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## A new oviraptorid (Dinosauria: Theropoda) from the Upper Cretaceous of southern China

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### Abstract

This paper describes a new oviraptorid dinosaur taxon, *Ganzhousaurus nankangensis* gen. et sp. nov., based on a specimen collected from the Upper Cretaceous Nanxiong Formation of Nankang County, Ganzhou City, Jiangxi Province, southern China. This new taxon is distinguishable from other oviraptorids based on the following unique combination of primitive and derived features: relatively shallow dentary; absence of fossa or pneumatopore on lateral surface of dentary; weakly downturned anterior mandibular end; shallow depression immediately surrounding anterior margin of external mandibular fenestra; external mandibular fenestra subdivided by anterior process of surangular; dentary posteroventral process slightly twisted and positioned on mandibular ventrolateral surface; shallow longitudinal groove along medial surface of dentary posteroventral process; angular anterior process wider transversely than deep dorsoventrally; sharp groove along ventrolateral surface of angular anterior process; ventral border of external mandibular fenestra formed mainly by angular; ventral flange along distal half of metatarsal II; and arctometatarsal condition absent. Phylogenetic analysis places *Ganzhousaurus nankangensis* gen. et sp. nov. in the clade Oviraptoridae, together with *Oviraptor*, *Citipati*, *Rinchenia* and the unnamed Zamyn Khondt oviraptorid.

**Key words:** Oviraptoridae, Southern China, Theropoda, Upper Cretaceous

### Introduction

The oviraptorids are a group of oviraptorosaurian theropod dinosaurs characterized by a highly pneumatized skull, an elongated and dorsally positioned naris, a deep mandible, and a large external mandibular fenestra subdivided by a surangular process (Osmólska *et al.* 2004). The oviraptorid fossil record is mainly restricted to the Upper Cretaceous (Campanian-Maastrichtian) deposits of the Gobi Desert of Mongolia and of Inner Mongolia in China (Osborn 1924; Barsbold 1976; Longrich *et al.* 2010). This relatively small geographic area has yielded at least nine species: *Oviraptor philoceratops*, *Ingenia yanshini*, *Conchoraptor gracilis*, *Rinchenia mongoliensis*, *Citipati osmolskae*, *Khaan mckennai*, *Nemegtomaia barsboldi*, *Machairasaurus leptonychus* and the new Bayan Mandahu oviraptorid (Osborn 1924; Barsbold 1981, 1986, 1997; Clark *et al.* 2001, 2002; Lü *et al.* 2004, 2005; Longrich *et al.* 2010; Fanti *et al.* 2012; Xu *et al.* in press). Two additional valid oviraptorosaur species, *Nomingia gobiensis* and *Gigantoraptor erlianensis*, may also be referable to Oviraptoridae (Barsbold *et al.* 2000; Xu *et al.* 2007).

Over the last decade, several definite and possible oviraptorids have also been discovered in central and southern China, including *Heyuannia huangi* (Lü 2002, 2005), *Shixinggia oblita* (Lü and Zhang 2005), *Luoyanggia liudianensis* (Lü *et al.* 2009), and *Banji long* (Xu and Han, 2010). These discoveries have extended the geographic distribution of oviraptorids southward and even made southern China a prime location, alongside the Gobi Desert of Mongolia, for new oviraptorid discoveries. Despite the limited distribution of Oviraptoridae, this clade is relatively diverse over the short stratigraphic range in which it occurs (Longrich *et al.* 2010). In the present paper, we report a new oviraptorid specimen from the Upper Cretaceous Nanxiong Formation of Nankang County near Ganzhou City, Jiangxi Province, China.

## Geological Setting

This specimen was brought from a fossil dealer who is not willing to reveal his identity. The only information concerning the provenance of the specimen provided by this dealer is that the specimen was collected in the Nankang Basin near Ganzhou City, Jiangxi Province, and the precise locality information is not clear. The Nanxiong Formation comprises the main part of the strata that crop out in the Nankang Basin, Ganzhou area, and consists mainly of purplish-red and brick-red sandstone, siltstone and mudstone. Vertebrate fossils that have been recovered from this stratigraphic unit include the turtle *Nanhsiungchelys*, the titanosaurian *Titanosaurus* sp., the oviraptorid *Banji long*, and the dinosaur oospecies *Oölithes spheroids* and *Oölithes rugustus*, whereas invertebrate fossils include gastropods *Truncatella maxima* and *Rubeyella carinate* (Bureau of Geology and Mineral Resources of Jiangxi Province 1984; Xu and Han 2010). The presence of *Truncatella maxima* and *Rubeyella carinate* suggests that the Nanxiong Formation was deposited toward the end of the Late Cretaceous (Bureau of Geology and Mineral Resources of Jiangxi Province 1984; Xu and Han 2010). The relatively basal position of *Banji long* among the Oviraptoridae suggests that the fossil-bearing beds of the Ganzhou Basin are older than those of the Nanxiong Basin of Guangdong Province, which contains the relatively derived oviraptorid *Heyuannia* (Lü 2002; 2005).

**Institutional Abbreviations:** **HYM**, Heyuan Museum, Guangdong, China; **IVPP**, Institute of Vertebrate Paleontology & Paleoanthropology, Chinese Academy of Sciences, Beijing, China; **IGM**, Institute of Geology, Mongolia; **SDM**, Shandong Museum, Jinan, China.

