Journal of Vertebrate Paleontology 25(1):107–118, March 2005

THE SMALL THEROPOD DINOSAURS *TUGULUSAURUS* AND *PHAEDROLOSAURUS* FROM THE EARLY CRETACEOUS OF XINJIANG, CHINA

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ABSTRACT—The type material of the small theropod dinosaurs *Tugulusaurus faciles* and *Phaedrolosaurus ilikensis* from the Lower Cretaceous (?Valanginian–Albian) Lianmugin Formation of Xinjiang, north-western China, is reviewed. Although based on an incomplete and rather poorly preserved specimen, *Tugulusaurus* can be shown to be valid on the basis of strongly broadened caudal vertebrae with an anteriorly placed neural arch and a short and highly asymmetrical metacarpal I. *Phaedrolosaurus*, based on an isolated tooth, must be considered a nomen dubium. A partial hind limb originally referred to this taxon can be demonstrated to be a distinct taxon of theropod on the basis of a posteriorly expanded fibular condyle on the proximal tibia and a longitudinal groove on the anterior side of the proximal end of the fibula. It is made the type of a new taxon, *Xinjiangovenator parvus* gen. et sp. nov. Whereas *Tugulusaurus* is the most basal coelurosaur known, *Xinjiangovenator* represents a maniraptoran.

INTRODUCTION

Although the Late Cretaceous theropod faunas from central and eastern Asia are well known from numerous finds in Mongolia and China, the evolution of this group in the Lower Cretaceous of Asia was poorly understood until recently.

Several theropod taxa have been found in predominantly Aptian–Albian aged sediments in Mongolia and China in the last twenty years (e.g., Barsbold and Perle, 1984; Barsbold et al., 1987; Russell and Dong, 1993a, b). In eastern Asia, the discovery of numerous non-avian theropod fossils of Barremian age (Swisher et al., 1999) from the Yixian Formation (= Chaomidianzi Formation of Ji et al., 1999) in Liaoning, China, has greatly improved our understanding of coelurosaur evolution in the early parts of the Early Cretaceous (e.g., Chen et al., 1998; Ji et al., 1999; Xu, Tang, and Wang, 1999; Xu, Wang, and Wu, 1999; Xu et al., 2000, 2002).

Several Early Cretaceous theropods from China and Mongolia show close phylogenetic relationships with taxa of similar age from Europe (e.g., ornithomimosaurs: Barsbold and Perle, 1984; Pérez-Moreno et al., 1994), as is the case with other vertebrates (e.g., ornithopods: Norman, 1998; multituberculates: Hahn and Hahn, 1992) and close biogeographic relationships and faunal exchanges between the two continents in the Early Cretaceous have often been suggested (e.g., Russell, 1993; Upchurch et al., 2001). Unfortunately, however, the central Asian fossil record of Early Cretaceous theropods is extremely poor.

In 1973, Dong described three theropod taxa from the Lianmugin Formation of Xinjiang, China, as *Kelmayisaurus petrolicus*, *Phaedrolosaurus ilikensis*, and *Tugulusaurus faciles*. The material comes from the Wuerho area, where pterosaur remains were first discovered by local geologists in 1963. The theropod material was collected during an Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) expedition in 1964, during which five sites were excavated in the Wuerho area. Site 64041 has yielded not only *Phaedrolosaurus* and *Tugulusaurus*, but also the pterosaurs *Dsungaripterus weii* and *Noripterus complicidens*, the sauropod cf. *Asiatosaurus mongoliensis*, and the turtle *Sinemys wuerhoensis*. An articulated partial theropod hindlimb from a different locality was also referred to *Phaedrolosaurus* (Dong, 1973; Sues 1977). The type specimens of *Phaedrolosaurus ilikensis* and *Tugulusaurus faciles* were collected from gray sandy mudstones and light green-gray sandstones of the lower part of the Lianmugin Formation, Tugulu Group (Zhao, 1980).

Coming from the westernmost part of China, these remains are of great interest in terms of their relationships with East Asian and European theropods from the Lower Cretaceous. However, they have received little attention since their original description, presumably due to the fragmentary nature of the type specimens. *Kelmayisaurus*, the only large theropod known from the Lianmugin Formation, was considered valid by Molnar et al. (1990), although the species is based only on a fragmentary maxilla and dentary. *Phaedrolosaurus* and *Tugulusaurus* were listed as nomina dubia by Norman (1990), but not discussed in the text.

In the present paper, the small theropods from the Lianmugin Formation, *Tugulusaurus* and *Phaedrolosaurus*, are reviewed and the phylogenetic relationships of the material are discussed. *Kelmayisaurus* is not taken into consideration here; because of the fragmentary nature of the type material and the lack of clearly diagnostic characters, this taxon should be regarded as a nomen dubium.

For sources of data in the comparative statements provided in the descriptions and discussion, see the literature in appendix I and the list of material examined in Rauhut (2003).

