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Authors: Lü, Junchang, Xu, Li, Liu, Yongqing, Zhang, Xingliao, Jia, Songhai, et al.

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A new troodontid theropod from the Late Cretaceous of central China, and the radiation of Asian troodontids

JUNCHANG LÜ, LI XU, YONGQING LIU, XINGLIAO ZHANG, SONGHAI JIA, and QIANG JI

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A new troodontid dinosaur, *Xixiasaurus henanensis* gen. et sp. nov., from the Upper Cretaceous Majiacun Formation of the Xixia Basin, Henan Province, is erected, based on a partial skull. It is characterized by bearing 22 maxillary teeth, a distinct opening on the lateral surface of the base of nasal process of the premaxilla, the rostral end of the upper jaw forming a tapered U-shape, and the mandibular symphyseal region slightly inflected medially. *Xixiasaurus* is most closely related to the Mongolian *Byronosaurus* among troodontids. *Byronosaurus*, *Urbacodon*, and *Xixiasaurus* may form a new clade, suggesting an endemic radiation of troodontids across Asia, including multiple taxa without dental serrations. The discovery of *Xixiasaurus* in the Xixia Basin may imply that the *Xixiasaurus*-bearing Majiacun Formation is Campanian in age.

Key words: Theropoda, Troodontidae, *Xixiasaurus*, Late Cretaceous, Henan Province, China.

Junchang Lü [Lujc2008@126.com], Yongqing Liu [liu_cags@126.com], and Qiang Ji [jirod@cags.net.cn], Institute of Geology, Chinese Academy of Geological Sciences, Beijing 100037, China;
Li Xu [zhzhxuli@sina.com], Xingliao Zhang [zhxliao@sina.com], and Songhai Jia [jiasonghai@163.com], Henan Geological Museum, Zhengzhou 450016, Henan Province, China.

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Introduction

Troodontidae is a clade of small, bird-like, lightly built maniraptoran theropods known from Cretaceous deposits of Asia and North America. They are characterized by a dorsoventrally flattened internarial bar, a large number of teeth, close packing of the dentary teeth, a depression on the ventral surface of the postorbital process of the laterosphenoid, reduced basal tubera that lie directly ventral to the occipital condyle (reversed in *Troodon formosus*), and elongate transverse processes (Makovicky and Norell 2004). Most of them have serrated teeth though a few have teeth lacking serrations. They have raptorial hands and an enlarged sickle-shaped claw on the foot, indicative of a predatory lifestyle. They bear one of the highest encephalization quotients among nonavian dinosaurs and had keen senses, as indicated by their enlarged orbits and well developed middle ear. Compared with other small theropod dinosaurs, the remains of troodontid dinosaurs are extremely rare, and only thirteen taxa have been described, mostly from central Asia (Osmólska and Barsbold 1990; Russell and Dong 1993; Makovicky and Norell 2004; Xu and Wang 2004). A new troodontid found from the Upper Cretaceous of Xixia County, Henan Province of central China is described here (Fig. 1). It represents the first *Byronosaurus*-like troodontid outside of the Gobi Region and northern China in Asia.

Institutional abbreviation.—HGM, Henan Geological Museum, Zhengzhou, Henan Province, China.

Systematic paleontology

Theropoda Marsh, 1881
Tetanurae Gauthier, 1986
Maniraptora Gauthier, 1986
Troodontidae Gilmore, 1924

Genus *Xixiasaurus* nov.

Etymology: *Xixiasaurus* refers to the theropod dinosaur found in the Chinese administrative unit Xixia County of Henan Province.

Type species: *Xixiasaurus henanensis* sp. nov.

Diagnosis.—As for the only species.

Xixiasaurus henanensis sp. nov.

Figs. 2–4.

Etymology: The specific name refers to Henan Province, in which the holotype site in Xixia County is found.

Holotype: A partial skull, an anterior portion of the lower jaw, and central portions of the ulna and radius, and a partial right manus with a complete first digit.

Type locality: Songgou Village, Zhangying of Wuliqiao Town, northeast region of Xixia County.