## Systematic paleontology

### Theropoda Marsh, 1881

### Oviraptorosauria Barsbold, 1976

### Oviraptoridae Barsbold, 1976

### *Ganzhousaurus nankangensis* gen. et sp. nov.

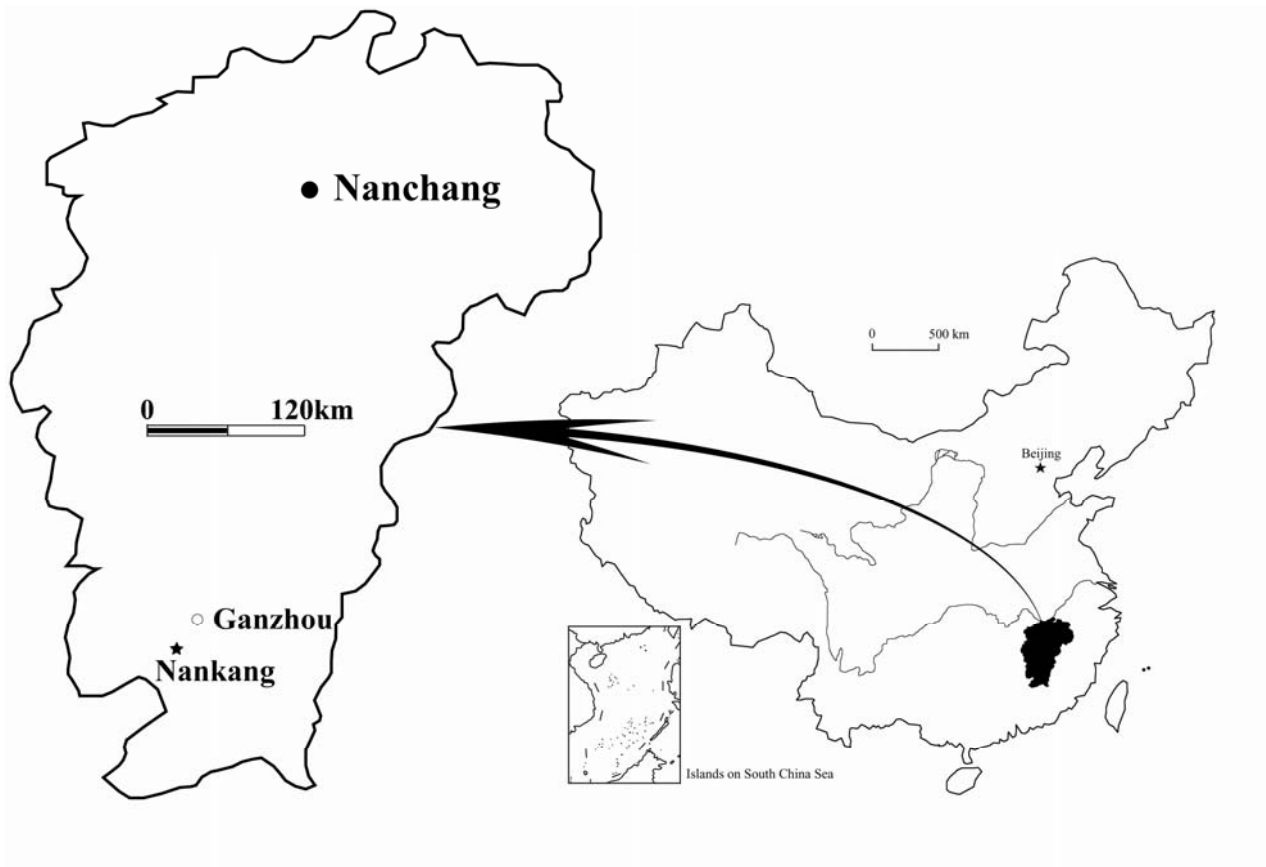
**Holotype:** SDM 20090302, a partial semi-articulated skeleton including the following elements: incomplete mandible, three articulated posterior caudal vertebrae, left partial ilium, midshaft portion of right tibia, and nearly complete articulated right pes (including metatarsals I-III, phalanges I-1, I-2, II-1, II-2, III-1 and IV-1, and parts of phalanges II-3, III-2 and IV-2).

**Type locality and horizon:** Upper Cretaceous Nanxiong Formation, Nankang County, near Ganzhou City, Jiangxi Province, China (Fig. 1).

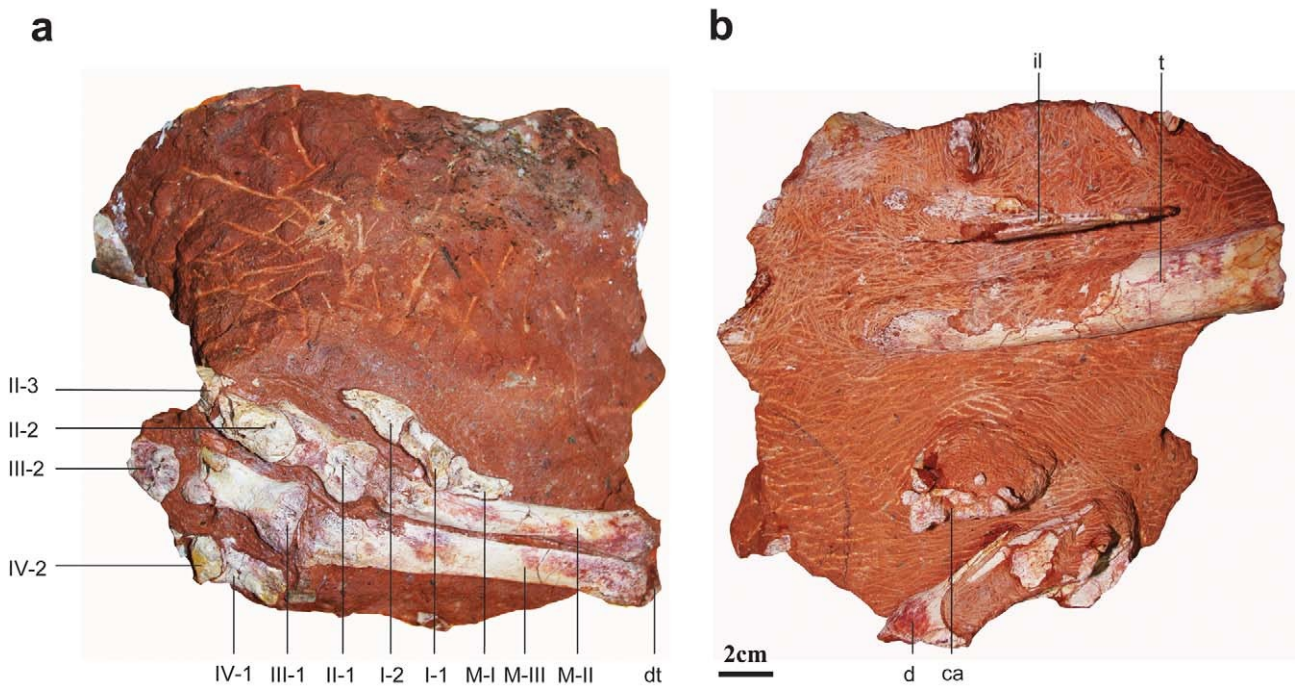
**Etymology:** The genus and species names both refer to the geographic location where the type specimen was found. The suffix of the genus name is derived from the Greek word *sauros*, lizard.

