguishable from *Pelecanimimus* by the tooth distribution pattern and the primitive configuration of the hand where digit I is shorter than digits II and III.

## DESCRIPTION

### Skull

The left side of the snout is well preserved, whereas the right side is crushed and displaced postmortem (fig. 4). The orbital and braincase regions are flattened and the left frontal and parietal are flipped under the right. The left squamosal is isolated and lies adjacent to the caudal end of the lower jaw. The left mandible appears to be intact and well preserved.

The premaxilla has a relatively short body, and the premaxillary buccal margin is only as long as the external naris. The internarial bar is dorsoventrally flat and is formed mainly by the premaxillae, with only a minor contribution from the nasals. The posterodorsal process of the premaxilla is elongate as in other ornithomimids, and it overlaps the nasomaxillary suture well posterior to the caudal end of the naris. It is broadest at its base but tapers caudally. Although incomplete distally, it does not appear to have reached the level of the antorbital fossa. The labial sur-

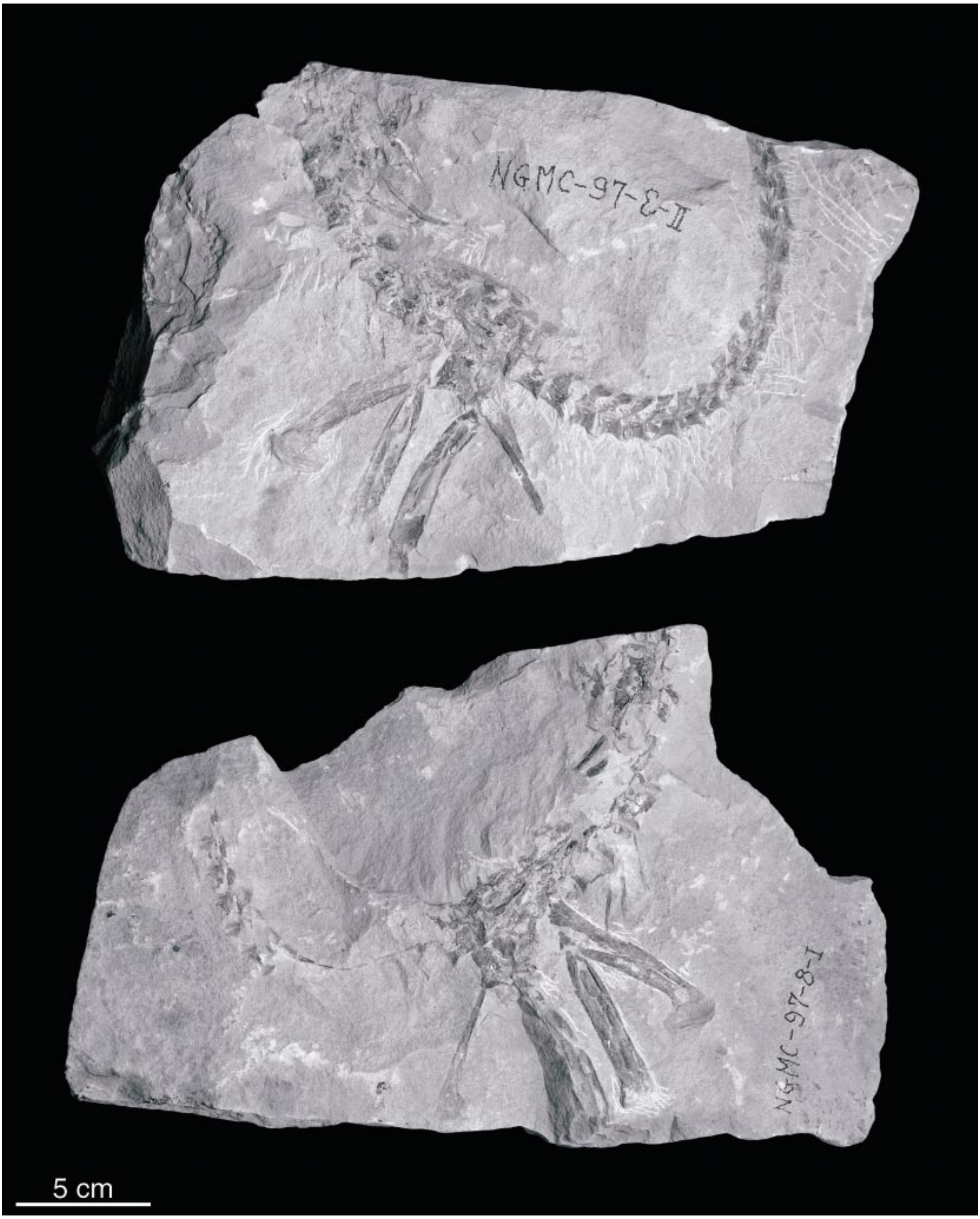


Fig. 1. NGMC 97-4-002 before preparation.


Fig. 2. The holotype skeleton of *Shenzhousaurus orientalis* as preserved on the main block, with parts in counterblock reattached. Abbreviations: g, gastralia; ga, gastroliths; lf, left femur; li, left ilium; lis, left ischium; lp, left pubis; lu, ungual of left hand; pb, pubic boot; r-dI, right digit I; r-dII, right digit II; r-dIII, right digit III; rf, right femur; rp, right pubis.


Fig. 3. The fossil locality.

face of the subnarial part of the premaxilla is marked by a few neurovascular foramina, the largest of which is located at the base of the internarial bar.

The maxilla is very elongate and bears a large antorbital fossa that is perforated by a larger antorbital and a smaller accessory fenestra. The rostral 40% of the maxilla lies anterior to the antorbital fenestra and has a flat lateral surface marked only by a few foramina, presumably for neurovascular transmission. The buccal margin is slightly sinuous in this region and rises gently toward the front. The buccal margin of the maxilla is very shallow beneath the antorbital fossa. A large maxillary palatal shelf is visible along the anterior two-thirds of the antorbital fossa. The fossa appears to be bordered by the nasal for a short stretch dorsal to the antorbital fenestra, although the maxilla is not complete in this region. Posterior to this the dorsal edge of the antorbital fenestra is bordered by the elongate anterior ramus of the lacrimal. The accessory fenestra perforates a depressed medial lamina of the maxilla that walls off the anterior third of the antorbital fossa medially. The posterior part of this lamina, which forms the interfenestral bar, bears dorsal and ventral embayments along the posterior border, perhaps indicating some type of interfenestral connection as in troodontids (Norell et al., 2000; Makovicky et al., 2003).

The jugal is poorly preserved, and articular contacts with the maxilla and lacrimal

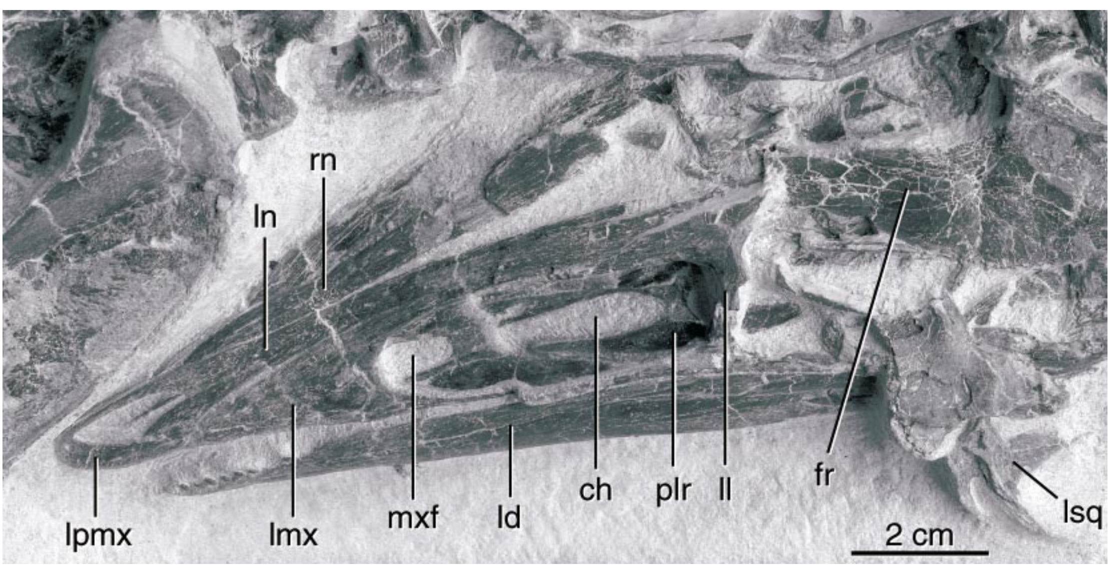


Fig. 4. Close-up of the left side of the skull of *Shenzhousaurus orientalis*. Abbreviations: ch, choana; fr, frontal; ld, left dentary; ll, left lacrimal; lmx, left maxilla; ln, left nasal; lpmx, left premaxilla; lsq, left squamosal; mxf, maxillary fenestra; plr, palatine recess; rn, right nasal.

cannot be traced. The orbital portion of the jugal is very slender, and the anteroventral corner of the orbit appears to have had a right-angled rather than a rounded shape. Posteriorly, the jugal is obscured by other elements.