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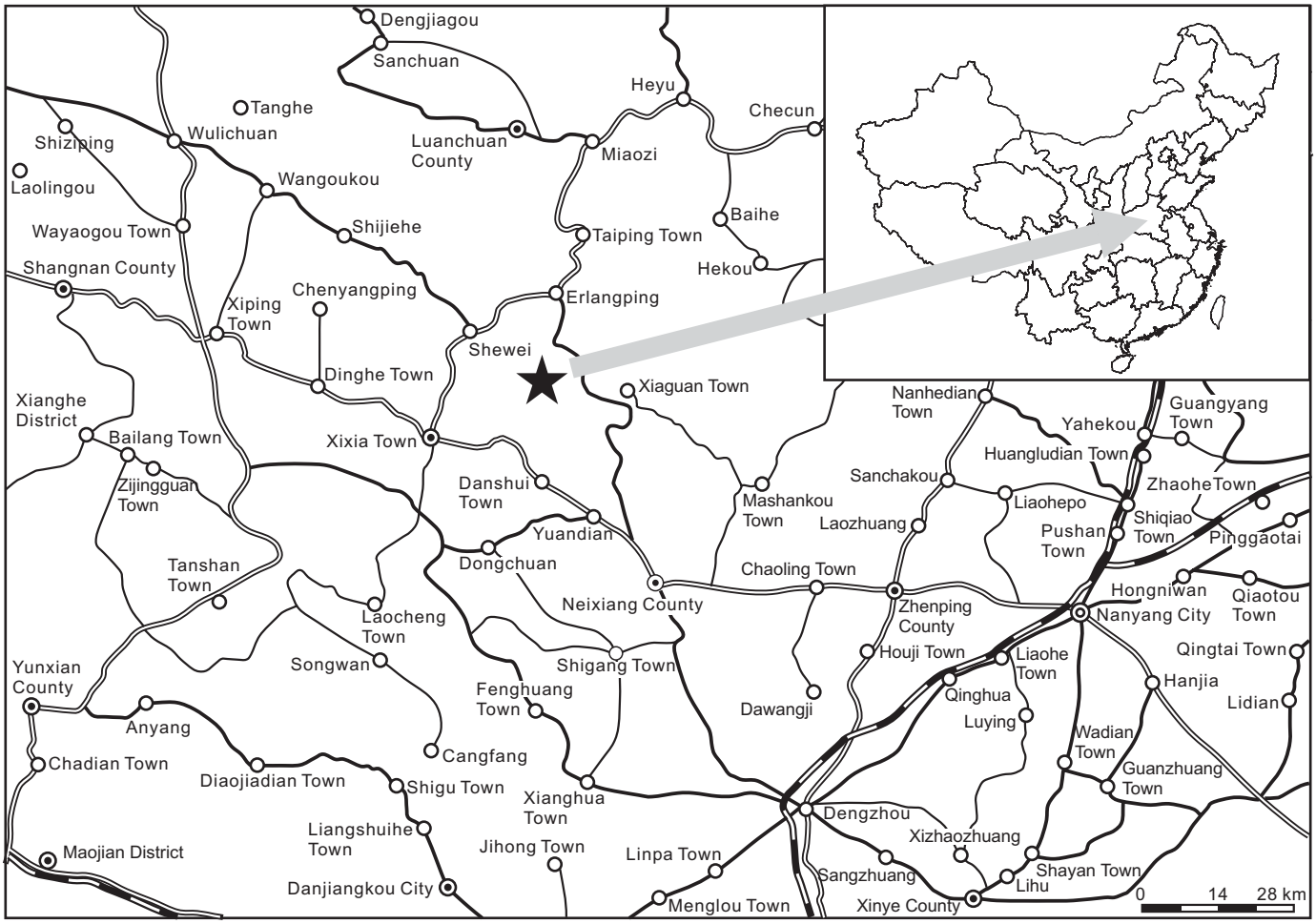


Fig. 1. The type locality of *Xixiasaurus henanensis* gen. et sp. nov.; lower to middle part of the Majiacun Formation (Upper Cretaceous: Coniacian–Campanian). The solid pentagon represents the fossil site near Songgou Village, Henan Province.

Type horizon: Mid-lower part of the Majiacun Formation (Coniacian–Campanian) (Wang et al. 2006; Chen et al. 2007; Pan et al. 2007).

Diagnosis.—Differs from other troodontids by having fewer maxillary teeth (which total 22) than *Byronosaurus* (> 30; Makovicky et al. 2003) and *Mei* (24; Xu and Norell 2004), but more than *Sinornithoides youngi* (18; Makovicky and Norell 2004), *Zanabazar junior* (20; Makovicky and Norell 2004; Norell et al. 2009), and *S. mongoliensis* (19; Makovicky and Norell 2004). It also has a distinct opening on the lateral surface of the base of the nasal process of the premaxilla, the rostral end of the upper jaw shows a more tapered U-shape than in *Byronosaurus*, and the mandibular symphyseal region is slightly inflected medially. Like *Byronosaurus*, *Mei*, *Urbacodon*, and *Anchiornis*, this new taxon has unserrated teeth, and like *Byronosaurus* it has a heterodont dentition and an extensive secondary bony palate. An extensive palate is also scored for *Saurornithoides mongoliensis* and *Troodon formosus* (see Varricchio 1997).

Description.—The skull is almost complete except for its posterior portion (Fig. 2). It is long and generally similar to that of *Byronosaurus*. The connection between nasals and frontals is displaced by preservation. Part of the braincase is missing; however, most of the rostral portion is preserved. The right side of the upper dentition is well-preserved. The posterior teeth are missing, but the tooth sockets are preserved. Thus, the tooth number can be determined accurately.

Both premaxillae are well-preserved and not fused to each other (Fig. 2A, B). The alveolar margin of the upper jaw forms a tapered U-shape in ventral view (Fig. 2C). The nasal process of the premaxilla extends posteriorly and is wedged between the premaxillary processes of the nasals. The nasal process of the premaxilla ends at the level of the posterior margin of the external narial opening. The process is quadrangular rather than triangular in cross-section, as seen in *Byronosaurus jaffei* (Makovicky et al. 2003). The nasal process of the premaxilla forms the anterodorsal corner of the external narial opening and has a distinct opening on the lateral surface at its base (Fig. 2B, premaxillary opening). A few small pits are present on the lateral surface of the premaxilla. The premaxilla/maxilla suture curves gently upward and straightens out below the nares in lateral view. The posteriorly tapering maxillary process of the premaxilla wedges between a small anteriorly extended process of the maxilla