**Diagnosis:** An oviraptorid differing from other taxa in having the following unique combination of plesiomorphic and derived features: relatively shallow dentary (ratio of maximum anteroposterior length to maximum dorsoventral depth 1.90); absence of fossa or pneumatopore on lateral surface of dentary (as in oviraptorids but in contrast to *Gigantoraptor*, *Chiostenotes* and *Caenagnathasia*); weakly downturned anterior mandibular end (as in *Khaan*, but contrasting with strongly downturned end in *Nemegtomaia* and *Heyuannia*); shallow depression immediately surrounding anterior margin of external mandibular fenestra (as in *Gigantoraptor*, *Nemegtomaia* and *Heyuannia*, but feature absent in *Citipati* and *Khaan*); external mandibular fenestra subdivided by anterior process of surangular (as in all oviraptorids); dentary posteroventral process slightly twisted and positioned on mandibular ventrolateral surface (as in *Nemegtomaia*; process not twisted and positioned on lateral surface in *Citipati* and *Heyuannia*); shallow longitudinal groove along medial surface of dentary posteroventral process (present in *Microvenator celer*; condition uncertain in other oviraptorosaurs); angular anterior process wider transversely than deep dorsoventrally (unknown in other oviraptorosaurs); sharp groove along ventrolateral surface of angular anterior process (absent in most oviraptorosaurs, but present in *Chiostenotes*, *Gigantoraptor* and *Khaan*); ventral border of external mandibular fenestra formed mainly by angular (feature absent in other oviraptorids but present in *Chiostenotes* and *Gigantoraptor*); ventral flange along distal half of metatarsal II (absent in *Citipati*, the new Bayan Mandahu oviraptorid and *Heyuannia* but present in *Avimimus*); and

arctometatarsal condition absent (as in most oviraptorids, but in *Avimimus*, *Chirostenotes* and *Elmisaurus* the pes is arctometatarsal).



**FIGURE 1.** Map showing fossil locality that produced *Ganzhousaurus nankangensis* gen. et sp. nov.



**FIGURE 2.** Photographs of holotype of *Ganzhousaurus nankangensis* gen. et sp. nov. (SDM 20090302). **a**, ventral view of right pes; **b**, reverse side of block, showing ilium, tibia, right mandible and caudal series. Abbreviations: ca, caudal series; d, dentary; dt, distal tarsal; il, ilium; t, tibia; MI-III, metatarsal I-III. Roman numerals I-IV identify pedal digits, and Arabic numerals 1-3 identify phalanges within each digit in order from proximal to distal. Scale bar=2cm.

## Description and Comparisons

The specimen was originally preserved in one block, with the nearly complete articulated right pes exposed on one side (Fig. 2a) and the partial ilium, fragmentary right tibia, three articulated caudal vertebrae and partial mandible exposed on the other (Fig. 2b). In order to reveal more of the morphological features preserved in this specimen, we dismantled the block and prepared the mandible and caudal vertebrae free of matrix.

**Mandible.** The mandible is represented by the anterior half of the right ramus and some fragments of the left one. Preserved elements include most of the right dentary, as well as parts of the right angular, surangular and splenial (Fig. 3a, b).

The middle part of the mandible is slightly convex laterally in dorsal view, while its ventral margin lacks the convexity seen in *Nemegtomaia* (Lü *et al.* 2004). The external mandibular fenestra is tall (ratio of maximum height to maximum length around 1.0) and is surrounded by the dentary, angular and surangular as in other oviraptorids (Osmólska *et al.* 2004; Fig. 3a). The anterior margin of the external mandibular fenestra of the new taxon is located just posterior to the point at which the ventral margin of the dentary begins to curve downward, whereas the fenestra extends much farther anteriorly in *Banji* (Xu and Han 2010). The main part of the ventral border of the fenestra is formed by the angular.

The right dentary is nearly complete, lacking only the anterior end and the distal part of the posterodorsal branch. To some degree, the edentulous dentary is deep as in other oviraptorids. However, the ratio of the maximum anteroposterior length of the dentary (74mm, from the estimated position of the anterior end of the dentary to the posterior end of the posteroventral process) to its maximum dorsoventral depth (39mm, from the ventral margin of the dentary to the estimated position of the posterior end of the posterodorsal process) is 1.9, compared to 1.50 in *Citipati* (Clark *et al.* 2001, 2002), 1.74 in *Khaan* (Clark *et al.* 2002) and 1.38 in *Nemegtomaia* (Lü *et al.* 2004). This indicates that the dentary is shallower in the new taxon than in most other oviraptorids. The anterior part of the dentary curves medially, making the mandible U-shaped in dorsal view. The anterior end of the dentary is only slightly downturned, rather than strongly downturned as in *Nemegtomaia* and *Heyuannia* (Lü *et al.* 2004; Lü 2002, 2005). Some small air-filled chambers are revealed by the broken surface at the anterior end of the dentary, indicating that this part of the bone is highly pneumatized as in other oviraptorids (Osmólska *et al.* 2004). There are several small, irregularly arranged pits on the lateral surface of the dentary (Fig. 3d), although in *Ganzhousaurus nankangensis* this surface lacks both the pneumatopore seen in *Chirostenotes pergracilis* and *Caenagnathasia martinsoni* (Currie *et al.* 1993) and the sizeable anterior and posterior fossae seen in *Gigantoraptor erlianensis* (Xu *et al.* 2007). The small pits probably represent vascular foramina, and indicate that the dentary was probably covered by a keratinous rhamphotheca (Osmólska *et al.* 2004; Balanoff *et al.* 2009). A shallow depression lies immediately anterior to the external mandibular fenestra (Fig. 3d), but is much shallower than the corresponding feature in *Nemegtomaia* and *Heyuannia* (Lü *et al.* 2004; Lü 2002, 2005). A comparable depression is present in *Gigantoraptor* and is also present in *Microvenator* (Makovicky & Sues 1998: fig. 1). The posterodorsal branch of the dentary is much less dorsally directed than in other oviraptorids (Clark *et al.* 2001). The slender posteroventral process of the dentary is twisted so that the lateral surface faces ventrolaterally, and the medial surface of the process bears a shallow longitudinal groove. The latter feature is presumably shared with *Microvenator celer* (Makovicky & Sues 1998: fig. 1; and Longrich personal communication). A wide, shallow, ventrally facing groove is also present on the medial surface of the posterodorsal dentary branch, extending forward and downward (Fig. 3b). Anteriorly, this groove extends onto the anterior, medially curved part of the dentary, and remains subparallel to the ventral margin of the bone. A similar groove is also present in *Citipati*, but not in *Nemegtomaia* (Lü *et al.* 2004).

The angular is missing only its posterior end. The anterior process of the angular is wider transversely than deep dorsoventrally, and contributes most of the ventral border of the external mandibular fenestra (Fig. 3a). This configuration is also present in oviraptorosaurs such as *Chirostenotes pergracilis* and *Gigantoraptor erlianensis* (Sternberg 1940; Currie *et al.* 1993; Xu *et al.* 2007), but in previously known oviraptorids the posteroventral branch of the dentary forms almost all the ventral border of the external mandibular fenestra. A wide longitudinal groove that receives the posteroventral branch of the dentary is present along the ventrolateral edge of the angular anterior process, and gradually becomes shallower posteriorly (Fig. 3c). A similar condition is present in *Khaan* (Balanoff *et al.* 2012), *Gigantoraptor* (Xu *et al.* 2007) and *Chirostenotes* (Sternberg 1940).