The lacrimal bears an elongate anterior process that borders the caudal half of the antorbital fenestra dorsally. A short, pointed posterior process is present on the lacrimal. It may have inserted into a notch on the dorsal surface of the prefrontal as in *Gallimimus*, but the prefrontal cannot be identified. Neither large fossae nor hornlike structures are present on the lacrimal.

A short section of the right postorbital is exposed in dorsal view, and it forms the anterior part of the intertemporal bar. It is relatively massive compared to the postorbital contribution to the intertemporal bar in other ornithomimid taxa. The postorbital of *Shenzhousaurus orientalis* does not reveal the characteristic anterodorsal curvature seen in maniraptorans.

The right frontal is exposed in dorsal view (fig. 5). A coronally directed crack extending through the frontal just anterior to the articulation of the postorbital may be the result of dorsoventral crushing of a strongly flexed part of the frontal. The frontals of other ornithomimid taxa are domed near the posterior part of the orbit, forming a flexure between the flat parts of the frontal and parietals. Anterior to the extensive orbital rim, the lateral edge of the frontal is sinuous and the medially inflected portion may mark a depression for the reception of a prefrontal.

The parietals appear paired and unfused. The dorsal surface of the parietal is flat and lacks a sagittal crest. A laterally concave flexure marks the medial edge of the supratemporal fenestra and separates the dorsal surface of the parietal from the lateral surface that forms parts of the adductor chamber. The frontoparietal suture is sinuous in dorsal view, as in *Gallimimus* (Osmólska et al., 1972).

The left squamosal is disarticulated and lies adjacent to the caudal end of the left mandible. It is exposed in lateral view, and the proximal end of the quadrate is preserved in articulation with the squamosal. The squamosal is tetraradiate, with two processes extending anteriorly around the caudal end of the supratemporal fenestra, a rostroventrally directed quadrate process that adheres to the anterior edge of the quadrate shaft, and a short lateral process. The intertemporal process of the squamosal is longer than the medial supratemporal process. The dorsal surface of the squamosal between these two processes is incised by a caudal extension of the supratemporal fenestra, bordered by a sharp rim, as in *Gallimimus* (IGM 100/1133). The quadrate process of the squamosal is triangular. The posterolateral process extends posterior to the quadrate articulation, but its length cannot be determined because it is overlapped by a disarticulated piece of the braincase. The articulation with the quadrate is not exposed in lateral view in *Shenzhousaurus orientalis*, as it is in *Gallimimus* (IGM 100/1133) and *Ornithomimus*.

Parts of the palate, including parts of both palatines and possibly the left pterygoid, are exposed. The palatine bears two anteriorly elongate processes that almost enclose the internal choana. The medial, interchoanal process is longer than the lateral one, in contrast to *Allosaurus* (Madsen, 1976), but similar to *Sinraptor* (Currie and Zhao, 1993) and *Deinonychus* (Witmer, 1997), and it extends at least as far rostrally as the interfenestral bar. The interchoanal process of the left side rises dorsomedially to meet its counterpart on the right side and form the interchoanal bar, possibly with participation of the pterygoids. The interchoanal bar is unlike the large, lobate structure of *Allosaurus* (Madsen, 1976), but is more slender and curves anteriorly from the posterior end of the choana as in *Velociraptor* (Barsbold and Osmólska, 1999). The dorsal surface of the palatine bears a deep fossa, the palatine recess (Witmer, 1995), near the base of the maxillary process just rostral to the level of the lacrimal (fig. 5). The palatine recess in *Shenzhousaurus orientalis* is in a similar position to palatine recesses observed in dromaeosaurs such as *Deinonychus* (Witmer, 1995: fig. 32) and *Velociraptor* (IGM 100/982). The recess invades the palatine body mediodorsally in *Shenzhousaurus orientalis* rather than posterodorsally as in the two dromaeosaurid taxa. Part of the pterygoid process of the palatine

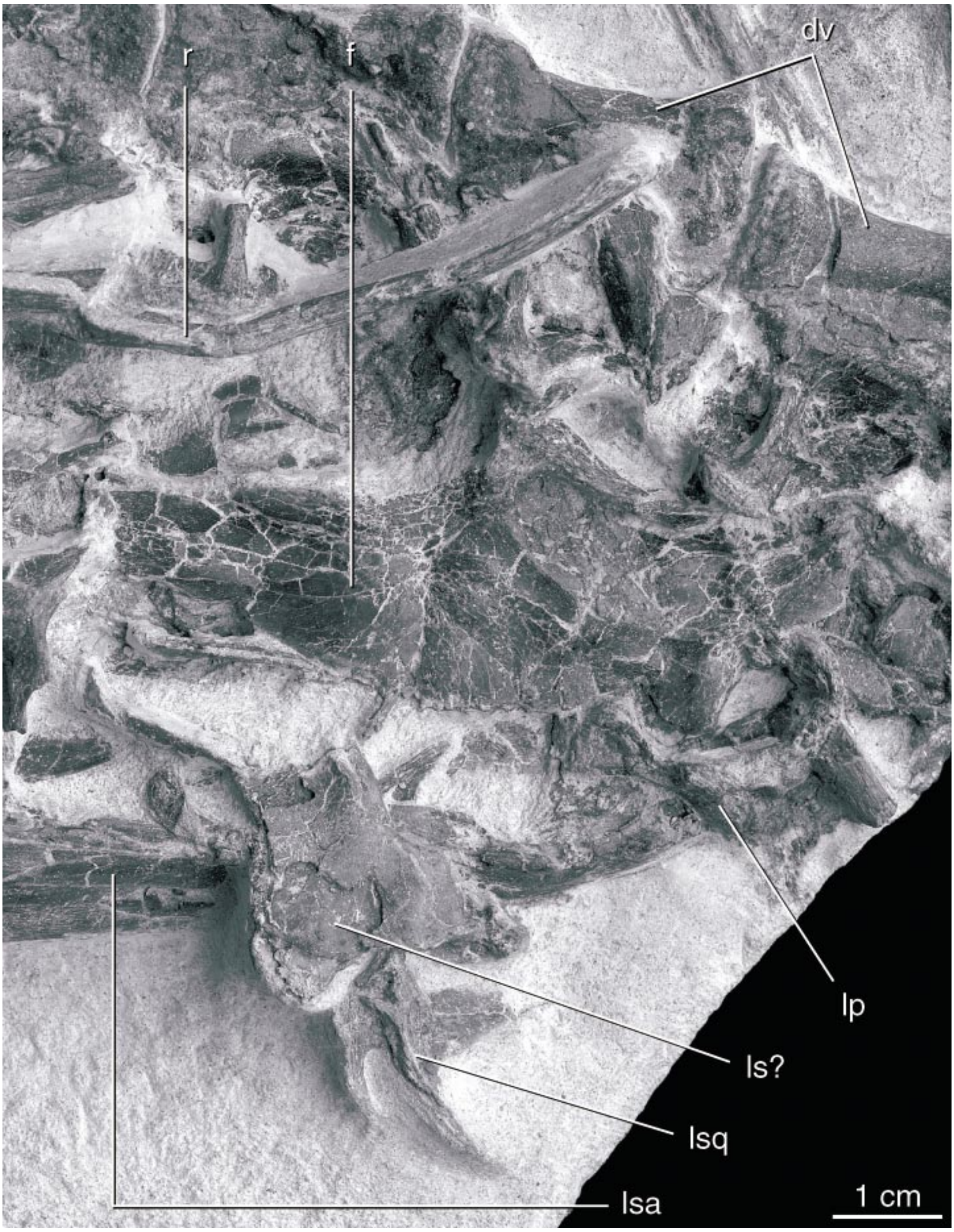


Fig. 5. Closeup of braincase. Abbreviations: dv, dorsal vertebra; f, frontal; lp, left prootic, ls?, left laterosphenoid, lsa, left surangular, lsq, left squamosal; r, rib.

is exposed within the orbit, posterior to the lacrimal.