Institutional abbreviation—IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842
SAURISCHIA Seeley, 1887
THEROPODA Marsh, 1881
TETANURAE Gauthier, 1986
COELUROSAURIA Huene, 1914
TUGULUSAURUS Dong, 1973
TUGULUSAURUS FACILES Dong, 1973

Tugulusaurus faciles Dong, 1973:48
Coelurosauria indet: Norman, 1990:282
Theropoda indet: Weishampel, 1990, p. 106
Tugulusaurus faciles Dong: 1992:104
Tugulusaurus faciles Dong: Sun et al., 1992:127
Tugulusaurus faciles Dong (nomen dubium): Lucas, 2002:165, 167

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Holotype—IVPP V 4025, fragmentary postcranial skeleton, comprising caudal vertebrae, a dorsal rib, the first digits of both mani, and partial hindlimbs.

Locality and Horizon—Wuerho, Lianmugin Formation, Xinjiang, China.

Age—?Valanginian–Albian (Shen and Mateer, 1992).

Diagnosis—Small theropod (femur length c. 215 mm); proximal mid-caudal vertebrae with neural arch placed only on anterior two thirds of centrum and centrum considerably broader than high (ratio width/height ca. 1.5); caudal centra rapidly increasing in length distally; minimal length of metacarpal I less than width of this bone; tibia with pronounced, semicircular lateral expansion of lateral malleolus.

Description

The type of *Tugulusaurus faciles* is incomplete and some elements are poorly preserved, but it nevertheless shows many characters that help to clarify its systematic position.

Axial skeleton—Four caudal vertebrae are represented by their centra and fragments of the fused neural arches (Fig. 1). The most complete and proximal-most vertebra has the right side of the neural arch preserved, but is missing the neural spine, the postzygapophysis and most of the prezygapophysis.

The presence of a reduced transverse process on the proximal-most vertebra suggests that this element comes from the middle of the caudal series (in other basal coelurosaurs the transverse processes are usually lost distal to caudal 15, suggesting that the vertebra in question pertains to this region of the caudal series). The other three vertebrae are more distal caudals. However, based on the closely corresponding sizes of their articular surfaces, they are probably also derived from the middle part of the series and might even represent a natural succession.

The vertebral centra are amphi-platycoelous, spool-shaped, and relatively stout, with a significantly greater transverse width than height (Fig. 1). The ratio between width and height, measured at the distal articular facet, is approximately 1.5 in all vertebrae preserved, although there seems to be a slight tendency towards further broadening in the distal-most vertebrae. The lengths of the centra also increase distally; however, whereas the increase from the first to the third vertebra is only from 23 mm to 25 mm, the last vertebra preserved has a central length of 34 mm. If one accepts the reasoning given above that there may not be any vertebrae missing between the four preserved elements, this indicates an abrupt lengthening of the caudal vertebrae in the middle region of the tail.

A ventral longitudinal groove is present on all vertebrae, but it is very faint in the proximal-most element preserved and becomes more pronounced in more distal vertebrae, where it is especially deep towards the articular ends of the centra (Fig. 1B). Chevron facets are present, but poorly developed in all centra. They also become more conspicuous in the distal vertebrae.

The base of the neural arch overhangs the lateral side of the centrum in all vertebrae and thus forms a longitudinal ridge on the dorsal part of this side (Fig. 1A). In the proximal-most preserved vertebra, a small, triangular and slightly ventrally directed transverse process is present at mid-height of the centrum, just behind its mid-length. Transverse processes are missing on all other vertebrae. The neural arch is restricted to the anterior two thirds of the centrum in the two proximal vertebrae, whereas it increases in relative length in the more distal elements and covers almost the entire length of the centrum in the distal-most vertebra. The bases of the prezygapophyses are preserved on all vertebrae. The attachments are expanded and massive, thus indicating that the prezygapophyses were considerably elongated, as is the case in other coelurosaurs.

One dorsal rib is present. It has a T-shaped cross section in its upper part, with a flat lateral part supported by a medial lamina that is perpendicular to the lateral side. Distally, the cross section becomes more U-shaped, with the opening facing posteriorly.

Forelimb—The complete first digits of both hands are the only elements preserved of the forelimbs (Fig. 2).

Metacarpal I is notably short and stout (Fig. 2A-C). The maximal length of the left element is 26 mm (measured perpendicular to the proximal articular surface), whereas the maximal width is 19 mm. However, the element is parallelogram-shaped in dorsal view, with the medial side entirely being situated more proximally then the lateral one (Fig. 2C), so that the minimal length of the metacarpal is only 16 mm. Thus, the element does not notably narrow between the articular ends, as is the case in most other theropods.

The lateral side of the metacarpal is higher than the medial side and laterally flattened to slightly concave dorso-ventrally (Fig. 2B), indicating that metacarpal I was closely appressed to the proximal half of metacarpal II, as it is in many tetanurans (Gauthier, 1986). Medially, the bone becomes lower, so that the medio-dorsal side forms a sharp ridge (Fig. 2A). Thus, the cross sections of the shaft and the proximal articular facet are triangular in outline, with the basis of the triangle running from the latero-ventral edge to the medio-dorsal corner. The proximal articular facet consists of a dorso-ventrally high, but transversely narrow lateral part that is separated from the lower, much broader and transversely convex medial part by a distinct step, the medial part being more proximal than the lateral one. The lateral side of the facet is further subdivided into a dorsal and ventral part by an incision of the lateral margin.