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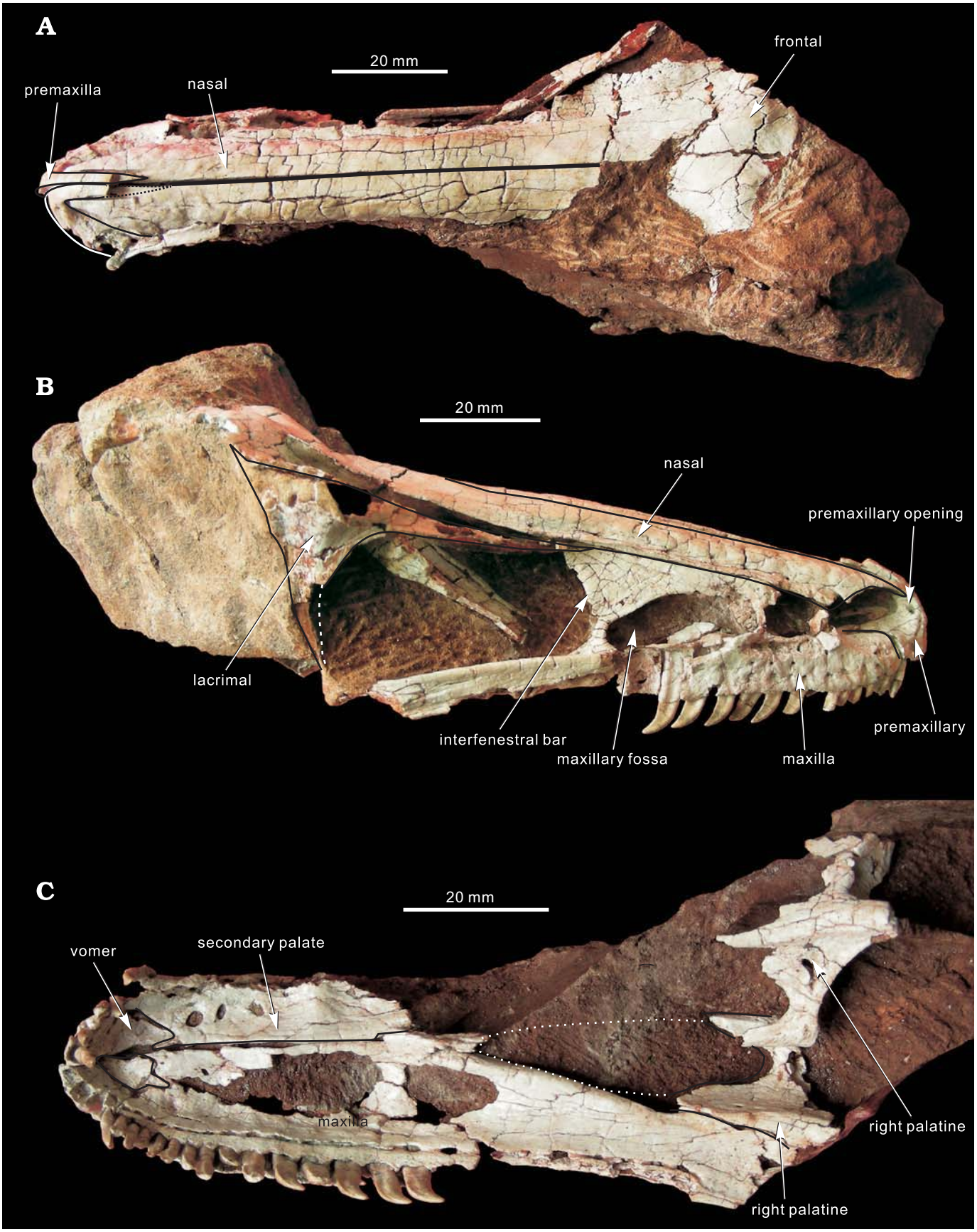


Fig. 2. Skull of troodontid theropod *Xixiasaurus henanensis* gen. et sp. nov. (HGM 41HIII-0201; holotype), lower– middle Majiacun Formation (Upper Cretaceous: Coniacian–Campanian), Henan Province, China; in dorsal (**A**); lateral (**B**), and ventral (**C**) views.

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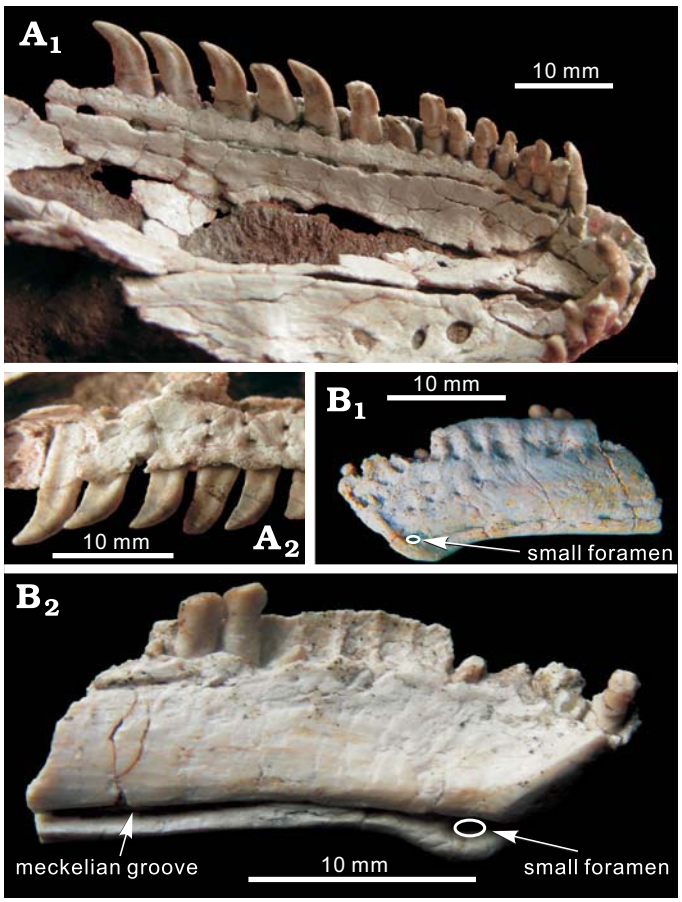


Fig. 3. A troodontid theropod *Xixiasaurus henanensis* gen. et sp. nov. (HGM 41HIII-0201; holotype), lower–middle Majiacun Formation (Upper Cretaceous: Coniacian–Campanian), Henan Province, China. **A**. Rostrum of skull in palatal (A_1) and right lateral (A_2) views. **B**. Anterior part of left dentary in lateral (B_1) and medial (B_2) views.