The hooked jugal process is the only visible part of the ectopterygoid and is exposed within the orbit slightly posterior to the pterygoid process of the palatine. A narrow sliver of bone dorsal to the jugal process of the ectopterygoid to this may represent a part of the pterygoid.

A large, crushed bone that overlaps the posterior part of the mandible may be a laterosphenoid. We interpret a large broken element posterior to the right parietal as the left prootic with its anterior surface (laterosphen-


Fig. 6. The dentition of *Shenzhousaurus orientalis* as preserved in the left dentary.

oid articulation) facing upward (fig. 5). A well-delimited depression on the lateral surface appears to be the dorsal tympanic recess. Medial to it, the posterior border of the floccular recess is visible. Part of the border of a large foramen, which is surrounded by a wide fossa on the lateral surface of the braincase, is visible anteroventral to the floccular recess and is here interpreted as the exit for the trigeminal nerve.

The complete left mandible is preserved, but much of the postdentary region is covered by the unidentifiable braincase element. The dentary is elongate but shallow and spans about two-thirds the length of the jaw. The dentary is deepest below the middle of the antorbital fenestra. It tapers gently rostral to this point, up to a point just posterior to the toothrow, where it deflects rostroventrally. The buccal margin is deflected anteroventrally at the symphysis, as in other ornithomimosaurs except *Pelecanimimus* (Pérez-Moreno et al., 1994). The lateral surface of the dentary is pocked by three roughly linear rows of neurovascular foramina (fig. 6). These extend posteriorly to the end of the abbreviated toothrow. Farther caudally, a shallow groove follows the dorsal margin of the dentary until it reaches the rostrodorsal process of the surangular.

As in other ornithomimosaurs, the external mandibular fenestra is reduced. It is bordered dorsally by the surangular that has a long, splintlike process overlapping the dentary. Fragments of the angular are exposed along the ventral border of the external mandibular fenestra. The glenoid and retroarticular process are exposed. A flattened area just rostral to the glenoid may correspond to the dorsal trough or sulcus seen on the surangular of many theropods, including *Velociraptor*, *Tyrannosaurus*, and *Ornitholestes*. As in other ornithomimids, an everted tab forms the anterolateral margin of the glenoid. In these taxa, such as *Gallimimus*, this tab articulates with an elongate, curved extension of the lateral quadrate condyle. The retroarticular process is crushed, but it appears to be expanded medially.

## Teeth

Six minute tooth crowns and a broken root are preserved at the deflected anterior tip of the left dentary. Gaps between the preserved teeth suggest the presence of one or two additional tooth positions. The teeth are conical and project slightly anteriorly. They do not have a constriction between the root and crown. A thin layer of enamel is preserved on the teeth. There is no trace of either carinae or serrations.

## Axial Skeleton

### Cervical Vertebrae

No cervical vertebrae can be identified on the specimen.


Fig. 7. Dorsal vertebrae of *Shenzhousaurus orientalis*.

### Dorsal Vertebrae

An articulated series of the last eight dorsal vertebrae are preserved in articulation with the sacrum. The centra are elongate and spool-shaped and are devoid of pneumatic foramina (fig. 7). The anteriormost centrum, which is broken anteriorly, bears a faint keel ventrally. Neural arches bear large pneumatic infraprezygapophyseal, infradiapophyseal, and infrapostzygapophyseal fossae below the transverse processes. The infraprezygapophyseal fossae are especially large and appear to extend into the prezygapophyses. The neural spines are long, tall anteroposteriorly expanded distally. The neurocentral sutures are fused but not obliterated. In no case is a neural arch separated from its corresponding centrum.

Parts of 10 dorsal ribs are preserved on the block, but none is complete. Two left ribs, which probably articulated with the fourth and fifth dorsals in the preserved series, have anteroposteriorly flared shafts as in other ornithomimids (Barsbold and Osmólska, 1990).

### Sacral Vertebrae

Parts of five sacral vertebrae are exposed but are partly obscured by the pelvic elements and the left femur. The centra appear to be fused, but the sutural lines are still evident. A constricted pit is visible on the exposed lateral surface of both the third and fourth sacrals. Such noninvasive depressions are also present on the sacral vertebrae of other ornithomimid taxa, including *Ornithomimus* (Makovicky, 1995), *Gallimimus* (Osmólska et al., 1972), *Struthiomimus*, and *Archaeornithomimus* (Makovicky, 1995). The ilium appears to be slightly displaced from the sacrum, thus exposing the transverse processes of the last sacral in lateral view. As in other ornithomimosaurs, the transverse processes of this element flare widely distally where they meet the medial border of the brevis fossa, and they may have contributed to the insertion area of the caudifemoralis brevis musculature. The neural spine of the last sacral appears to have been freestanding, but it cannot be determined whether the neural spines of the remaining sacrals formed a lamina as in some other ornithomimosaurian specimens.

### Caudal Vertebrae

A section of the tail comprising 15 articulated caudal vertebrae is preserved, curving posterodorsally from the sacrum (fig. 8). All the preserved caudals possess transverse processes or traces thereof, indicating that the transition point lies distal to the preserved section of the tail. Centrum length increases distally in the preserved section, whereas centrum height decreases distally.

The transverse processes are distally expanded and backswept. Their distal ends are rounded. In the second and third caudal vertebrae, a thin lamina extends anteriorly from the transverse process on to the lateral face of the prezygapophysis, where it forms a distinct ridge bounding a shallow fossa. This connection between the transverse process and prezygapophysis is also present in *Ornithomimus*. The neural spines of the first 12 vertebrae are obscured by transverse processes. Those of the remaining three caudals are parallelogram-shaped and lean posteriorly, extending beyond the caudal end of their respective centra.

### Chevrons

The first chevron is situated between the first and second caudals. It is rod-shaped, but its length is indeterminate, as the second chevron covers it distally. The second to fifths chevron are very elongate, slender, and rod-shaped with a slight posterior curvature that becomes more pronounced in more dis-

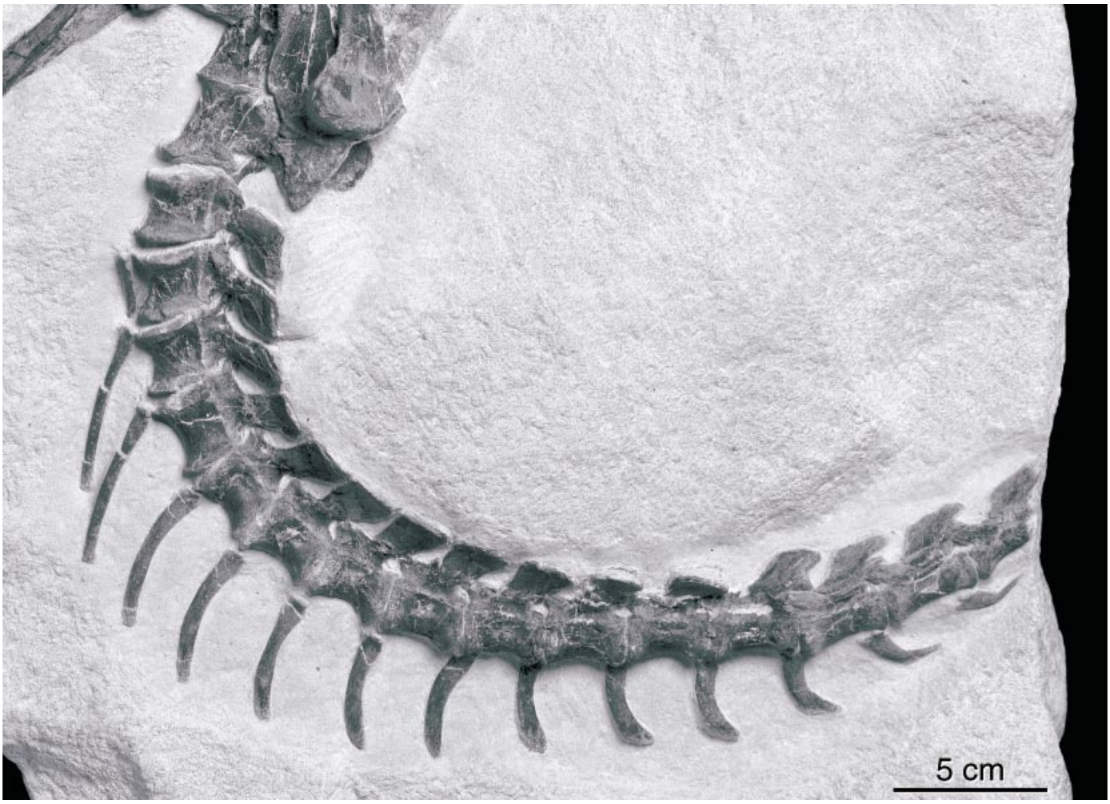


Fig. 8. Anterior caudal vertebrae of *Shenzhousaurus orientalis*.

tal elements. Posterior to this, the chevrons become progressively wider, mediolaterally compressed, shorter, and more hooked. The last two chevrons are strongly hooked and end in a point distally.