The distal articular end of the metacarpal is also strongly asymmetrical. The lateral condyle of the articulation extends much farther distally than the medial side (Fig. 2C). It is also

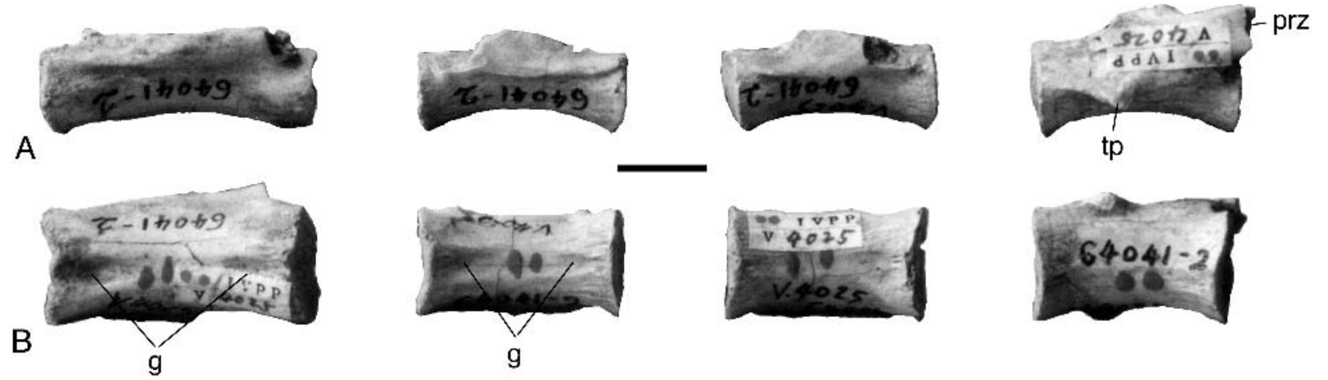

FIGURE 1. Caudal vertebrae of *Tugulusaurus faciles* (IVPP V 4025, holotype). **A**, right lateral view (second vertebra in left lateral view); **B**, ventral view. **Abbreviations**: **g**, ventral groove; **prz**, prezygapophysis; **tp**, transverse process. Scale bar equals 1 cm.