and the main body of the same bone. It excludes the maxilla medially from participation in the margin of the narial opening. The maxillary process of the premaxilla extends posteriorly to the same level as the nasal process. As in most theropod dinosaurs, there are four, closely packed premaxillary teeth, of which two crowns are missing on the left side, and three are missing on the right side. The tooth alveoli are sub-oval. The premaxillary teeth are smaller than the posterior maxillary teeth. There is a distinct constriction between the crown and root of the premaxillary teeth and the anterior ten maxillary teeth. The teeth are unserrated, with sharp, smooth carinae (Fig. $3A_1$, A_2) like those of *Byronosaurus jaffei* (Norell et al. 2000). The buccal surfaces of the tooth crowns are convex and the lingual surfaces are moderately concave. The ventral portions of the premaxillae are not fused, leaving a fissure along the mid-line of the premaxilla. Two small openings are present on the medial surface near the base of the third and fourth premaxillary teeth, but none is present near the first and second premaxillary teeth. These two small openings are connected by a shallow groove.

The maxilla is much longer than high and forms most of the lateral surface of the skull. Anteriorly, it forms nearly half of the floor of the external naris. The naris is suboval, with long axis parallel to the ventral margin of the maxilla (Fig. 2B). The maxilla rises gently posteriorly from the narial floor. The lateral surface below the narial chamber is covered with small pits and foramina as in *Byronosaurus jaffei* (Makovicky et al. 2003). This row of small pits and small openings is just dorsal and parallel to the dentigerous margin (Fig. $3A_2$), but they do not lie in a groove, differing from the case in *Byronosaurus jaffei*, where the pits lie in a groove (Makovicky et al. 2003). The lateral surface of the maxilla is perforated by three large, elongated openings (anterior, maxillary, and antorbital fenestrae). The anterior fenestra is probably completely enclosed by the maxilla as it is in *Byronosaurus jaffei* (Makovicky et al. 2003), but because of preservation damage, this is not definite. Two rows of small pits are present on the lateral surface of the maxilla below the first opening. The maxillary fenestra is backed by a perforated osseous wall, which is called the interfenestral bar (Fig. 2B). The wall separates the maxillary fenestra from the antorbital fenestra as in *Byronosaurus jaffei* (Makovicky et al. 2003). The antorbital fenestra lacks an osseous floor and is large and rectangular in lateral view, although the shape of the posterior margin of the antorbital fenestra is not clear due to poor preservation. Below the antorbital fenestra, the maxilla is low dorsoventrally and is devoid of the small foramina that are so conspicuous anteriorly. The dentition underlies most of the lower margin of the antorbital fenestra.

Ventrally, the longitudinally extensive shelf of the maxilla contributes to the large secondary palate and it extends posteriorly from the contact with the premaxilla and are joined by a median vomer at the anterior border of the choanae. Only a portion of the vomer is preserved. A portion of the palatine is preserved in both sides. The shape of the palatine is not clear due to the poor preservation.

There are three small openings on the anterior portion of the left palatal shelf of the maxilla. There is a row of nutrient foramina that lie in a groove just dorsal and parallel to the dentigerous margin (Fig. $3A_1$). The total number of maxillary teeth is 22 (8 are shown by alveoli only). The anterior 7 teeth are much smaller than the posterior ones and are closely packed, with distinct constrictions between the tooth crowns and tooth roots. The anterior and posterior carinae of the crowns are sharp but lack serrations. The lingual surfaces of crowns have distinct grooves adjacent to the carinae, which is similar to the teeth of *Urbacodon* (Averianov and Sues 2007) and *Mononykus* (Chiappe et al. 1996). Posterior to the tenth maxillary tooth, the bases of the crowns are less expanded, and the teeth curve posteriorly and are laterally compressed (Fig. $3A_2$). The maxillary teeth are heterodont, with the fifteenth tooth largest, based on the width of the tooth socket. More posterior teeth are smaller based on the widths of the tooth sockets.

The nasals are very elongated and not fused, indicating that the specimen represents an immature individual. The nasals are 99.9 mm long and 8.8 mm wide. They cover the top of the rostrum for most of its length. Anteriorly, the nasal forms the

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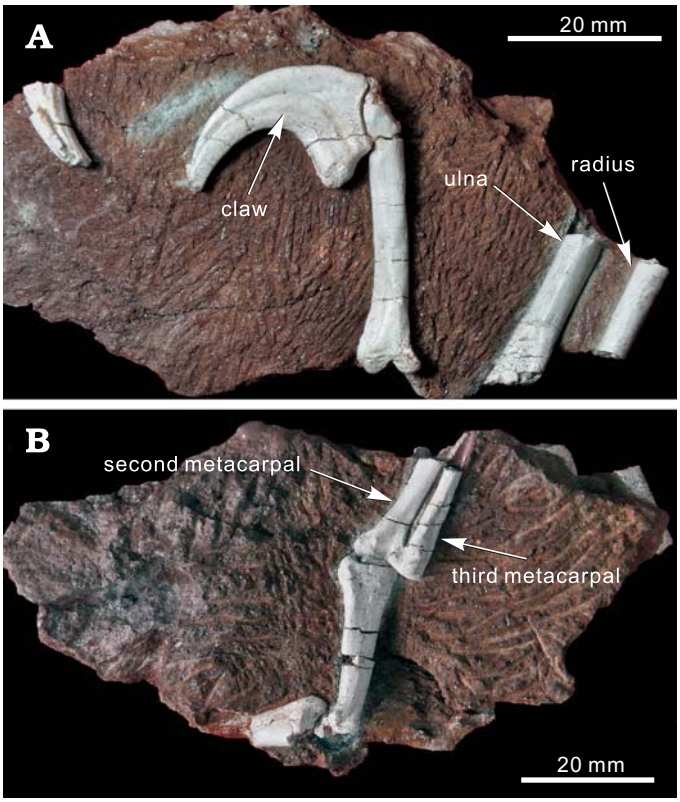


Fig. 4. A troodontid theropod *Xixiasaurus henanensis* gen. et sp. nov. (HGM 41HIII-0201; holotype), lower–middle Majiacun Formation (Upper Cretaceous: Coniacian–Campanian), Henan Province, China; partial right forelimb. **A**. First digit and partial ulna and radius. **B**. Distal ends of metacarpals II and III, first phalanx and proximal end of the second phalanx.

posterolateral boundary of the large external naris. Anteriorly, the nasal slopes dorsolaterally, while it flattens posteriorly.