GASTRALIA

Parts of eight gastral arches from the right side are preserved, but only one preserves both the complete medial and lateral segments (fig. 9). The medial segment has an expanded and dorsoventrally compressed midline end. It tapers distally and is overlapped anteriorly by the lateral element. The two elements are approximately equal in length, unlike those of higher ornithomimids, in which the medial elements are longer. The dorsal ends of the rodlike lateral elements are slightly expanded and curve dorsally. The last gastral element is three times wider than the preceding segments. The last gastral arch may have only comprised this medial element

APPENDICULAR SKELETON

PELVIS

The pelvis is present in semiarticulation although some elements were shattered when the slab was split. The ilium is about equal in length to the pubis, and the ischium is only slightly shorter (see table 1).

Most of the exposed dorsal surface of the ilium is shattered, as it lay on the contact between the slab and counterslab (fig. 10). Nevertheless, it can be determined that the anterior and posterior blades are roughly equivalent in length and that the iliac blade was dorsoventrally low. The ilia covered six vertebrae, less than in *Gallimimus* and *Ornithomimus* (Barsbold and Osmólska, 1990). Apparently the ilia met at the midline as in other ornithomimids (Makovicky et al., in

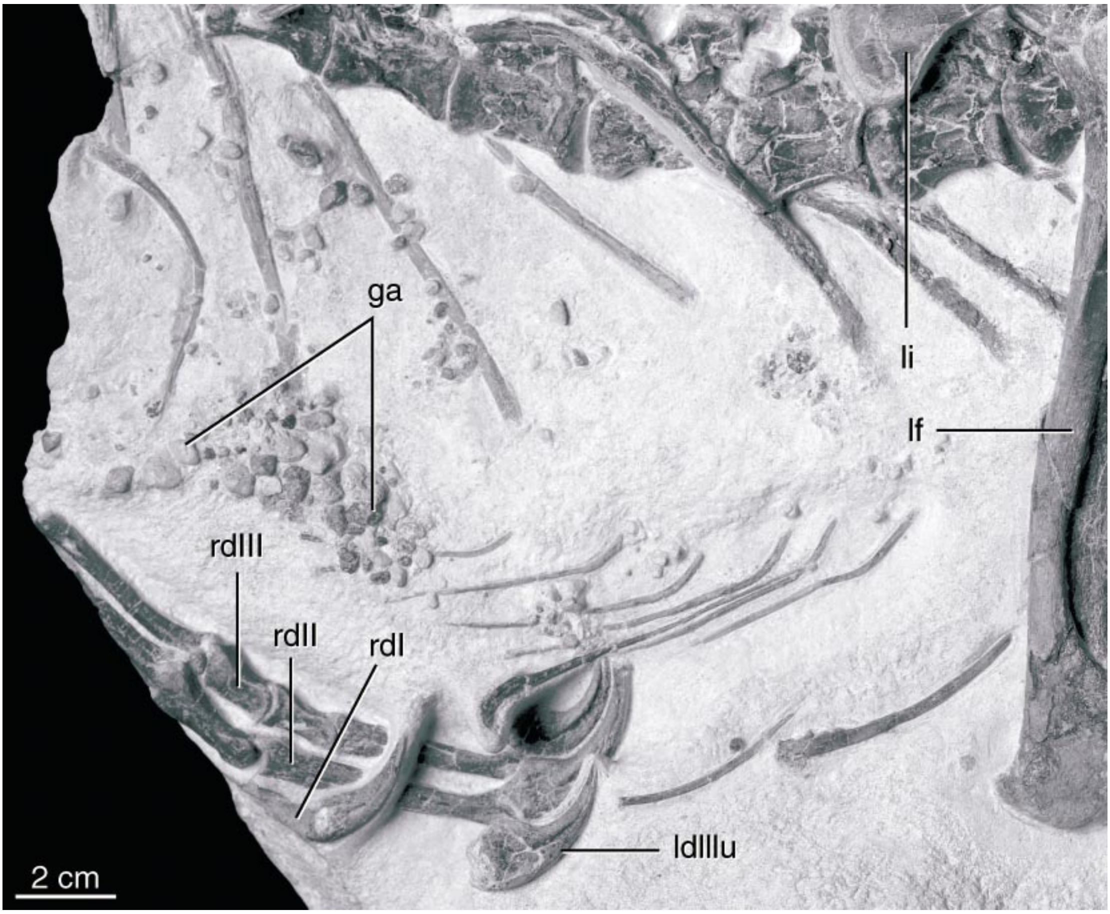


Fig. 9. Gastroliths of *Shenzhousaurus orientalis*. ga, gastroliths; ldIIIu, left digit 3 ungual; lf, left femur; li, left ilium; rdI, right digit 3, rdII; right digit 2; rdIII, right digit 3.

press; Barsbold and Osmólska, 1990). Both anterior and posterior blades also are rounded similar to the oviraptorosaur *Khaan mckennai* (personal obs.). This is unlike the condition in other ornithomimids where the ilium is dolichoiliac and the posterior blade is truncated rather than tapering to a point (Barsbold and Osmólska 1990). Although the anterior blade is hooked as in other ornithomimids, the hook is small as in *Khaan mckennai* (personal obs.), *Ornitholestes hermanni* (Osborn, 1903), and *Velociraptor mongoliensis* (Norell and Makovicky, 1997, 1999). Posterior to the acetabulum the lateral border of the brevis fossa is concave ventrally, giving it a slightly hooked appearance. This is unlike the condition in other ornithomimids where the lateral margin of the brevis fossa is straight (Barsbold and Osmólska 1990). The preacetabular apron is slightly concave and is separated from the main body of the ilium by a sharp ridge that continues anteriorly to form the lateral border of the deep cupedicus fossa. The acetabulum is marked by a large supra-acetabular crest that overhangs the acetabulum. As is typical of ornithomimosaurs, the supracetabular crest formed a hood or cap over the entire proximal femur. The ischiac peduncle is not wide, but is formed as a ventral conical process, as in other ornithomimids and tyrannosaurs, which inserts into a slot in the ischium. A large antitrochanter is present. The postacetabular apron is large and like the preacetabular apron is separated from the iliac blade by a large ridge that continues pos-

TABLE 1
**Measurements of Holotype of *Shenzhousaurus orientalis* (all measurements in millimeters)**

| | | | |
|---|---|---|---|
| Skull length | 185 | Chevron 1 | >21 |
| Left mandible | 154 | Chevron 2 | 48 |
| Naris length | 19 | Chevron 3 | 48 |
| Antorbital fossa length | 54 | Chevron 4 | 44 |
| Maxillary fenestra length | 11 | Chevron 5 | 41 |
| Antorbital fenestra length | 38 | Chevron 6 | 38 |
| Last dorsal vertebra[a] | 31 | Chevron 7 | 33 |
| 2 | 30 | Chevron 8 | 33 |
| 3 | 31 | Chevron 9 | >26 |
| 4 | 29 | Chevron 10 | >26 |
| 5 | 29 | Chevron 11 | >26 |
| 6 | 27 | Chevron 12 | >23 |
| 7 | 26 | Chevron 13 | 23 |
| | | Chevron 14 | 20 |
| Sacrum length | 140 | | |
| Caudal 1 | 20 | Ilium length | 153 |
| Caudal 2 | 19 | Pubis length | 169 |
| Caudal 3 | 19 | Ischium length | 153 |
| Caudal 4 | 22 | Femur length | 191 |
| Caudal 5 | 21 | Pubic boot length | 62 |
| Caudal 6 | 21 | | |
| Caudal 7 | 21 | P1 ungual 1 | >35 |
| Caudal 8 | 22 | p2-1 | 29 |
| Caudal 9 | 23 | p2-2 | 60 |
| Caudal 10 | 24 | p2 ungual | 45 |
| Caudal 11 | 24 | MC 3 | 50 |
| Caudal 12 | 26 | p3-1 | 19 |
| Caudal 13 | 25 | p3-2 | 18 |
| Caudal 14 | 28 | p3-3 | >43 |
| | | p3 ungual | >29 |
| | | p3 ungual left | 37 |

[a]Dorsal vertebrae are numbered from the last dorsal anteriorly.

teriorly to define the lateral edge of the brevis fossa. The brevis fossa is large and deep and expands posteriorly as a deep trough to the posterior limit of the ilium.