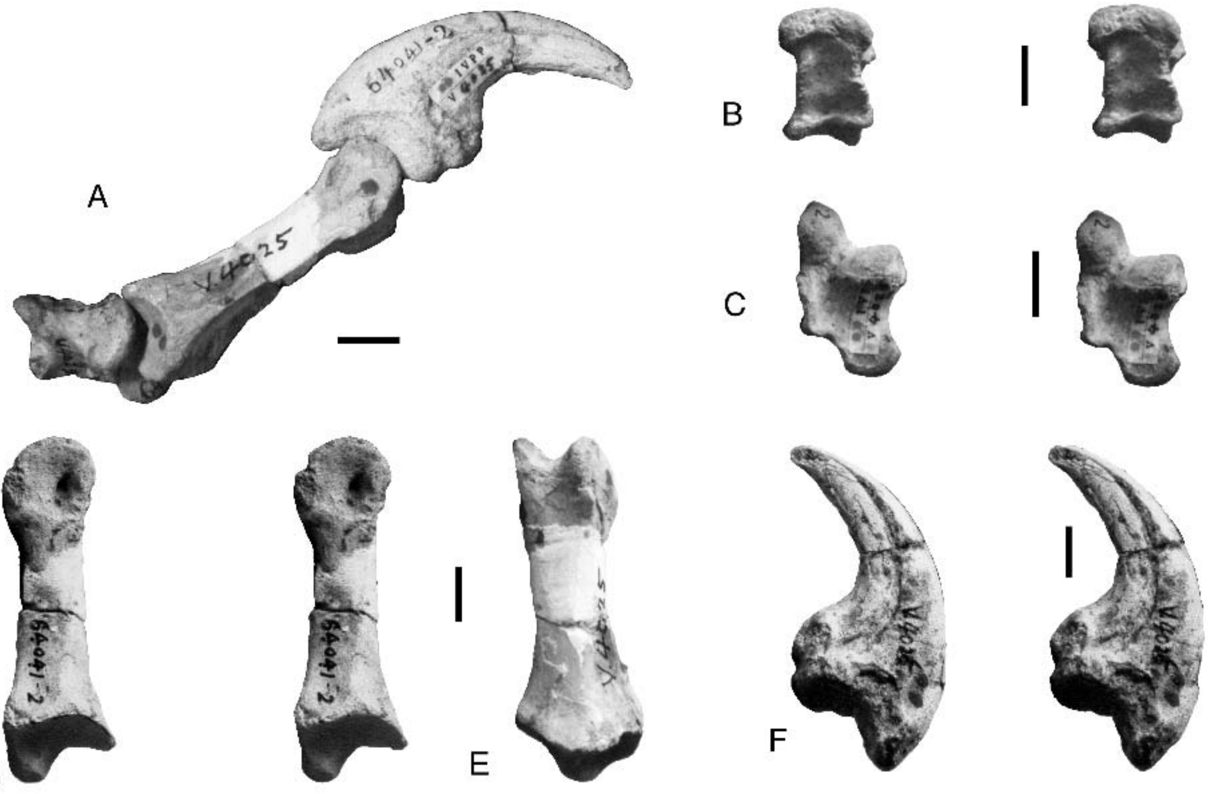

FIGURE 2. *Tugulusaurus faciles*, manual digit I (IVPP V 4025, holotype). **A**, articulated left digit I, medial view; **B**, **C**, left metacarpal I in (**B**) lateral and (**C**) dorsal views (stereopairs); **D**, **E**, left phalanx I-1 in (**D**) lateral and (**E**) dorsal views (**D**, stereopair); **F**, left ungual I in lateral view (stereopair). Scale bars equal 1 cm.

narrower, slightly higher and more convex transversely. The medial condyle is separated from the lateral condyle by a step rather than a groove and is almost flat transversely. The arches of the condyles extend approximately as far proximally on the dorsal as on the ventral side. In the medial condyle, the end of the articular surface is more sharply defined on the dorsal side than on the ventral one, probably indicating that extension of the digit was more restricted than flexion. No collateral ligament pits or dorsal extensor grooves are present.

The first phalanx of the first digit of the hand is elongate, but robust (Fig. 2A, D, E). Its proximo-distal length is approximately twice as long as the metacarpal (54 mm in the complete right element). The shaft of the phalanx is semi-oval in cross section, with a flattened to slightly concave ventral side. The proximal end is slightly expanded in both transverse and dorsolateral directions. The proximal articular facet shows two concavities that are separated by a longitudinal ridge. The shape of the articular facet is semi-oval. The concave facet for the lateral condyle of metacarpal I is slightly larger than that for the medial condyle and extends slightly more distally than the latter. Together with the asymmetric condyles of the metacarpal, this slightly asymmetric arrangement of the facets results in digit one pointing proximo-medially, rather than strictly proximally. As is the case in other theropods (Galton, 1971), this leads to partial opposability of the first digit during flexion.

The distal articular end is developed as a narrow ginglymus, with the ginglymoidal arch extending farther proximally ventrally than dorsally, as usual in phalanx I-1 in theropods. The collateral ligament fossae are small, deep and positioned far dorsally on the lateral side of the ginglymoidal arch.

The ungual of digit I is large, robust and strongly curved (Fig. 2F). It is 70 mm long, along the outer curve. The proximal articular end shows a broad medial ridge that separates two narrow concave facets. The claw grooves are symmetrical and run from the proximo-ventral end in a gentle arch distally, where they meet the dorsal margin of the bone just before the tip of the claw. The bone is not considerably broader below the grooves than above. The flexor tubercle is low, but robust, and separated from the proximal articular facet by a small and shallow transverse groove.

Hind Limb—The hind limb is represented by a complete left femur, the proximal end of the right femur, the left tibia, left astragalus and calcaneum, a fragment of the right astragalus, the distal ends of left metatarsals III and IV, a pedal phalanx, and a pedal ungual (Figs. 3, 4).

The femora and the tibia are poorly preserved, their shafts being mainly represented by sedimentary casts of their hollow centers (Fig. 3). The femur (Fig. 3A-D) is approximately 215 mm long, slender, and shows a slight sigmoidal curve in posterior view. In lateral view, it is only moderately flexed. The femoral head is medially and slightly anteriorly directed and is confluent with the greater trochanter in anterior view. On the posterior side of the head, an oblique ligament groove is present. The greater trochanter is antero-posteriorly narrow and not expanded into a trochanteric shelf. The lesser trochanter is broken, but it was obviously wing-like, proximally placed, and not fused to the greater trochanter. The fourth trochanter is represented by a stout ridge that is placed in the proximal third of the length of the femur. On the anterior side of the distal end, a large but shallow groove is present medially. The tibial condyle is slightly larger than the fibular condyle and the latter is slightly offset proximally from the distal end.

The tibia (Figs. 3E-H, 4A, B) is also slender and slightly longer than the femur (ca. 240 mm). The cnemial crest is only moder-