The surangular is mediolaterally thinner than in *Citipati*, *Nemegtomaia* and the new Bayan Mandahu oviraptorid (Xu *et al.* 2013), with a smooth outer surface. The suture between the surangular and the angular is not clear (Fig. 3a). The anterior surangular margin is damaged, but the middle portion of the margin appears to be drawn anteriorly at least to some degree. This suggests that an anterior surangular process was present in this

animal, and would have subdivided the external mandibular fenestra as in other derived oviraptorosaurs (Osborn 1924; Osmólska *et al.* 2004).

The splenial is a strap-like bone that contacts the dentary anteriorly and extends posteriorly along the medial surface of the angular. The splenial closely approaches the posterior end of the angular, although the exact position at which the former bone terminates posteriorly is hard to determine.

**Vertebrae.** Although heavily weathered, the three articulated vertebrae present in the specimen are morphologically informative except on the right lateral side (Fig. 3e). The general morphology of the vertebrae, and the absence of laterally positioned pneumatic foramina, indicate that they are from the distal caudal region (Barsbold *et al.* 1990). The vertebrae are generally short, and are not as elongated as the distal caudal vertebrae of other theropods (Holtz 2004). They are approximately square in lateral view, and are even anteroposteriorly shorter than the distal caudal vertebrae of *Citipati*.

Only the anteriormost of the three preserved vertebrae is sufficiently well preserved to reveal morphological details. The centrum of this vertebra is anteroposteriorly shorter than is typical in non-oviraptorosaurian theropods (Barsbold *et al.* 1990), and the other two preserved centra decrease successively in both length and width. The slightly concave cranial articular surface of the anteriormost centrum is elliptical in shape, being wider than deep. Although the posterior articular surface cannot be observed, the relative flatness of the anterior surface suggests that the centrum is amphiplatyan. The transverse processes are ridge-like, unlike the well developed transverse processes seen in the caudal vertebrae of *Chirostenotes* (Sues 1997), and located at the widest point of the centrum as seen in cranial view. Ventrally, the centrum has a shallow longitudinal groove, flanked by a pair of weak, subparallel longitudinal ridges (Osmólska *et al.* 2004).

The right prezygapophysis of the first preserved caudal vertebra is stout and laterally compressed, with a rounded distal end. This prezygapophysis extends anterodorsally for a distance that would probably have been less than half of the length of the preceding centrum, unlike the elongated and anteriorly oriented distal caudal prezygapophyses of most non-oviraptorosaurian theropods (Holtz 2004; Norell & Makovicky 2004). In *Citipati*, by contrast, the prezygapophyses are cylindrical structures with pointed distal ends. The left postzygapophysis of the first preserved centrum is clearly shorter than the prezygapophysis, and is distorted in a manner that causes it to be overlapped by the prezygapophysis of the succeeding vertebra in such a way that morphological details cannot be observed. Only the anterior margin of the neural spine is preserved, but this structure was apparently very low and posteriorly located on the neural arch. The anterior groove for the interspinous ligament is narrow transversely.

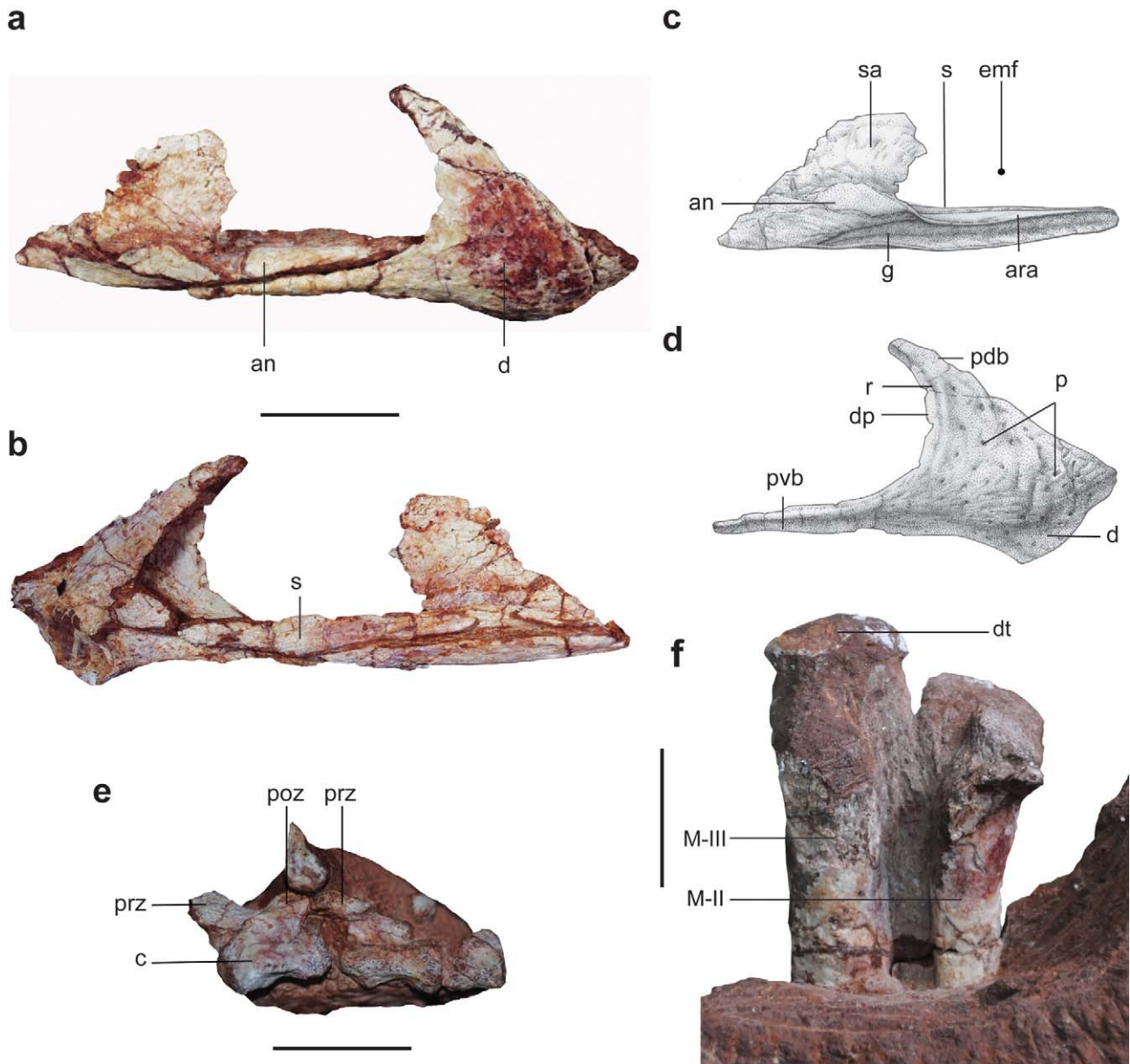
**Pelvis and Hindlimb.** The preserved iliac fragment probably represents the incomplete ischiadic peduncle of the left ilium, along with the ventral margin of the postacetabular process (Fig. 2b). A long bone fragment preserved near the partial ilium is interpreted as the middle part of the shaft of the right tibia (Fig. 2b). It is difficult to characterize the morphology of these bony elements due to their poor preservation.