The frontals (Fig. 2A) are 65 mm long and are not fused. Each frontal is triangular in dorsal view and reaches its maximum width at the point of contact with the postorbital, as in other troodontids. Rostrally, the lateral border of the frontal is overlapped by the nasal and lacrimal. The anteromedial portion of the frontal contacts the posterior end of the nasals. In lateral view, the posterior portion of the frontal is dome-like, indicating an enlarged braincase. The orbital rim is raised with weak notches along the margin. Medial to the orbital rim, a shallow trough is present on the lateral surface of the frontal.

A small portion of the ventral process of the right lacrimal is missing. The bone is T-shaped in lateral view. The anterior process of the lacrimal is very long, reaching the level of the anterior margin of the antorbital fenestra. It forms most of the posterodorsal border of the antorbital fenestra as in *Byronosaurus jaffei* (Makovicky et al. 2003).

A portion of the left squamosal is preserved. It contacts the parietal and postorbital medially. It is rod-like in dorsal view.

Only the anterior portion of the left dentary is preserved (Fig. $3B_1$, B_2). Thirteen tooth sockets (including three with broken teeth) are preserved. The preserved teeth and tooth sockets indicate that the teeth are small and closely packed. They are set in an open groove, as in other troodontids, rather than individual sockets (Currie 1987). The mandibular symphysis is short. The symphyseal region is slightly inflected medially. Two rows of nutrient foramina are present laterally, just below the anterior seven dentary teeth. Posterior to the seventh dentary tooth, only one row remains. The foramina lie in a labial groove, which is a diagnostic character of troodontid dinosaurs (Currie 1987). The medial surface of the dentary is smooth. A distinct deep, narrow groove (the Meckelian groove) is present just above the ventral margin of the dentary (Fig. $3B_2$). The Meckelian groove extends toward the mandibular symphysis and continues on the symphyseal surface almost to the anterior end of the dentary. Just posterior to the symphysis and ventral to the Meckelian groove, a distinct foramen is confluent with the inferior alveolar canal (Fig. $3B_1$, B_2). This is identical to the condition in *Urbacodon itemirensis* (Averianov and Sues 2007). On the lateral side of the bone at the same level as the Meckelian groove, there is a shallow groove with elongate pits.

A partial right forelimb (middle portion of the ulna and radius, distal ends of the second and third metacarpals, complete first digit, and first phalanx of the second digit) is preserved (Fig. 4). All the preserved parts are naturally articulated. The radius is much thinner than the ulna. The first metacarpal is missing. The third metacarpal is thinner than the second metacarpal and their distal ends are at the same level (Fig. $4A_2$), indicating that the second and third metacarpals are equal in length. The claw of the first digit is trenchant, with a large flexor tubercle. The first phalanx of the first digit is 3.6 cm long, and the first phalanx of the second digit is 3 cm long.

Stratigraphic and geographic range.—Only known from a single locality in the ?Campanian deposits of the Xixia Basin, Henan Province.

Discussion

Comparisons and familial allocation.—*Xixiasaurus* is assigned to the Troodontidae based on the following characters: a higher tooth count than most other theropods, including maniraptoran taxa such dromaeosaurids and avianlians; constriction between the tooth crown and root; close packing of dentary dentition near the rostral tip of the lower jaw; and presence of a distinct groove for the neurovascular foramina on the dentary (Currie 1987; Xu et al. 2002; Makovicky et al. 2003; Makovicky and Norell 2004). However, *Xixiasaurus* is different from most of troodontid dinosaurs, but similar to *Byronosaurus jaffei* (Norell et al. 2000), *Mei long* (Xu and Norell 2004) *Urbacodon itemirensis* (Averianov and Sues 2007) and *Anchiornis huxleyi* (Hu et al. 2009) in the dentition, which is unusual for theropod dinosaurs in that no serrations are found on the anterior or posterior carinae. This is also present in other theropods such as alvarezsaurids (Chiappe 1996), the ornithomimosaur *Pelecanimimus polyodon* (Pérez-Moreno et al.

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1994), the spinosaurid dinosaur *Spinosaurus aegyptiacus* (Stromer 1915), and toothed avialans (Makovicky et al. 2003). This obviously indicates that serrations were independently lost in several theropod lineages.

The tooth morphologies of the new troodontid are similar to those of *Byronosaurus* and *Urbacodon*, which were found at Ukhaa Tolgod, Mongolia (Norell et al. 2000; Makovicky et al. 2003) and Uzbekistan (Averianov and Sues 2007) respectively. This is the third troodontid dinosaur locality found in Asia outside of the Gobi Region and northern China.

Although *Xixiasaurus* is most similar to *Byronosaurus* in skull shape and tooth morphology, it differs in having fewer maxillary teeth (22 in *Xixiasaurus*, at least 30 in *Byronosaurus*), premaxillary teeth which are small but not so closely packed as in *Byronosaurus*; anterior end of the upper jaw of that is less U-shaped in ventral view, it is U-shaped in *Byronosaurus*. Moreover, the constrictions at the bases of the tooth crowns are much more distinct in *Xixiasaurus* than in *Byronosaurus*.