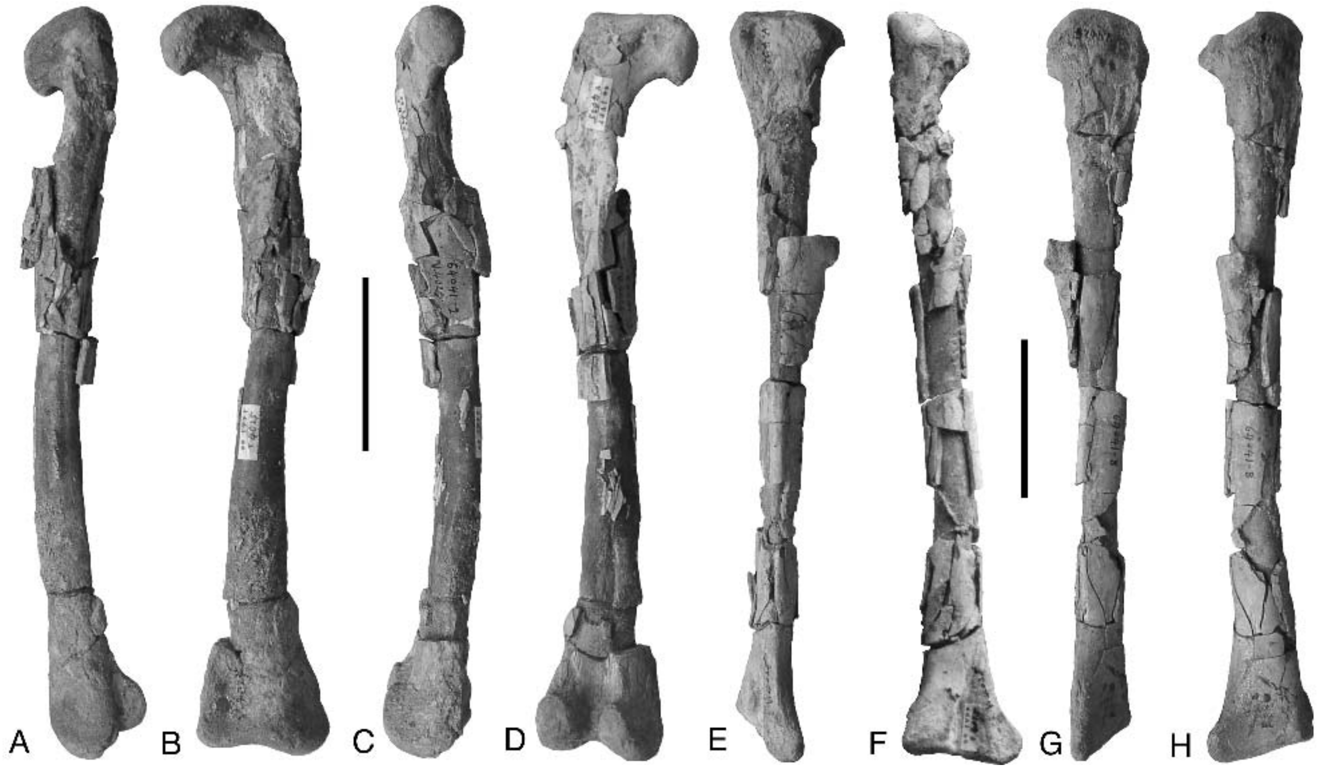

FIGURE 3. *Tugulusaurus faciles*, hind-limb elements (IVPP V 4025, holotype). **A**–**D**, left femur in (**A**) lateral, (**B**) anterior, (**C**) medial, and (**D**) posterior views; **E**–**H**, left tibia in (**E**) lateral, (**F**) anterior, (**G**) medial, and (**H**) posterior views. Scale bars equal 5 cm.

ately expanded and robust. Its anterior end is slightly hooked laterally, as it is the case in most theropods. The fibular condyle is small, more or less triangular and offset from the lateral side of the proximal end of the tibia by a notch posteriorly (Fig. 4A). It does not extend as far posteriorly as the medial side.

A lateral ridge for the attachment of the fibula on the proximal half of the tibial shaft was present, but it is too strongly damaged to be informative. As in all tetanurans, the ridge was clearly offset from the proximal articular facet of the tibia.

The distal end of the tibia is flattened antero-posteriorly and strongly expanded laterally, where the lateral malleolus ends in a semicircular flange. Anteriorly, the surface of the distal end is subdivided by an almost vertical, only very slightly proximolaterally inclined, step (Fig. 4B). This step seems to have extended distally to the distal end, unlike the situation in other basal tetanurans, where it curves medially distally. Although this may be a further autapomorphy of *Tugulusaurus*, it must be noted that the bone shows some signs of erosion in this area, leaving the possibility that this is a preservational artifact. In distal view, the distal articular facet is broadly triangular.

The left astragalus and calcaneum are well preserved, with only the tip of the ascending process of the astragalus missing (Fig. 4C, D). As in most coelurosaurs, the calcaneum is reduced: the astragalus is 32 mm wide, whereas the width of the calcaneum is only 6 mm, resulting in a astragalar width/calcaneum width ratio of 5.3. In proximal view (Fig. 4D), the astragalus is more or less trapezoidal in outline, with an expanded anteromedial edge ending in a slightly acute angle, and a constriction anteriorly between the lateral third of the bone and the medial two thirds. The facet for the tibia is antero-posteriorly concave and broader medially than laterally. Whereas it is facing mainly proximally medially, it faces proximo-posteriorly on its lateral side. Thus, the astragalar condyles are not entirely below the distal end of the tibia, but are facing antero-distally, as in all tetanurans.