The right pes is exposed in plantar view, and the proximal ends of metatarsals II and III are also visible after preparation. Metatarsals I–III are nearly complete, but metatarsals IV and V are missing. Most of the pedal elements are longer and more slender than in other oviraptorids, with the exception of *Citipati* (Table 1), and the pes is non-arctometatarsal.

**TABLE 1.** Measurements of selected pedal elements of *Ganzhousaurus nankangensis* gen. et sp. nov. and other oviraptorids. All values are in mm. Abbreviations: Kha, *Khaan mckennai* (IGM 100/1002); Cit, *Citipati osmolskae* (IGM 100/978); Hey, *Heyuannia huangi* (HYMV1-1); Wul, the new Bayan Mandahu oviraptorid (IVPP V 18409); Gan, *Ganzhousaurus nankangensis* gen. et sp. nov. (SDM 20090302). All measurements except those for *Heyuannia huangi* (which are from Lü 2005) were taken directly from the specimens listed.

Elements	Kha	Cit	Hey	IVPPV18409	Gan
Metatarsal I length	-	37	30	-	36
Metatarsal II length	91	176	110	119	125
Metatarsal III length	104	195	135	145	147
Metatarsal IV length	98	188	120	139	-
Metatarsal V length	35	-	-	-	-
Phalanx I-1 length	-	34	19	-	28
Phalanx II-1 length	-	-	35	-	41
Phalanx III-1 length	-	-	37	43	45





**FIGURE 3.** Mandible and postcranial skeleton of the holotype of *Ganzhousaurus nankangensis* gen. et sp. nov., SDM 20090302. **a**, lateral side of mandible; **b**, medial side of mandible; **c**, line drawing of angular and surangular in lateral view, showing the groove present on the anterior ramus of angular; **d**, line drawing of dentary in lateral view; **e**, distal caudal vertebrae; **f**, anterior view of proximal ends of metatarsals II and III. Abbreviations: an, angular; ara, anterior ramus of angular; c, centrum; d, dentary; dp, depression; dt, distal tarsal; emf, external mandibular fenestra; g, groove; p, pit; pdb, posterodorsal branch of dentary; poz, postzygapophyses; prz, prezygapophyses; pvb, posteroventral branch of dentary; r, ridge; s, splenial; sa, surangular; M-II–III, metatarsal II–III. Scale bar=2cm.

As in other oviraptorosaurs, the proximal end of the first metatarsal is reduced and positioned about one third of the way up the second metatarsal from the distal end (Zhou & Wang 2000; Zhou *et al.* 2000; Osmólska *et al.* 2004; He *et al.* 2008). However, the proximal end of metatarsal I is much more robust than in *Citipati* (Clark *et al.* 2001). Unlike in *Citipati* but in agreement with *Avimimus*, a prominent ventral flange is present along the distal half of metatarsal II, giving this bone a subtriangular mid-shaft cross-section. The proximal end of metatarsal II is greatly expanded mediolaterally as in other oviraptorids (Currie & Russell 1988; Osmólska *et al.* 2004). The proximal end of metatarsal III narrows slightly between metatarsals II and IV in anterior view (Fig. 3f), although there is much less narrowing than in *Citipati* and basal oviraptorosaurs (Zhou & Wang 2000; He *et al.* 2008). The cross-section of metatarsal III is rectangular as in *Heyuannia* (Lü 2005).

Only one distal tarsal is preserved, on the proximal end of the third metatarsal. The distal tarsal is a round, proximodistally flattened element preserved in articulation with the metatarsal, but the two bones are not co-ossified. This differs from the condition seen in *Avimimus*, in which the distal tarsals are co-ossified with the metatarsals (Kurzanov 2000; Vickers-Rich *et al.* 2002; Osmólska *et al.* 2004).

Except in digit V and the distal portions of digits II-IV (including phalanges III-3, III-4, IV-3, IV-4, IV-5, and the distal part of II-3), the pedal phalanges are preserved almost in natural articulation. The phalanges are short and robust, and the proximal phalanx is the longest in each digit. The first metatarsal bears two phalanges. Phalanx I-1 is more robust and slightly more medially curved than in *Chirostenotes* (Currie & Russell 1988), and much shorter and more slender than in *Citipati* (Clark *et al.* 2001). The collateral ligament fossae are located near the centers of the medial and lateral surfaces of the distal condyles, as seen in phalanges II-1 and II-2. Phalanx III-1 is the longest phalanx in the foot, measuring approximately 30% of the length of the third metatarsal as in *Heyuannia*, IVPPV18409 and the non-oviraptorid *Chirostenotes* (Currie & Russell 1988; Lü 2005; Xu *et al.* in press; Table 1). This ratio is 25% in *Similicaudipteryx* (He *et al.* 2008), indicating that larger values may be characteristic of caenagnathids and oviraptorids.

Comparisons with *Machairasaurus* (Longrich *et al.* 2010), *Shixinggia* (Lü & Zhang 2005) and *Luoyanggia* (Lü *et al.* 2009) are impossible due to the lack in these taxa of preserved elements that are equivalent to those known for *Ganzhousaurus nankangensis*.

## Discussion

*Ganzhousaurus nankangensis* is referable to the Oviraptorosauria based on the following combination of features: large external mandibular fenestra; dentary with two long posterior processes; caudal vertebrae with short amphiplatyan centra and anterodorsally directed prezygapophyses. This species can be identified as an oviraptorid based on the presence of the following derived features: deep edentulous mandible (Fig. 3a); tall external mandibular fenestra, with ratio of maximum height to maximum length about 1.0; and proximal end of metatarsal III robust (Osmólska *et al.* 2004).