The left ischium is preserved in near articulation with the ilium and can be observed in lateral view. The iliac process is long and is angled posterodorsally from the shaft. On its posteroproximal lateral surface is a large triangular scar as in other ornithomimosaurs and tyrannosaurs (Buffetaut et al., 1996). The surface of the acetabulum that lies in between the iliac and pubic processes is smooth and crescent-shaped. The pubic process is short, relatively shorter than in other ornithomimids. In fact, the pubic contact lies along the same axis as the shaft of the ischium. Just ventral to the pubic contact lies a large hook-shaped obturator process. It is possible that this process may have completely enclosed a foramen; however, breakage in this area prevents confirmation. Distally the ischium tapers and then expands on its distal end into a small triangular boot that projects anteriorly.

The left pubis and part of the right are exposed laterally and are in near articulation with the ilia and ischia. The overlying femur obscures most of its proximal features. However, the articulation with the ilium indicates that it was propubic. Near the iliac contact the pubis is flat, becoming thin and rodlike distally. It is slightly anteriorly convex, and laterally it is marked by a small sinuous longitudinal ridge or crest which extends nearly half the length of the shaft. This crest divides

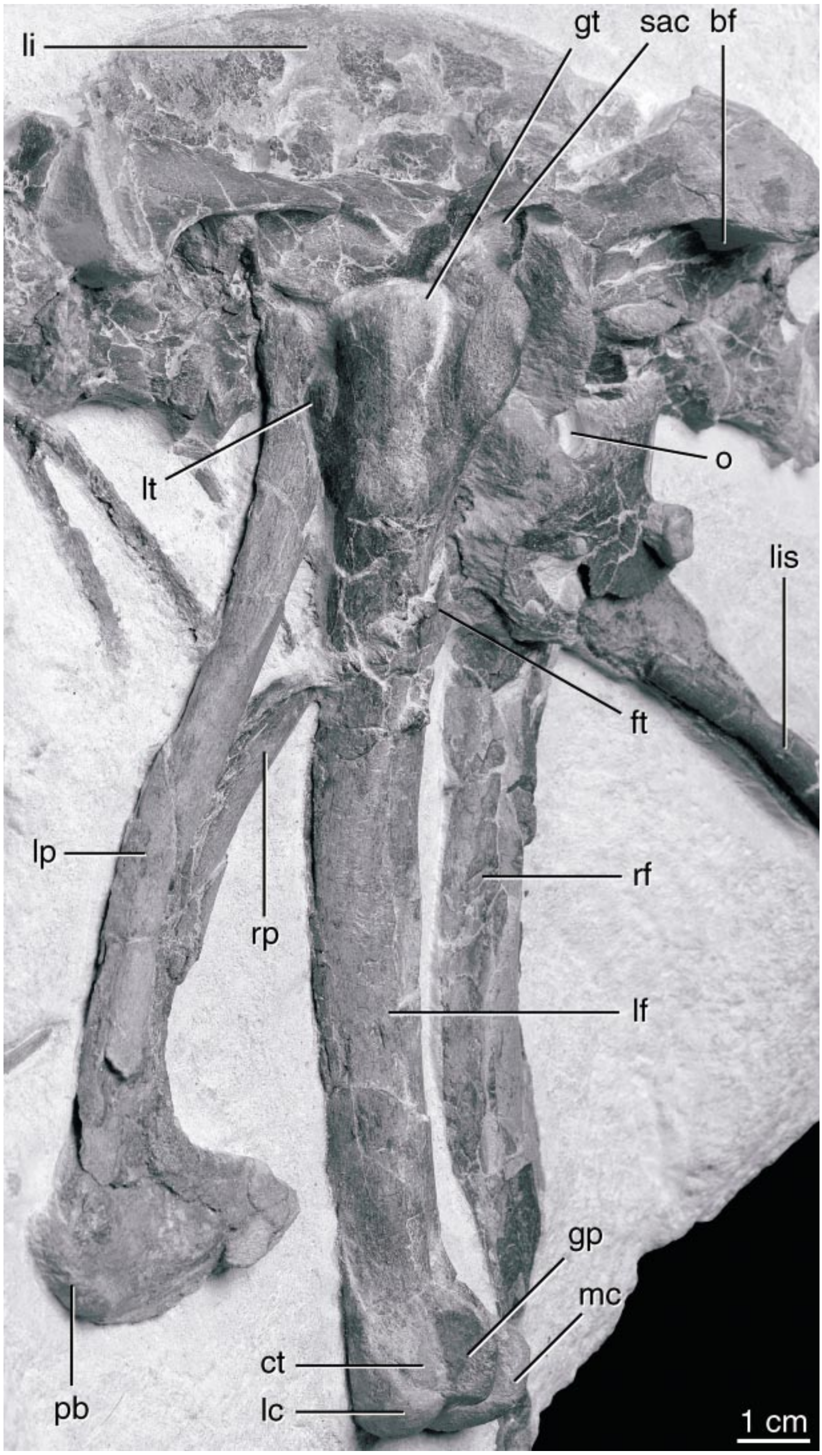


Fig. 10. Pelvis of *Shenzhousaurus orientalis*. Abbreviations: ct, ectocondylar tuber; ft, fourth trochanter; gp, gastrocnemius process; gt, greater trochanter; lc, lateral crest; lf, left femur; lp, left pubis; li, left ilium; lis, left ischium; lt, lesser trochanter; mc, medial crest; o, obturator foramen; pb, pubic boot; rf, right femur, rp, right pubis; sac, sacrum.

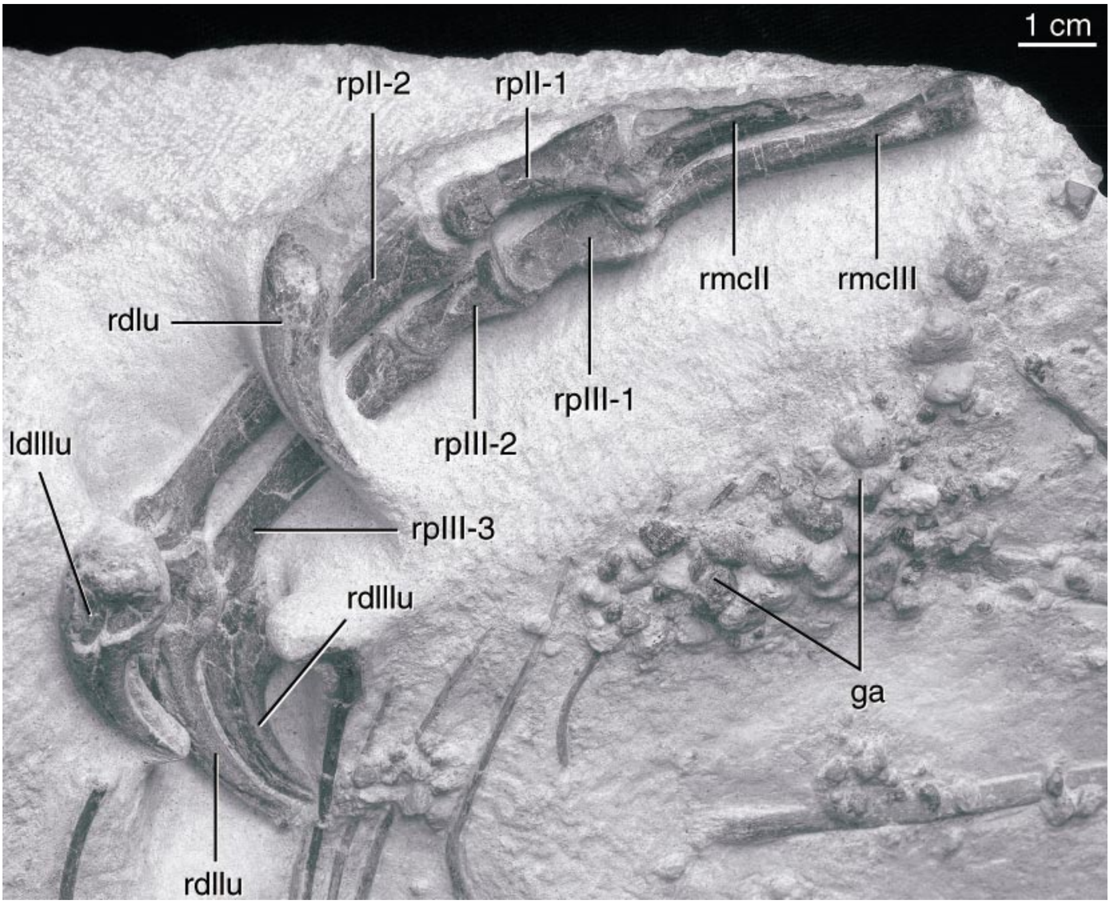


Fig. 11. Manus of *Shenzhousaurus orientalis*. ga, gastroliths; ldIIIu, left digit 3 ungual; rmcII, right metacarpal 2; rmcIII, right metacarpal 3; rpII-1, right digit 2 first phalanx; rpII-2, right digit 2 second phalanx; rpIII-1, right digit 3 first phalanx; rpIII-2, right digit 3 second phalanx; rpIII-3, right digit 3 third phalanx, rdIu, right digit 1 ungual; rdIIu, right digit 2 ungual; rdIIIu, right digit 3 ungual.