The ascending process of the astragalus is sheet like, but restricted to the lateral half of the astragalar body (Fig. 4C, D). As in coelurosaurs, it is slightly offset from the anterior border of the astragalar body by a shallow semilunate groove on its basis (Fig. 4C). Its exact height cannot be determined due to its broken proximal end; however, it was certainly lower than in other coelurosaurs and most probably only insignificantly higher than the astragalar body. On the lateral side of the process, a facet for the fibula is present. As in all coelurosaurs, it is strongly reduced and steeply inclined, facing only laterally.

In anterior view, the ventral side of the astragalus is strongly concave, with the highest point of the arch at approximately the same part where the anterior constriction is found in proximal view. The condyles are well rounded and there is no anterior horizontal groove across them, as is present in neoceratosaurs and many basal tetanurans.

The calcaneum is disc like and strongly convex distally. Proximally, it shows a flat, antero-posteriorly long trapezoidal facet for the fibula. This facet is separated from the smaller, posteriorly placed, deeply concave facet for the tibia by an oblique ridge (Fig. 4D). The contact between the calcaneum and astragalus is developed as a simple butt joint, with the astragalus showing a slight concavity medially on its lateral side (Fig. 4C).

The preserved elements of the pes are fragmentary and not very informative (Fig. 4E-M). Of the left metatarsals III and IV, only the distal articular ends are preserved. The end of metatarsal III (Fig. 4E-G) forms a broad, very slightly ginglymoidal articular facet that is slightly higher on the medial than on the lateral side. Well-developed and approximately centrally placed collateral ligament fossae are present on both sides. The shaft is broadly oval at the break; whether the pes was arctometatar-