Xixiasaurus differs from *Mei* (Xu and Norell 2004) in having a more elongate snout, fewer maxillary teeth (22 in *Xixiasaurus*, and 24 in *Mei*) and its larger size.

Xixiasaurus shares with *Urbacodon itemirensis* (Averianov and Sues 2007) the unserrated teeth and a small foramen confluent with the inferior alveolar canal in the dentary; the latter is also present in *Troodon formosus* (Currie 1987). However, only the lower jaw and dentary teeth are known for *Urbacodon*, and only the anterior part of the lower jaw (with four incomplete teeth) is preserved in *Xixiasaurus*. The preserved partial tooth crowns of *Xixiasaurus* display smooth surfaces both on the lingual and labial sides. The lingual surfaces of the tooth crowns of *Urbacodon* display distinct striations, which is different from those of *Xixiasaurus*.

Xixiasaurus differs from *Sinornithoides* (Russell and Dong 1993) in that the alveolar margin of the upper jaw forms a tapered U-shape in ventral view, whereas it is a very elongate U-shape in *Sinornithoides* (Russell and Dong 1993); premaxillary teeth and maxillary teeth do not bear denticles (= serrations) in *Xixiasaurus*; however, denticles are present in *Sinornithoides*.

Xixiasaurus differs from *Sinusonasus* (Xu and Wang 2004) and *Sinovenator* (Xu et al. 2002) in the absence of serrations on both anterior and posterior carinae of teeth, while serrations are present in *Sinusonasus* (Xu and Wang 2004) and *Sinovenator* (Xu et al. 2002). *Xixiasaurus* differs from *Saurornithoides* (Barsbold 1974) in the absence of serrations on all the teeth.

Jinfengopteryx elegans was initially regarded as a basal avian (Ji et al. 2005; Ji and Ji 2007), but currently it is regarded as a troodontid dinosaur (Xu and Norell 2006; Turner et al. 2007). The teeth of *Jinfengopteryx* lack serrations, which are similar to those of *Xixiasaurus*; however, the tooth morphologies and the skull shapes are different. The skull of *Jinfengopteryx* is more or less triangular, with a relatively shorter and higher preorbital portion (Ji and Ji 2007), and the tooth crowns are conical, different from those of *Xixiasaurus*, whose preorbital portion is distinctly long and low, and the teeth are laterally compressed.

Anchiornis huxleyi is the oldest troodontid reported so far (Hu et al. 2009). *Xixiasaurus* differs from *Anchiornis* in that the skull of *Anchiornis* is sub-triangular with a relatively shorter and higher preorbital portion in lateral view; the preorbital portion of the skull of *Xixiasaurus* is distinctly long and low. The teeth of *Anchiornis* lack serrations, which are similar to those of *Xixiasaurus*; however, the tooth morphologies are different in the two taxa.

The radiation of Asian troodontid dinosaurs.—Troodontid dinosaurs are largely restricted to the Northern Hemisphere. To date, twelve species belonging to ten genera of troodontids have been reported from Asia. They are *Saurornithoides mongoliensis* (see Osborn 1924) from the ?middle Campanian, *Zanabazar junior* (see Barsbold 1974; Norell et al. 2009) from the early Maastrichtian, *Borogovia gracilicrus* (see Osmólska 1987) from the early Maastrichtian, *Tochisaurus nemegtensis* (see Kurzanov and Osmólska 1991) from the early Maastrichtian, *Sinornithoides youngi* (see Russell and Dong 1993) from Late Cretaceous, *Byronosaurus jaffei* (see Norell et al. 2000) from the ? middle Campanian, *Sinovenator changii* (see Xu et al. 2002) from the Barremian, *Mei long* (see Xu and Norell 2004) from the Early Cretaceous, *Sinusonasus magnodens* (see Xu and Wang 2004) from the Hauterivian, *Jinfengopteryx elegans* (Ji et al. 2005; Ji and Ji 2007; Xu and Norell 2006; Turner et al. 2007) from the Early Cretaceous, *Urbacodon itemirensis* from the Cenomanian (see Averianov and Sues 2007), and *Anchiornis huxleyi* from the earliest Late Jurassic Tiaojishan Formation of western Liaoning (Xu et al. 2009; Hu et al. 2009). *Sinovenator* was once regarded as a basal troodontid dinosaur (Xu et al. 2002), and its more distal teeth bear small denticles like those of dromaeosaurids, and unlike the enlarged denticles of derived troodontids (Makovicky and Norell 2004). However, *Anchiornis* represents the oldest troodontid reported so far (Hu et al. 2009). The discovery of the troodontid *Anchiornis* from the earliest Late Jurassic deposits confirms that Troodontidae have had a long independent history that preceded the Early Cretaceous, as Currie and Dong (2001) thought. The serrationless teeth of *Anchiornis* indicate that the earliest troodontid forms (teeth with serrations) may be traced back to at least in the early Jurassic. Ever increasing fossil discoveries also suggest that troodontid dinosaurs reached their greatest diversity, especially in the variety tooth morphologies, during the Campanian in Asia.

The functional significance of the loss of serrations on the teeth of some troodontid dinosaurs.—Troodontid dinosaurs are considered to have been carnivorous based on the following characters: individual denticles curve distally toward the tip of the tooth, are sharply pointed, and have razor-sharp enamel ridges between the adjacent denticles, and have blood grooves at the base (Currie and Dong 2001). However, Holtz et al. (1998) suggested the possibility that troodontids may have been herbivorous, because the size of

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their serrations is similar to those of herbivorous dinosaurs rather than other carnivores. This idea has not been widely accepted (Currie and Dong 2001). The lack of serrations on the anterior and posterior carinae of the teeth in *Byronosaurus*, *Urbacodon*, and *Xixiasaurus* may indicate that the loss may be related to the change of food sources. The teeth lost their typical meat-slicing function. At least in some troodontid dinosaurs, such as *Byronosaurus*, *Urbacodon*, and *Xixiasaurus*, the teeth may indicate that these animals were either herbivorous or omnivorous.