To confirm the phylogenetic position of *G. nankangensis*, we conducted a phylogenetic analysis including this taxon using a modified version of the oviraptorosaur matrix of Longrich *et al.* (2010). The matrix was expanded by adding four characters and two taxa, for a total of 185 characters and 19 taxa (Appendix). The two added taxa are *Banji long* and *Ganzhousaurus nankangensis*, while the four newly added characters include:

182. Depression on lateral surface of dentary immediately anterior to external mandibular fenestra: absent (0) or present (1);

183. Ventral border of the external mandibular fenestra formed primarily by dentary (0) or angular (1);

184. Groove on ventrolateral edge of angular to receive posteroventral branch of dentary: absent (0) or present (1);

185. Posteroventral branch of dentary twisted so that lateral surface of branch faces somewhat ventrally: absent (0) or present (1);

The data file is available at DRYAD (<http://datadryad.org/doi:10.5061/dryad.dh546>). The data matrix was analyzed using the program TNT (Goloboff *et al.*, 2008), with three characters treated as ordered (Longrich *et al.* 2010). The analysis yielded nine most parsimonious trees, each with a length of 338 steps, a consistency index of 0.645 and a retention index of 0.701. In the strict consensus of these trees, oviraptorid interrelationships are well-resolved and *G. nankangensis* falls within the oviraptorid clade Oviraptorinae (Fig. 4). Oviraptorinae are characterized by large body size in comparison to Ingeniine oviraptorids (Table 1), a spur-like anterior process on the surangular, dorsal expansion of the frontonasal crest, and a relatively long forelimb and highly curved unguals resembling the caenagnathid condition (Longrich *et al.* 2010). Moreover, *Oviraptor* and *Ganzhousaurus* both have a relatively shallow dentary in comparison to ingeniine oviraptorids.

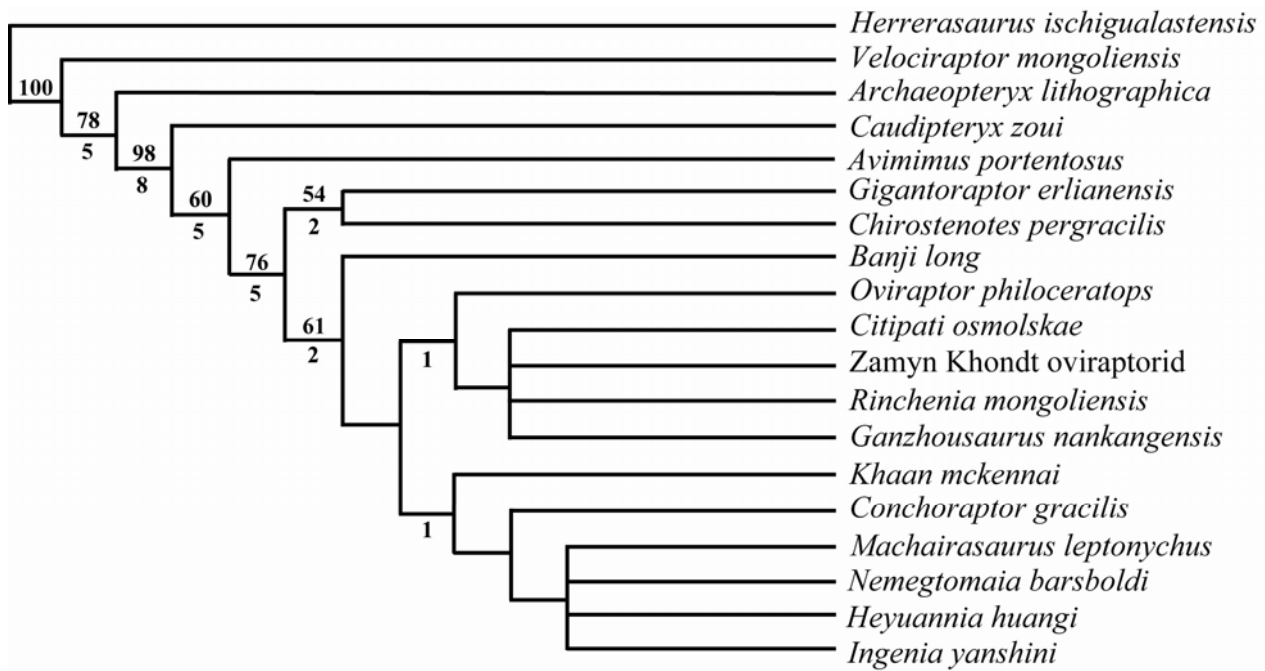
This phylogenetic hypothesis is weakly supported statistically. Bootstrap and Bremer support values for nodes within Oviraptoridae are low, although the monophyly of Oviraptoridae is more strongly supported (bootstrap value of 61). Accordingly, *Ganzhousaurus* appears to be an oviraptorid, but placement of this taxon within Oviraptorinae is tentative (Fig. 4). Interestingly, *Ganzhousaurus* shares some features with caenagnathids and with *Gigantoraptor*, which we recovered as the sister taxon of the one caenagnathid (*Chirostenotes*) included in the

analysis. These features include a shallow groove along the ventrolateral surface of the angular anterior process, and the fact that the angular forms almost all of the ventral border of the external mandibular fenestra. However, our analysis suggests that these features evolved independently in the *Gigantoraptor*-caenagnathid clade and in *Ganzhousaurus*. The shallow groove on the angular anterior process is also present in the oviraptorid *Khaan*, possibly indicating a third independent acquisition of this character.