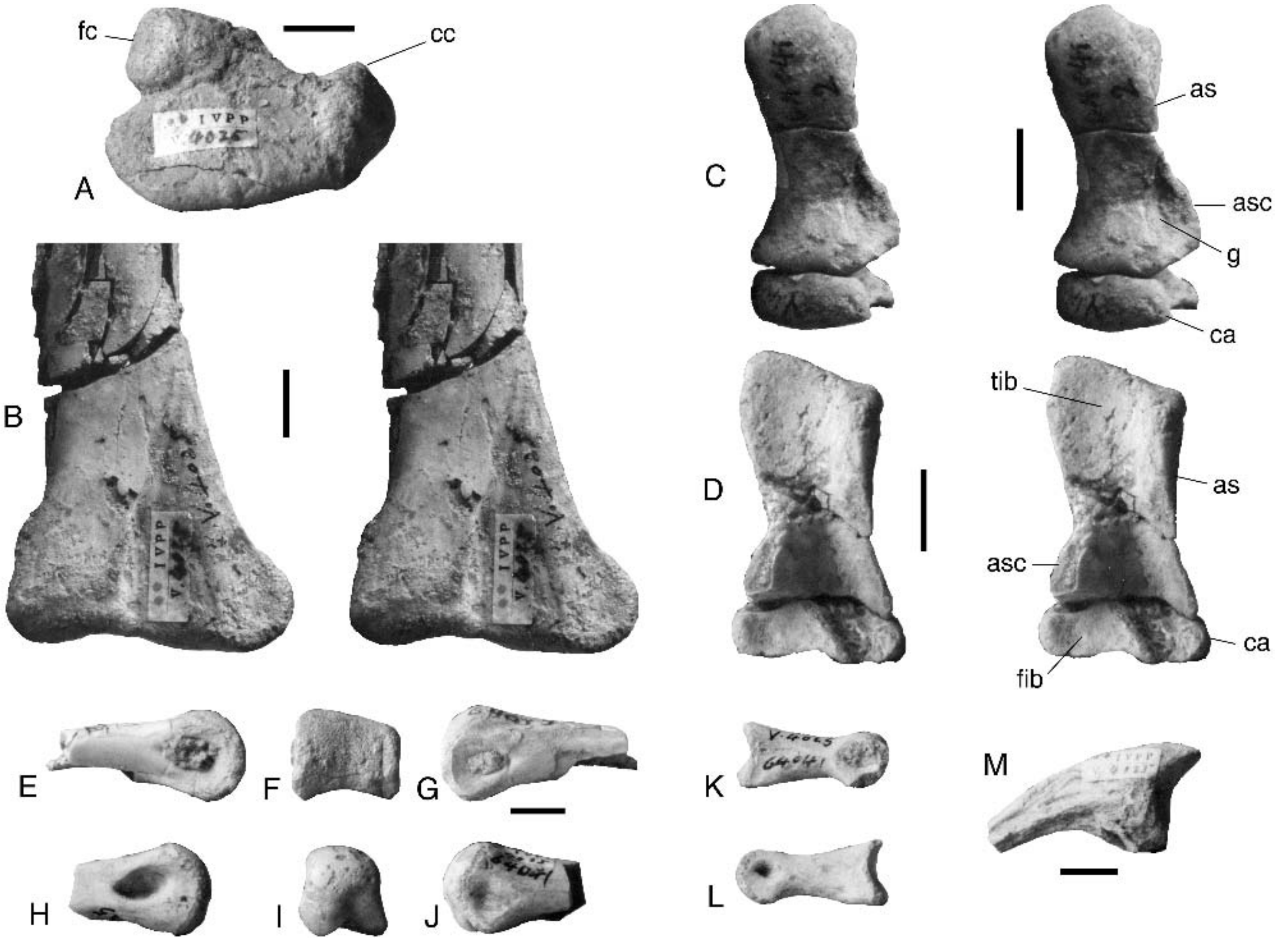

FIGURE 4. *Tugulusaurus faciles*, hind-limb elements (IVPP V 4025, holotype). **A**, left tibia in proximal view; **B**, distal end of left tibia in anterior view; **C**, **D**, left astragalus and calcaneum in (**C**) anterior and (**D**) proximal views (stereopairs); **E**–**G**, distal end of left metatarsal III in (**E**) medial, (**F**) distal, and (**G**) lateral views; **H**–**J**, distal end of left metatarsal IV in (**H**) medial, (**I**) distal, and (**J**) lateral views; **K**, **L**, pedal phalanx in (**K**) medial and (**L**) lateral views; **M**, pedal ungual in lateral view. **Abbreviations**: **as**, astragalus; **asc**, ascending process of the astragalus; **ca**, calcaneum; **cc**, cnemial crest; **fc**, fibular condyle; **fib**, fibular facet; **g**, anterior groove at the base of the ascending process; **tib**, tibial facet. Scale bars equal 1 cm.

salian or not cannot be said on the basis of this fragment (contra Dong, 1973).

The distal end of metatarsal IV is higher than broad and strongly convex distally (Fig. 4H-J). The articular facet is subdivided posteriorly by a groove that separates the medial part of the facet from a latero-posteriorly expanded flange. A large and deep collateral ligament fossa is present on the medial side, whereas the lateral side only exhibits a slight concavity.

The two preserved phalanges are typical theropod pedal elements. One of the phalanges is 27 mm long and relatively small (Fig. 4K, L). It is flattened ventrally, with a triangular proximal articular facet and a ginglymoidal distal articulation. Based on its small size, this is probably one of the distal phalanges of digit IV. The other phalanx is a pedal ungual (Fig. 4M). It is flattened ventrally and only moderately curved. The claw grooves are arranged symmetrically. It is too large to be of digit IV and thus might represent the ungual of digit III.

Discussion

Despite the fragmentary nature of the holotype of *Tugulusaurus faciles*, this species can be demonstrated to be a valid taxon with certainty. The anteriorly placed and posteriorly reduced neural arches of the mid-caudal vertebrae, the extremely shortened metacarpal I and the semicircular lateral expansion of the distal end of the tibia are unknown in any other theropod dinosaur and thus constitute autapomorphies of this taxon. Furthermore, the astragalus shows a mixture of primitive (low ascending process, arising out of the lateral half of the astragalar body) and advanced characters (fibular facet reduced and steeply inclined laterally, semilunate groove at the basis of the ascending process) that is also unique among known theropod dinosaurs.

PHAEDROLOSAURUS Dong, 1973
PHAEDROLOSAURUS ILIKENSIS Dong, 1973
(nomen dubium)

Phaedrolosaurus ilikensis Dong:46
Phaedrolosaurus ilikensis Dong (nomen vanum): Sues, 1977:182
Coelurosauria indet: Norman, 1990:282
Theropoda indet: Weishampel, 1990:106
Phaedrolosaurus ilikensis: Dong, 1992:104
Phaedrolosaurus ilikensis Dong: Sun et al., 1992:127
Phaedrolosaurus ilikensis Dong (nomen dubium): Lucas, 2002: 165, 167