Geological age of the Majiacun Formation.—In previous studies, the Majiacun Formation was described as Cenomanian to Turonian (Zhou et al. 1983) in age on the bases of spores and pollens, and dinosaur egg fossils. Later, Wang et al. (2006) thought that the Majiacun Formation correlated with the Coniacian–Santonian. Based on studies of bivalves and gastropods, the Majiacun Formation is regarded as Coniacian to Campanian (Chen et al. 2007), and Santonian to Maastrichtian, respectively (Pan et al. 2007). *Byronosaurus* is found in Campanian age sediments (Norell et al. 2000; Makovicky and Norell 2004), and *Xixiasaurus* is more closely related to *Byronosaurus* than other troodontid dinosaurs. Thus it is inferred that the geological age of the Majiacun Formation may be Campanian, which agrees with the ranges suggested by Chen et al. (2007) and Pan et al. (2007). The minimum age for the dispersal of the *Troodon* lineage to North America from Asia was regarded to be Campanian or earlier (Makovicky and Norell 2004). Greatest diversity of troodontid dinosaurs was achieved during the Campanian.

Comments on the status of *Byronosaurus*.—*Byronosaurus* is assigned to Troodontidae on the basis of the following characters: numerous densely packed teeth (more than 22 upper and 17 lower teeth; this is fewer than 19 and 17, respectively, in dromaeosaurid dinosaurs; although there are 24 maxillary teeth and 40 dentary teeth in some therizinosauroids, the tooth morphologies are different from those of troodontids); constriction between the tooth crown and root; close packing of dentary dentition near the rostral tip of the lower jaw, presence of a distinct groove for the neurovascular foramen on the dentary and a dorsoventrally flattened internarial bar (Currie 1987; Xu et al. 2002; Makovicky et al. 2003; Clark et al. 2004; Makovicky and Norell 2004; Norell and Makovicky 2004). However, *Byronosaurus* differs from other troodontid dinosaurs in that its teeth are devoid of serrations on the anterior and posterior carinae; and in having a horizontal groove with small foramina on the maxilla adjacent and parallel to the tooth row (Norell et al. 2000). The teeth of *Xixiasaurus* are similar to those of *Byronosaurus*, and they are not only heterodont, but also display a different shape. The discovery of *Xixiasaurus* suggests the possibility that *Byronosaurus*, *Urbacodon*, and *Xixiasaurus* may form a clade, indicating that there was a wide radiation of troodontids across Asia including multiple taxa without dental serrations.

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References

Averianov, A.O. and Sues, H.-D. 2007. A new troodontid (Dinosauria: Theropoda) from the Cenomanian of Uzbekistan, with a review of troodontid records from the territories of the Former Soviet Union. *Journal of Vertebrate Paleontology* 27: 87–98. http://dx.doi.org/10.1671/0272-4634(2007)27%5B87:ANTDTF%5D2.0.CO;2

Barsbold, R. 1974. Saurornithoididae, a new family of carnivorous dinosaurs from Central Asia and North America. *Palaeontologia Polonica* 30: 5–22.

Chen, J.H., Wang, D.Y., Feng, J.C., Fu, G.H., and Zhu, S.G. 2007. Late Cretaceous non-marine bivalves from the dinosaur egg-bearing strata of Xixia Basin, Henna, China [in Chinese with English abstract]. *Acta Palaeontologica Sinica* 46: 299–313.

Chiappe, L.M. 1996. Early avian evolution in the Southern Hemisphere: The fossil record of birds in the Mesozoic of Gondwana. *Memoirs of the Queensland Museum* 39: 533–554.

Chiappe, L.M., Norell, M.A., and Clark, J.M. 1996. Phylogenetic position of *Mononykus* (Aves: Alvarezsauridae) from the Late Cretaceous of the Gobi Desert. *Memoirs of the Queensland Museum* 39: 557–582.

Clark, J.M., Maryańska, T., and Barsbold, R. 2004. Therizinosauroidea. *In*: D.B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria* (Second Edition), 151–164. University of California Press, Berkeley.

Currie, P.J. 1987. Bird-like characteristics of the jaws and teeth of troodontid theropods (Dinosauria, Saurischia). *Journal of Vertebrate Paleontology* 7: 72–81.

Currie, P.J. and Dong, Z.M. 2001. New information on Cretaceous troodontids (Dinosauria, Theropoda) from the People's Republic of China. Results from the Sino-Canadian Dinosaur Project. Part 3. *Canadian Journal of Earth Sciences* 38: 1753–1766. http://dx.doi.org/10.1139/cjes-38-12-1753

Holtz, T.R., Brinkman, D.L., and Chandler, C.L. 1998. Denticle morphometrics and a possibly omnivorous feeding habit for the theropod dinosaur *Troodon*. *Gaia* 15: 159–166.

Hu, D., Hou, L.H., Zhang, L.J., and Xu, X. 2009. A pre-*Archaeopteryx* troodontid theropod from China with long feathers on the metatarsus. *Nature* 461: 640–643. http://dx.doi.org/10.1038/nature08322

Ji, Q., Ji, S., Lü, J.C., You, H.L., and Yuan, C.X. 2005. First avialan bird from China (*Jinfengopteryx elegans* gen. et sp. nov.). *Geological Bulletin of China* 24: 197–205.

Ji, S. and Ji, Q. 2007. *Jinfengopteryx* compared to *Archaeopteryx*, with comments on the mosaic evolution of long-tailed avialan birds. *Acta Geologica Sinica* (English Edition) 81: 337–343.