the pubis into anterior, and posterior-facing surfaces. Medially the pubic moietes meet to form the pubic apron, which is extensive, forming nearly two-thirds the length of the pubis. The pubic apron is posteriorly concave and is formed from crests that emanate from the anterior of the pubic shafts. Distally the pubes form a large pubic boot. At the terminus of the pubes the pubic boot appears to be transversally expanded. This boot is moderately expanded anteriorly, where it forms a pronounced point. Posteriorly the pubic boot is much more extensive. Ventrally the pubic boot is deeply convex, as opposed to the condition in *Gallimimus*, where the ventral edge of the boot is nearly straight.

## Forelimb

Only parts of the right hand, including all of digits II and III, and a single ungual of the left hand are preserved (fig. 11). The preserved elements of the right hand are in articulation, but the hand is situated at the edge of the block, and the missing parts were obviously lost during collection when the block was trimmed. The ungual and a partial impression of the penultimate phalanx are the only preserved parts of digit I. The ungual is slightly curved, not trenchant, and has a small flexor tubercle situated distal to the proximal articulation. A deep groove extends along the medial surface of the ungual, to the distal end of the ungual. The preserved ungual of digit I of the left manus shows a similar groove on the lateral surface, and these two grooves are parallel along the ungual, unlike the offset grooves on the unguals of dromaeosaurs. As preserved, the ungual of digit I does not reach the level of the proximal end of the unguals of digits II and III. Because the hand is articulated, the preserved position of ungual I-2 reflects the actual proportions of the digits in life and indicates that digit I is proportionately shorter than digits II or III, which is the primitive condition for Tetanurae (Gauthier, 1986; Sereno, 1997). Among ornithomimosaurs, the condition in *Shenzhousaurus* appears most like that of *Harpymimus* (Barsbold and Perle, 1984), in which digit I is short. The unguals are slightly curved, not trenchant, and bear small flexor tubercles distal to the proximal articulations as in other ornithomimosaurs (Osmólska, 1997; Sereno, 2001). In *Gallimimus* (Osmólska et al., 1972), *Struthiomimus* (Osborn, 1917; Nicholls and Russell, 1985; AMNH 5339), *Anserimimus* (IGM 100/300), *Pelecanimimus* (Pérez-Moreno et al., 1994), and *Ornithomimus* (Sternberg, 1933) the ungual of digit I reaches to at least the base of the unguals of digits II and III.

Only the distal part of metacarpal II is preserved, and it is exposed in ventral and medial views. The distal articulation is divided into two distinct tubercles ventrally. A pronounced flexor pit separates the two tubercles. Phalanx II-1 has a transversely flat ventral surface, with a pronounced arch in lateral view. The proximal articulation is extensive, and a small posteromedial lappet forms a small heel extending ventral to the distal end of the metacarpal. The distal articulation is divided into two widely separated tubercles in ventral view, and the articulation appears ginglymous, although it is poorly preserved.

Phalanx II-2 is elongate, slender, and has a nearly straight shaft that is oval in cross section. The proximal articulation is formed as a deep arc in lateral view, with dorsal and ventral parts of the articulation projecting far posteriorly. In contrast to *Gallimimus*, the ventral end of the articulation extends farther proximally than the dorsal tip. A small, midline process or tuber is present on the ventral surface of the phalanx II-2, adjacent to proximal articulation. The apparently ginglymous distal articulation describes an arc of approximately 180° and has a small, elliptical collateral ligament pit. The ungual of digit II is similar to that of digit I, except that is slightly longer.

Metacarpal III is almost complete. It appears to be almost as thick as the preserved part of metacarpal II, as in *Harpymimus* (Barsbold and Osmólska, 1990). The proximal end is triangular in proximal view, with a slightly concave area where it was apressed against the shaft of metacarpal II. The shaft of metacarpal III appears to curve slightly laterally. The distal articulation divides into two tubera ventrally.

Phalanx III-1 is short and blocky, with flat medial and ventral faces that are set perpendicular to each other. As in phalanx II-1, the medioventral end of the proximal articulation extends for a short distance below the end of metacarpal III. Distally, the medial collateral ligament pit is very weak. The distal articulation is apparently ginglymoid. Phalanx III-2 is almost identical to phalanx III-1, except for being more slender and lacking the short heel on the proximal articulation. Phalanx III-3 is longer than the combined lengths of digits III-1 and III-2, as in derive ornithomimids (Barsbold and Osmólska, 1990). Proximally, phalanx III-3 is similar to II-2, including the presence of a small tubercle just ventral to the proximal articulation. The shaft thins distally and is thinnest just adjacent to the distal articulation, which is offset ventrally from the shaft. The medial collateral ligament fossa is deep but not displaced dorsally as in many other theropods. The ungual is similar to those of digits I and II and is roughly as long as that of digit II. It appears to have a more pronounced groove for the claw sheath than do the other unguals.

### Hindlimb

Both right and left femora are preserved; however, the right is severely damaged (fig. 10). The left femur lies in articulation with the acetabulum, and proximal lateral and distal proximal surfaces are exposed. Hindlimb elements distal to the femur are not preserved.

As in other ornithomimids, the femur is

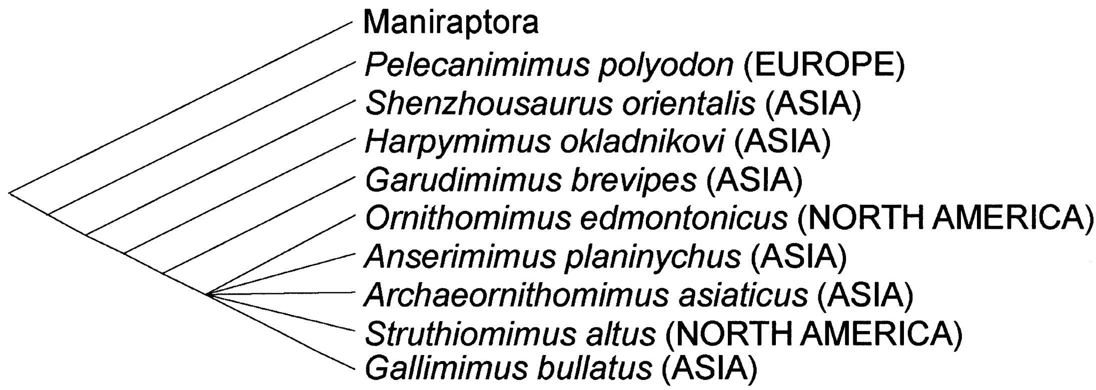


Fig. 12. Strict consensus of 432 most parsimonious trees depicting relationships among ornithomimosaur species derived from parsimony analysis of 220 characters in 50 coelurosaurian species (see http://research.amnh.org/users/norell/index.html). Tree statistics for shortest trees are (TL = 586, CI = 45, and RI =75). Continental distributions are listed after taxon names.

slightly bowed (contra Barsbold and Osmólska, 1990), but not to the level of Maniraptora. The proximal end is exposed in lateral view. The greater trochanter is higher than the lesser trochanter. The lesser trochanter is alariform and is separated from the greater trochanter by a deep cleft that extends approximately 28 mm down the femoral shaft. This cleft ends in the bump, which apparently does not continue down the femoral shaft as the lateral ridge as in maniraptoriforms like *Velociraptor* (Norell and Makovicky, 1997, 1999). A small ridge divides the lesser trochanter into anterior and posteriorly oriented surfaces. A weakly developed fourth trochanter lies distal and medial to the posterior trochanter. Distally the femur is twisted to expose the posterior surface. The medial condyle is much larger than the lateral one, is bulbous, and extends medial to the axis of the femoral shaft. A thin crest, or buttress, extends proximally up the shaft of the femur from the medial condyle. The medial and lateral condyles are separated by a deep wide popliteal fossa that is not closed distally by lateral or medial expansions. The gastrocnemius process that lies posterior to the lateral condyle is unusual in that it is thin and its lateral surface is nearly flat. It contacts the shaft of the femur nearly at a right angle and borders a flat, triangular surface on the femoral shaft that extends to the edge of the lateral condylar surface. A very low ectocondylar tuber is also present at the lateral apex of the lateral condyle.