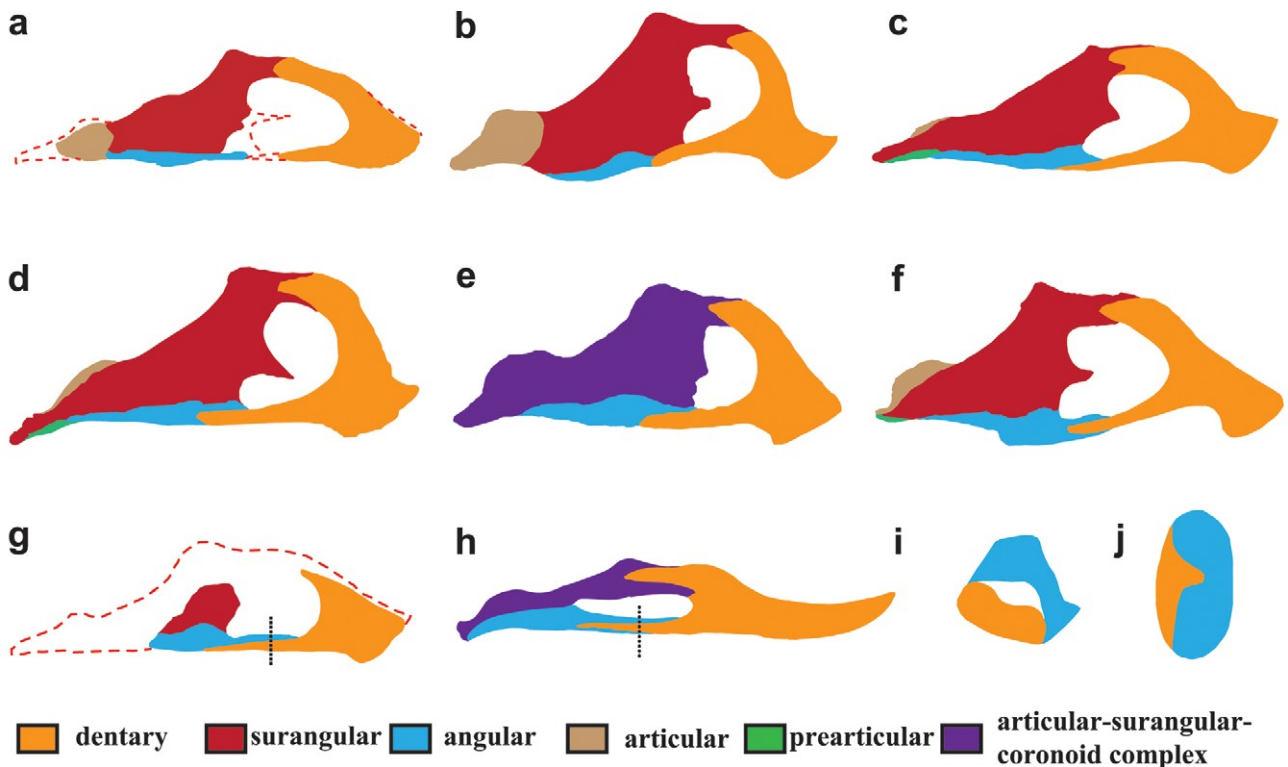
These resemblances to the *Gigantoraptor*-caenagnathid clade could be interpreted as evidence that *Ganzhousaurus* is a member of this lineage (Longrich personal communication). However, the dorsoventrally tall external mandibular fenestra of *Ganzhousaurus* is an equally compelling resemblance to oviraptorids, and one that contrasts sharply with the dorsoventrally lower fenestra seen in both *Gigantoraptor* and caenagnathids. Additionally, the deep mandible and proximally robust metatarsal III of *Ganzhousaurus* distinguish this taxon sharply from caenagnathids, though admittedly not from *Gigantoraptor*, and agree with the oviraptorid condition. Furthermore, the ventrolateral groove on the angular anterior process and the fact that the angular forms most of the ventral margin of the external mandibular fenestra are not entirely independent features in morphological terms, in that both are related to the extent and articular relationships of the angular anterior process. *Ganzhousaurus* and the caenagnathid-*Gigantoraptor* grouping may simply have independently evolved an unusual type of angular, characterized by a long anterior process that is appressed to the dorsomedial surface of the posteroventral branch of the dentary, and develops a ventrolateral groove to accommodate this contact. The relationships of *Ganzhousaurus* require further testing, ideally on the basis of more complete material and a data matrix including more caenagnathids, but we believe that referral of this taxon to the Oviraptoridae is the best supported hypothesis at present.

Variation in the configuration of the external mandibular fenestra region is extensive among oviraptorosaurs, and *Ganzhousaurus* makes a noteworthy contribution to this morphological diversity. *Incisivosaurus*, *Caudipteryx* and *Chirostenotes* have shallow and elongated lower jaws (Sternberg 1940; Zhou *et al.* 2000; Xu *et al.* 2002; Balanoff *et al.* 2009), and most derived oviraptorids have relatively short, deep mandibles with tall external mandibular fenestrae (Osmólska *et al.* 2004; Lü 2005). The composition of the ventral border of the external mandibular fenestra is variable among oviraptorosaurs (Fig. 5). In *Ingenia* and *Oviraptor*, the fenestra is largely bordered by the dentary and surangular. The posteroventral branch of the dentary extends along almost the entire ventral margin of the fenestra and overlaps the anterior end of the lateral surface of the angular, almost excluding this bone from the border of the fenestra in lateral view (Barsbold *et al.* 1990; Fig. 5a, b). In other oviraptorids, such as *Khaan* (Fig. 5c), *Citipati* (Fig. 5d), and *Heyuannia* (Fig. 5f), the external mandibular fenestra is surrounded by the dentary, angular and surangular in lateral view (Osborn 1924; Clark *et al.* 2001, 2002; Osmólska *et al.* 2004; Lü 2005). The dentary then borders the fenestra anterodorsally, ventrally and anteriorly, while the surangular forms most of the posterodorsal border. The angular makes only a slight contribution to the margin of the fenestra, near the posteroventral corner. In *Citipati* (Fig. 5d) and *Heyuannia* (Fig. 5f), however, the angular anterior process extends anteriorly between the splenial and the dentary, terminating at approximately the level of the anterior border of the external mandibular fenestra (Clark *et al.* 2001, 2002; Osmólska *et al.* 2004; Lü 2005). Thus, the angular anterior process cannot normally be seen in lateral view. In *Khaan*, the anterior process of the angular has a shallow longitudinal groove along its ventrolateral edge. The posteroventral dentary branch occupies this groove, but passes ventral to the angular posteriorly. In *Nemegtomaia*, the fenestra is surrounded by the dentary, the angular and the articular-surangular-coronoid complex. The articular-surangular-coronoid complex forms the posterodorsal border of the fenestra, while the dentary forms the anterior and ventral borders (Lü *et al.* 2004; Fig. 5e). In *Chirostenotes*, the same elements contribute to the border of the fenestra, but the articular-surangular-coronoid complex and the angular respectively form the dorsal and ventral margins. The posteroventral branch of the dentary is subtriangular in cross-section, and fits into a narrow groove along the lateral edge of the angular anterior process (Sternberg 1940; Fig. 5j). The dentary contributes only the anterior margin of the fenestra (Sternberg 1940; Currie *et al.* 1993; Fig. 5h). In *G. nankangensis*, the fenestra is surrounded by the dentary, angular and surangular as in most oviraptorids. However, the nature of the contact between the dentary posteroventral process and the angular anterior process resembles that seen in *Chirostenotes*, even though the mandible is much shorter and deeper in *G. nankangensis* (Fig. 5g). Thus, *G. nankangensis* resembles *Chirostenotes*, and differs from typical oviraptorids, in that most of the ventral margin of the external mandibular fenestra is formed by the angular rather than the dentary.





**FIGURE 4.** Strict consensus of oviraptorosaur interrelationships. The phylogenetic analysis resulted in 9 most parsimonious trees of 338 steps, each with a consistency index of 0.645 and a retention index of 0.701. Values above nodes represent bootstrap percentages (%), values below nodes represent Bremer support values. Bootstrap values lower than 20 are not shown.