Kurzanov, S.M. and Osmólska, H. 1991. *Tochisaurus nernegtensis* gen. et sp. n., a new troodontid (Dinosauria, Theropoda) from Mongolia. *Acta Palaeontologica Polonica* 36: 69–76.

Makovicky, P.J. and Norell, M.A. 2004. Troodontidae. *In*: D.B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria* (Second Edition), 184–195. University of California Press, Berkeley.

doi: 10.4202/app.2009.0047

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Makovicky, P.J., Norell, M.A., Clark, J.M., and Rowe, T. 2003. Osteology and relationships of *Byronosaurus jaffei* (Theropoda: Troodontidae). *American Museum Novitates* 3402: 1–32. http://dx.doi.org/10.1206/0003-0082(2003)402%3C0001:OAROBJ%3E2.0.CO;2

Norell, M.A. and Makovicky, P.J. 2004. Dromaeosauridae. *In*: D.B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria* (Second Edition), 196–209. University of California Press, Berkeley.

Norell, M.A., Makovicky, P.J., and Clark, J.M. 2000. A new troodontid from Ukhaa Tolgod, Late Cretaceous, Mongolia. *Journal of Vertebrate Paleontology* 20: 7–11. http://dx.doi.org/10.1671/0272-4634(2000)020%5B0007:ANTTFU%5D2.0.CO;2

Norell, M.A., Makovicky, P.J., Bever, G.S., Balanoff, A.M., Clark, J.M., Barsbold, R., and Rowe, T.B. 2009. A review of the Mongolian Cretaceous dinosaur *Saurornithoides* (Troodontidae, Theropoda). *American Museum Novitates* 3654: 1–63.

Osborn, H.F. 1924. Three new Theropoda, *Protoceratops* zone, central Mongolia. *American Museum Novitates* 144: 1–12.

Osmólska, H. 1987. *Borogovia gracilicrus* gen. et sp. n., a new troodontid dinosaur from the Late Cretaceous of Mongolia. *Acta Palaeontologica Polonica* 31: 133–150.

Osmólska, H. and Barsbold, R. 1990. Troodontidae. *In*: D.B. Weishampel, P. Dodson, and H. Osmólska (eds), *The Dinosauria*, 259–268. University of California Press, Berkeley.

Pan, H.Z., Wang, D.Y., Feng, J.C., Fu, G.H., and Zhu, S.G. 2007. Late Cretaceous non-marine Gastropoda from the dinosaur egg-bearing strata of Xixia Basin, Henna [in Chinese with English abstract]. *Acta Palaeontologica Sinica* 46: 293–298.

Pérez-Moreno, B.P., Sanz, J.L., Buscalioni, A.D., Moratalla, J.J., Ortega, F., and Raskin-Gutman, D. 1994. A unique multitoothed ornithomimosaur from the Lower Cretaceous of Spain. *Nature* 370: 363–367. http://dx.doi.org/10.1038/370363a0

Russell, D.A. and Dong, Z.M. 1993. A nearly complete skeleton of a new troodontid dinosaur from the Early Cretaceous Ordos Basin, Inner Mongolia, People's Republic of China. *Canadian Journal of Earth Sciences* 30: 2163–2173.

Stromer, E. 1915. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltier-Reste der Baharîje-Stufe (unterstes Cenoman). 3. Das Original des Theropoden *Spinosaurus aegyptiacus* nov. gen., nov. spec. *Abhandlungen der Königlich Bayerischen Akademie der Wissenschaften, Mathematisch-physikalische Klasse* 28 (3): 1–32.

Turner, A.H., Pol, D., Clark, J.A., Erickson, G.M., and Norell, M.A. 2007. A basal dromaeosaurid and size evolution preceding avian flight. *Science* 317: 1378–1381. http://dx.doi.org/10.1126/science.1144066

Varricchio, D.J. 1997. Troodontidae. *In*: P.J. Currie and K. Padian (eds.), *Encyclopedia of Dinosaurs*, 749–754. Academic Press, San Diego.

Wang, D.Y., Chen, P.J., Chen, J.H. , Cao, M.Z., Pan H.Z., Li, G., Zhu, S.G., Feng, Z.J., Wu, S.Q., Pang, F.J., and Li, G.W. 2006. Discovery of invertebrate fossils from the dinosaurian egg-bearing strata in the Xixia Basin of Henan, China [in Chinese with English abstract]. *Acta Palaeontologica Sinica* 45: 494–497.

Xu, X. and Norell, M.A. 2004. A new troodontid dinosaur from China with avian-like sleeping posture. *Nature* 43: 838–841. http://dx.doi.org/10.1038/nature02898

Xu, X. and Norell, M. 2006. Non-avian dinosaur fossils from the Lower Cretaceous Jehol Group of western Liaoning, China. *Geological Journal* 41: 419–437. http://dx.doi.org/10.1002/gj.1044

Xu, X. and Wang, X.L. 2004. A new troodontid (Theropoda: Troodontidae) from the Lower Cretaceous Yixian Formation of Western Liaoning, China. *Acta Geologica Sinica* 78: 22–26.

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

Xu, X., Zhao, Q., Norell, M., Sullivan, C., Hone, D., Erickson, G., Wang, X., Han, F., and Guo, Y. 2009. A new feathered maniraptoran dinosaur fossil that fills a morphological gap in avian origin. *Chinese Science Bulletin* 54: 430–435. http://dx.doi.org/10.1007/s11434-009-0009-6

Zhou, S.Q., Han, S.J., and Zhang, Y.C. 1983. Late Cretaceous Strata of Xixia Basin, Henan Province. *Journal of Stratigraphy* 7: 64–70.

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