### Gastroliths

The thoracic cavity of *Shenzhousaurus orientalis* contains numerous pebbles, which are best interpreted as gastroliths. The uniform matrix surrounding the skeleton is devoid of lithic clasts of a comparative size. The pebbles are distributed unevenly in the thoracic cavity, with a concentration just anterior to the preserved part of the gastral basket. Less concentrated amounts of gastroliths occur throughout the rest of the thoracic cavity, and some are dispersed posteriorly across the femur and proximal end of the left ischium and sacrum. The gastroliths are heterogeneous in size, shape, and composition. Whereas some are smooth and rounded, others are highly angular and/or pockmarked. Gastroliths have been previously reported in ornithomimosaurs (Kobayashi et al., 1999).

## DISCUSSION

Phylogenetic analysis posits *Shenzhousaurus* near the base of Ornithomimosauria (Makovicky et al., in press), being more advanced than the Barremian *Pelecanimimus* (fig. 12). Ornithomimosaurs are monophyletic and are the sister group to a clade composed of Maniraptora (including *Ornitholestes*) (Gauthier, 1986; Sereno, 1997; Xu et al., 2002b). No support was found for a close relationship between ornithomimosaurs and troodontids (Holtz, 1994). Alvarezsaurids, which have been postulated as close ornithomimosaur relatives (Sereno, 2001), are found to be the sister group of all other Maniraptora except *Ornitholestes*. *Shenzhousaurus* and other ornithomimosaurs are more derived than *Pelecanimimus* in the progressive loss of teeth from the upper jaws and all but the tip of the dentary (*Shenzhousaurus*, *Harpymimus*) or complete loss of teeth (higher ornithomimosaurs). *Harpymimus* and *Shenzhousaurus* are similar in having primitive manual proportions in which metacarpal I is much shorter than either II or III, but *Harpymimus* shares a derived curvature of the ischium with higher ornithomimids.

Except for the Spanish taxon *Pelecanimimus*, most ornithomimids are known from Central Asia and western North America. Examining distributions within the context of the phylogeny (fig. 12) demonstrates that early ornithomimids have an extensive evolutionary history in eastern Asia, yet the center of origin is ambiguous because of the European range of *Pelecanimimus*. Several other dinosaur clades, including tyrannosaurs (Hutt et al., 2001) and pachycephalosaurs (Sereno, 1999), whose derived members are mainly known from Asia and North America, also have basal taxa from the Early Cretaceous of Europe predating the formation of the Turgai Straits. Among higher ornithomimosaurs, a single dispersal across Beringia is required to account for the distribution of taxa between North America and Asia if North American ornithomimids form a monophyletic taxon. Otherwise, two dispersals are required to explain the known geographic diversity of this clade.

Advanced ornithomimosaurs lack teeth and had beaks (Osborn, 1917, Norell et al., 2001b). The edentulous nature of their beaks has been used along with gastroliths (Kobayashi et al., 1999) to suggest that the diet was highly specialized. According to our phylogenetic analysis, the advanced ornithomimid condition progressed through stages of loss of the upper and posterior dentary teeth initially as seen in the reduced maxillary toothrow in the basal form *Pelecanimimus*. *Shenzhousaurus* and *Harpymimus* illustrate a more progressive state in which maxillary teeth are absent and the dentary only bears teeth near the symphysis.

Although tooth loss is common among coelurosaurs (Chiappe et al., 1999), the pattern is disparate among groups. Therizinosauroids and hesperornithiformes have edentulous premaxillae, but retain maxillary and dentary teeth. Although advanced oviraptorosaurs are edentulous, the basal *Caudipteryx* has teeth restricted to the premaxilla. Nevertheless, the ornithomimosaur pattern where the lower jaw is toothed anteriorly and the entire upper jaw is edentulous appears unique as a phylogenetic precursor to toothlessness among theropod dinosaurs, with the possible exception of the basal avialan *Shenzhouraptor* (Ji et al., 2002b and 2003, Zhou and Zhang, 2002).

## ACKNOWLEDGMENTS

We thank the National Geological Museum of China. Mick Ellison prepared the illustrations, and Brian Roach prepared the specimen with the consultation of Marilyn Fox. The Division of Paleontology at the American Museum, Byron, Lynette, and Richard Jaffe, Vivian Pan, and the Field Museum Department of Geology provided support for this project.

## REFERENCES

Barsbold R., and H. Osmólska. 1990. Ornithomimosauria. *In* D.B. Weishampel, P. Dodson, and H. Osmólska (editors), The Dinosauria: 225–244. Berkeley: University of California Press.

Barsbold, R., and H. Osmólska. 1999. The skull of *Velociraptor* (Theropoda) from the Late Cretaceous of Mongolia. Acta Palaeontologica Polonica 44(2): 189–219.

Barsbold, R., and A. Perle. 1984. The first record of a primitive ornithomimosaur from the Cretaceous of Mongolia. Palaeontologicheskii Zhurnal 1984(2): 121–122. [Translated from Russian]

Buffetaut, E., V. Suteethorn, and H. Tong. 1996. The earliest tyrannosaur from the Lower Cretaceous of Thailand. Nature 381: 689–691.

Chen, P.J., Z.-M. Dong, and S.-N. Zhen. 1998. An exceptionally well preserved theropod dinosaur from the Yixian Formation of China. Nature 391: 147–152.

Chiappe, L.M., M.A. Norell, and J.M. Clark. 1996. Phylogenetic position of *Mononykus*

(Aves: Alvarezsauridae) from the Late Cretaceous of the Gobi Desert. Memoirs of the Queensland Museum 39(3): 557–582.

Chiappe, L.M., S.-A. Ji, Q. Ji, and M.A. Norell. 1999. Anatomy and systematics of the Confuciusornithidae (Theropoda: Aves) from the Late Mesozoic of northeastern China. Bulletin of the American Museum of Natural History 242: 1–89.

Clark, J.M., M.A. Norell, and R. Barsbold. 2001. Two new oviraptorids (Theropoda: Oviraptorosauria) from the Late Cretaceous Djadoktha Formation, Ukhaa Tolgod, Mongolia. Journal of Vertebrate Paleontology 21(2): 209–213.

Currie, P.D., and X.-J. Zhao. 1993. A new carnosaur (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People's Republic of China. Canadian Journal of Earth Sciences. 25: 972–986.

Gao, K., S. Evans, Q. Ji, M.A. Norell, and S.-A. Ji. 2000. Exceptional fossil material of a semiaquatic reptile from China: the resolution of an enigma. Journal of Vertebrate Paleontology 20: 417–421.

Gauthier, J.A. 1986. Saurischian monophyly and the origin of birds. *In* K. Padian (editor), The origin of birds and the evolution of flight. Memoirs of the California Academy of Sciences 8: 1–55.

Holtz, T.R., Jr. 1994. The phylogenetic position of the Tyrannosauridae: implications for theropod systematics. Journal of Paleontology 68: 1100–1117.

Hou, L. 1997. Mesozoic birds of China. Phoenix Valley Provincial Aviary of Taiwan. 228 pp. Taipei.

Hutt, S., D. Naish, D.M. Martill, M.J. Barker, and P. Newberry. 2001. A preliminary account of a new tyrannosauroid from the Wessex Formation (Early Cretaceous) of southern England. Cretaceous Research 22: 227–242.

Ji, Q., and S.-A. Ji 1996. On discovery of the earliest bird fossil in China and the origin of birds. Chinese Geology 17: 30–33.

Ji, Q., P.J. Currie, S.-A. Ji, and M.A. Norell. 1998. Two feathered dinosaurs from northeastern China. Nature 393: 753–761.

Ji, Q., Z.-X. Luo, and S.-A. Ji. 1999. A Chinese triconodont mammal and mosaic evolution of the mammalian skeleton. Nature 398: 326–330.