**FIGURE 5.** Camera lucida drawings of oviraptorosaur mandibles in lateral view: **a**, *Oviraptor philoceratops*; **b**, *Ingenia yanshini*; **c**, *Khaan mckennai*; **d**, *Citipati osmolskae*; **e**, *Nemegtomaia barsboldi*; **f**, *Heyuannia huangi*; **g**, *Ganzhousaurus nankangensis* gen. et sp. nov.; **h**, *Chirostenotes pergracilis*; **i**, cross-section of bar ventral to external mandibular fenestra in *Ganzhousaurus nankangensis* gen. et sp. nov. (SDM 20090302), located 20 mm posterior to anterior end of angular; **j**, cross-section of bar ventral to external mandibular fenestra of *Chirostenotes pergracilis*, located 20 mm posterior to anterior end of angular (after Sternberg 1940); red dashed lines in **a** and **g** represent approximate estimated outline of complete mandible; black dashed lines in **i** and **j** mark positions of cross-sections. **a**, **d** after Clark *et al.* (2002); **b** after Barsbold *et al.* (1990); **c** after Clark *et al.* (2001); **f** after Lü (2005) and **h**, **j** after Sternberg (1940) and Currie *et al.* (1993). Not to scale.

The discovery of *G. nankangensis* not only increases the known diversity of oviraptorids, but more specifically represents the third definite oviraptorid reported so far from a small geographic area straddling the border between Guangdong and Jiangxi Provinces in southern China (Lü 2002, 2005; Lü & Zhang 2005; Xu & Han 2010). *Heyuannia huangi* and the controversial oviraptorid *Shixinggia oblita* were collected from northern Guangdong, geographically close to the city of Ganzhou (Lü 2002, 2005; Lü & Zhang 2005), while *Banji long*, *G. nankangensis* and three taxonomically indeterminate oviraptorid embryos were recovered from Ganzhou City itself (Cheng *et al.* 2008; Xu & Han 2010). Based on these finds, northern Guangdong and southern Jiangxi can be regarded as a new prime location for oviraptorid discoveries.

It is worth noting that an unnamed oviraptorid housed in the Nanxiong Museum (Nanxiong Museum No. E-1) resembles *G. nankangensis* in some respects (Lü 2005). This specimen comprises an incomplete lower jaw, two articulated posterior cervical vertebrae, some articulated dorsal vertebrae, and an incomplete right pes (Lü 2005). The length to height ratio of the lower jaw of the unnamed specimen is greater than in any other known oviraptorid, but still less than in Caenagnathidae. The maximum height/maximum length ratio of the external mandibular fenestra of this unnamed specimen is around 1.0 (measurement from Lü 2005), as in *G. nankangensis*. However, the ventral border of the external mandibular fenestra of the unnamed specimen has not been figured or described. Hence, further comparisons between *G. nankangensis* and the unnamed specimen will be necessary in order to determine whether they represent distinguishable taxa.

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**APPENDIX.** (Continued)

Taxa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1			
	7	7	7	7	7	7	7	7	7	8	8	8	8	8	8	8	8	8	8	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	
<i>Herrerasaurus ischigualastensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	?	
<i>Velociraptor mongoliensis</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	1	0	
<i>Archaeopteryx lithographica</i>	?	1	0	0	0	0	1	1	2	1	0	0	0	0	1	1	-	0	1	0	0	0	0	0	0	0	2	0	1	0	0	?	?	?	0	1	0	
<i>Avimimus portentosus</i>	0	?	1	?	?	1	1	?	?	?	0	1	?	?	?	?	?	1	1	0	0	0	?	?	?	?	2	1	?	1	1	0	0	0	1	1		
<i>Caudipteryx zoui</i>	?	0	?	?	1	1	1	?	?	?	2	?	?	?	0	0	0	1	?	?	?	?	?	?	?	1	?	?	?	0	2	1	0	?	?	?	?	?
<i>Chirostenotes pergracilis</i>	1	1	2	1	0	1	1	0	0	2	0	1	1	1	0	0	1	1	1	1	0	0	0	0	0	0	2	?	2	1	?	?	?	?	?	0	?	
<i>Gigantoraptor erlianensis</i>	1	1	2	1	1	1	1	2	0	2	0	1	1	1	0	0	1	1	1	1	1	1	1	1	?	?	?	?	1	?	1	?	?	?	?	?	?	
<i>Rinchenia mongoliensis</i>	1	1	1	1	1	1	1	2	1	2	?	0	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	2	1	2	1	1	1	1	1	0	0	1
Zamyn Khondt oviraptorid	1	1	1	1	1	1	1	2	1	2	2	0	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	2	1	2	1	1	1	1	1	0	1	1
<i>Conchoraptor gracilis</i>	1	1	1	1	1	1	1	2	1	2	?	0	1	1	0	0	1	1	1	1	1	1	1	1	1	1	2	1	2	1	1	1	1	1	1	0	1	1
<i>Ingenia yanshini</i>	1	1	1	1	1	1	1	2	1	2	?	0	1	1	0	0	1	1	1	1	1	1	1	1	1	1	2	1	2	1	?	1	1	0	0	1		
<i>Citipati osmolskae</i>	?	1	1	?	1	1	1	2	1	2	2	0	?	1	0	0	1	1	1	1	1	1	1	1	1	1	1	2	1	?	?	?	?	?	?	?		
<i>Khaan mckennai</i>	?	1	?	?	1	1	?	2	1	2	1	0	?	1	0	0	1	1	1	1	1	1	1	?	?	?	?	1	2	1	1	?	1	0	1	1		
<i>Machairasaurus leptonychus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Heyuannia huangi</i>	?	?	?	?	1	?	?	2	1	2	1	?	?	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	2	1		
<i>Nemegtomaia barsboldi</i>	1	?	1	1	1	1	1	2	1	2	?	1	1	1	0	0	1	1	1	1	1	1	?	1	1	?	1	2	1	1	?	?	?	?	?	1		
<i>Oviraptor philoceratops</i>	?	?	?	?	1	?	1	2	1	2	2	?	?	1	0	0	1	1	?	?	?	1	?	?	?	?	?	2	1	?	?	?	?	0	?	?		
<i>Banji long</i>	1	1	?	?	1	1	?	2	1	2	1	?	?	0	0	0	1	1	0	?	?	?	?	?	?	?	1	2	1	?	1	?	?	?	?	?		
<i>Ganzhousaurus nankangensis</i>	?	?	?	0	1	1	?	?	1	?	2	0	?	?	0	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	

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