Ji. Q., S.-A. Ji, H.-B. Zhang, H.-L. You, J.-P. Zhang, L.-X. Wang, C.-X. Yuan, and X.-X. Ji. 2002a. A new avialan bird, *Jixiangornis orientalis* gen. et sp. Nov. from the Lower Cretaceous of western Liaoning, NE China. Journal of Nanjing University (Natural Sciences) 38(6): 723–736.

Ji, Q., S.-A. Ji, H.-L. You, J.-P. Zhang, C.-X. Yuan, X.-X. Ji, J.-L. Li, and Y.-X. Li. 2002b. Discovery of an avialan bird, *Shenzhouraptor sinensis* gen. et. sp. nov., from China. Geological Bulletin of China 21(7): 363–369. [in Chinese with English abstract]

Ji., Q., S.-A. Ji, H.-L. You, J.-P. Zhang, N.-J. Zhang, C.-X. Yuan, and X.-X. Ji. 2003. An Early Cretaceous Avialan bird *Shenzhouraptor sinensis* from Western Liaoning China. Acta Geologica Sinica 77(1): 21–26.

Kobayashi, Y., J.-C. Lu, Z.-M. Dong, R. Barsbold, Y. Azuma, and Y. Tomida. 1999. Herbivorous diet in an ornithomimid dinosaur. Nature 402: 480.

Lo, C.-H., P.-J. Chen, Y.-Y. Tsou, S.-S. Sun, and C.-Y. Lee. 1999. $^{40}Ar/^{39}Ar$ laser single-grain and K-Ar dating of the Yixian Formation, NE China. Palaeoworld 11: 328–340.

Madsen, J.M. 1976. *Allosaurus fragilis*: a revised osteology. Utah Geological Survey Bulletin 48: 27–31.

Makovicky, P.J. 1995. Phylogenetic aspects of the vertebral morphology of Coelurosauria (Dinosauria: Theropoda). Unpublished M.S. dissertation, Copenhagen University, Denmark.

Makovicky, P.J., and M.A. Norell. 1998. A partial ornithomimid braincase from Ukhaa Tolgod (Upper Cretaceous, Mongolia). American Museum Novitates 3247: 1–16.

Makovicky, P.J., M.A. Norell, J.M. Clark, and T. Rowe. 2003. Osteology of *Byronosaurus jaffei* (Theropoda: Troodontidae). American Museum Novitates 3402: 1–32.

Makovicky, P.J., Y. Kobayashi, and P.J. Currie. In press. Ornithomimosauria. *In* D.B. Weishampel, P. Dodson, and H. Osmólska (editors), The Dinosauria: 2nd ed., Berkeley: University of California Press.

Marsh, O.C. 1890. Description of New dinosaurian reptiles. American Journal of Science (Series 3) 39: 81–86.

Nicholls, E.L., and A.P. Russell. 1981. A new specimen of *Struthiomimus altus* from Alberta, with comments on the classificatory characters of upper Cretaceous ornithomimids. Canadian Journal of Earth Sciences 18: 518–526.

Nicholls, E.L., and A.P. Russell. 1985. Structure and function of the pectoral girdle and forelimb of *Struthiomimus altus* (Theropoda: Ornithomimidae). Palaeontology 28: 643–677.

Norell, M.A., and P.J. Makovicky. 1997. Important features of the dromaeosaur skeleton: information from a new specimen. American Museum Novitates 3215: 1–28.

Norell, M.A., and P.J. Makovicky. 1999. Important features of the dromaeosaur skeleton II: information from newly collected specimens of

*Velociraptor mongoliensis*. American Museum Novitates 3282: 1–45.

Norell, M.A., P.J. Makovicky, and J.M. Clark. 2000. A new troodontid from Ukhaa Tolgod, Late Cretaceous, Mongolia. Journal of Vertebrate Paleontology Rapid Communication 20(1): 7–11.

Norell, M.A., J.M. Clark, and P.J. Makovicky. 2001a. Relationships among Maniraptora: problems and prospects. *In* J.A. Gauthier and L.F. Gall (editors), New perspectives on the origin and early evolution of birds: 49–67. New Haven. CT: Peabody Museum of Natural History.

Norell, M.A., P.J. Makovicky, and P.J. Currie. 2001b. The beaks of ostrich dinosaurs. Nature 412: 873–874.

Osborn, H.F. 1903. *Ornitholestes hermani*, a new compsognathid dinosaur from the upper Jurassic. Bulletin of the American Museum Natural History 19: 459–464.

Osborn, H.F. 1917. Skeletal adaptations of *Ornitholestes*, *Struthiomimus*, *Tyrannosaurus*. Bulletin of the American Museum Natural History 35: 733.

Osmólska, H. 1997. Ornithomimosauria. *In* P.J. Currie and K. Padian (editors), Encyclopedia of Dinosaurs: 499–503. San Diego: Academic Press.

Osmólska, H., E. Roniewicz, and R. Barsbold. 1972. A new dinosaur, *Gallimimus bullatus* n. gen., n. sp. (Ornithomimidae) from the Upper Cretaceous of Mongolia. Palaeontologica Polonica 27: 103–143.

Pérez-Moreno, B.P., J.L. Sanz, A.D. Buscalioni, J.J. Moratalla, F. Ortega, and D. Rasskin-Gutman. 1994. A unique multitoothed ornithomimosaur from the Lower Cretaceous of Spain. Nature 370: 363–367.

Perle, A., M.A. Norell, L.M. Chiappe, and J.M. Clark. 1993. Flightless bird from the Cretaceous of Mongolia. Nature 362: 623–626.

Perle, A., L.M. Chiappe, R. Barsbold, J.M. Clark, and M.A. Norell. 1994. Skeletal morphology of *Mononykus olecranus* (Theropoda: Avialae) from the Late Cretaceous of Mongolia. American Museum Novitates 3105: 1–29.

Sereno, P.C. 1997. The origin and evolution of dinosaurs. Annual Review of Earth and Planetary Sciences 25: 435–489.

Sereno, P.C. 1999. The evolution of dinosaurs. Science 284: 2137–2147.

Sereno, P.C. 2001. Alvarezsaurids: birds or ornithomimosaurs? *In* J. A. Gauthier, and L.F. Gall (editors), New perspectives on the origin and early evolution of birds: 69–98 New Haven, CT: Peabody Museum of Natural History.

Sternberg, C.M. 1933. A new *Ornithomimus* with complete abdominal cuirass. Canadian Field-Naturalist 47(5): 80–83.

Swisher, C.C., X.-L. Wang, Z.-H. Zhou, Y.-Q. Wang, F. Jin, J.-Y. Zhang, X. Xu, F.-C. Zhang, Y. Wang. 2002. Further support for a Cretaceous age for the feathered dinosaur beds of Liaoning, China: new $^{40}$Ar/ $^{39}$Ar dating of the Yixian and Tuchengzhi Formations. Chinese Science Bulletin 47: 135–138.

Witmer, L.M. 1995. Homology of facial structures in extant archosaurs (birds and crocodilians) with special reference to paranasal pneumaticity and nasal conchae. Journal of Morphology 225: 269–327.

Witmer, L.M. 1997. The evolution of the antorbital cavity of archosaurs: a study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. Society of Vertebrate Paleontology Memoir 3: 1–73.

Xu, X., Z. Tang, and X. Wang. 1999a. A therizinosaurid dinosaur with integumentary structures from China. Nature 399: 350–354.

Xu, X., X. Wang, and X. Wu, 1999b. A dromaeosaurid dinosaur with a filamentous integument from the Yixian Formation of China. Nature 401: 262–266.

Xu, X., Z. Zhou, and X. Wang. 2000. The smallest known non-avian theropod dinosaur. Nature 408: 705–708.

Xu, X., M. A. Norell, X.-L. Wang, P. J. Makovicky, and X.-C. Wu. 2002a. A basal troodontid from the Early Cretaceous of China. Nature 415: 780–784.

Xu, X., Y.-N. Cheng, X.-L. Wang, and C.-H. Chang. 2002b. An unusual oviraptorosaurian dinosaur from China. Nature 419: 291–293.

Zhou, Z., and F. Zhang, 2002. A long-tailed, seed-eating bird from the Early Cretaceous of China. Nature 418: 405–409.

Recent issues of the *Novitates* may be purchased from the Museum. Lists of back issues of the *Novitates* and *Bulletin* published during the last five years are available at World Wide Web site http://library.amnh.org. Or address mail orders to: American Museum of Natural History Library, Central Park West at 79th St., New York, NY 10024. TEL: (212) 769-5545. FAX: (212) 769-5009. E-MAIL: scipubs@amnh.org