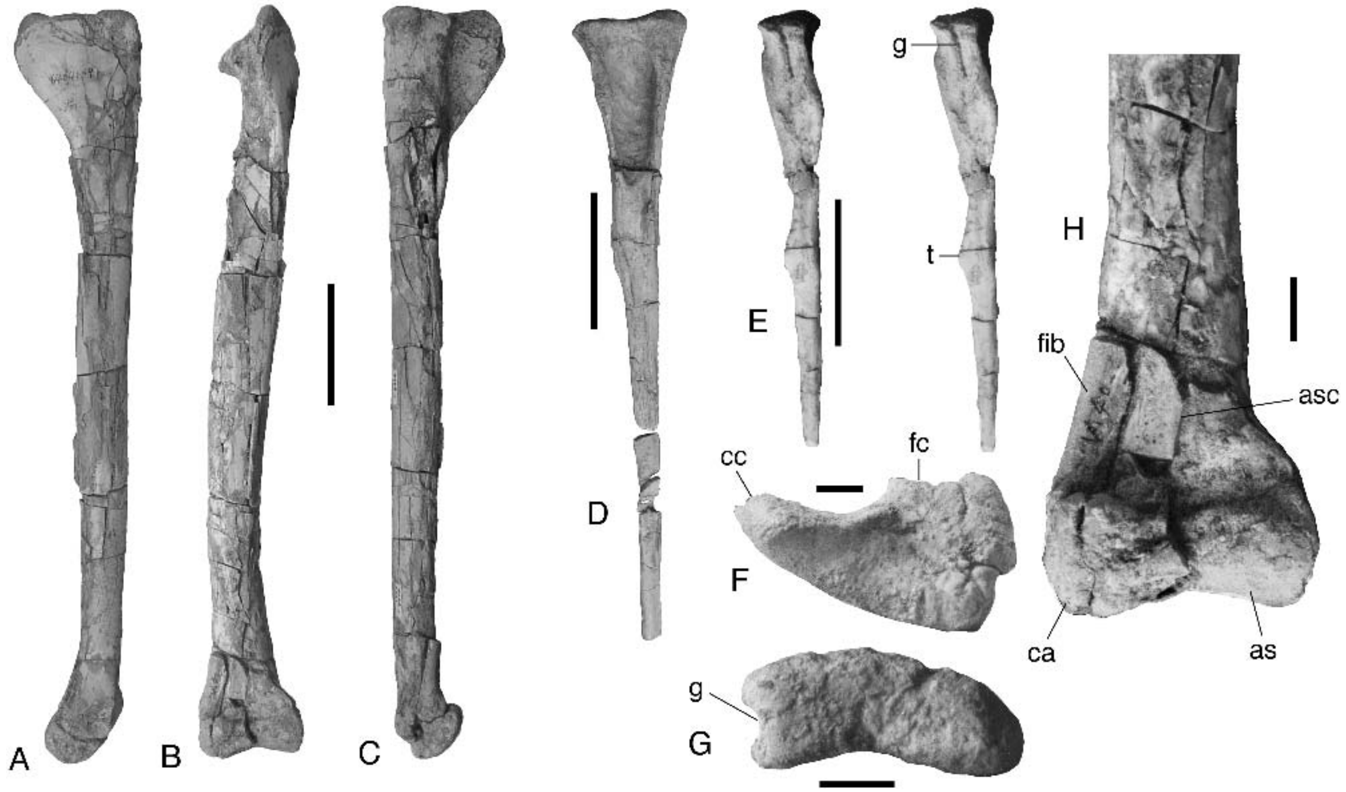

FIGURE 5. *Xinjiangovenator parvus* gen. et sp. nov., holotype (IVPP V 4024). **A**–**C**, right tibiotarsus in (**A**) medial, (**B**) anterior, and (**C**) lateral views; **D**, **E**, right fibula in (**D**) medial and (**E**) anterior views (**E**, stereopair); **F**, proximal articular surface of right tibia; **G**, proximal articular surface of right fibula; **H**, detail of distal right tibiotarsus in anterior view. **Abbreviations**: **as**, astragalus; **asc**, ascending process of the astragalus; **ca**, calcaneum; **cc**, cnemial crest; **fc**, fibular condyle; **fib**, fibula; **g**, groove on the anterior surface of the proximal fibula; **t**, tubercle for the insertion of the M. iliofibularis. Scale bars equal 5 cm (A–E) and 1 cm (F–H).

Lectotype—IVPP V 4024–1, isolated tooth.

Locality and Horizon—Wuerho, Lianmugin Formation, Xinjiang, China.

Age—?Valanginian–Albian (Shen and Mateer, 1992).

Comments—As discussed by Sues (1977), an isolated tooth described by Dong (1973) must be regarded as the type specimen of this species, and an articulated hind limb referred to the same species by Dong (1973) cannot be demonstrated to belong to the same taxon. The diagnosis given by Dong (1973:46; English translation in Sues, 1977:182) does not list any characters that distinguish this tooth from any other theropod teeth. Thus, *Phaedrolosaurus ilikensis* should be regarded as a nomen dubium, which leaves the hindlimb elements without a formal designation. Since these elements are taxonomically distinctive from all other theropods, they are here made the type of a new genus and species.

MANIRAPTORA Gauthier, 1986
XINJIANGOVENATOR, gen. nov.

Type species—*Xinjiangovenator parvus*, sp. nov.

Etymology—From the autonomous region of Xinjiang, China, and venator, Greek for hunter, gender masculine.

Diagnosis—As for type and only known species.

XINJIANGOVENATOR PARVUS, sp. nov.

Phaedrolosaurus ilikensis Dong, 1973:47 (partim)
Dromaeosauridae indet: Sues, 1977:182
Phaedrolosaurus ilikensis Dong: 1992:104 (partim)
Phaedrolosaurus ilikensis Dong: Sun et al., 1992:127 (partim)
Phaedrolosaurus ilikensis Dong (nomen dubium): Lucas, 2002: 165, 167 (partim)

Holotype—IVPP 4024–2, articulated partial right hind limb.

Locality and Horizon—Wuerho, Lianmugin Formation, Xinjiang, China.

Age—?Valanginian–Albian (Shen and Mateer, 1992).

Etymology—Parvus, Latin for small, referring to the small size of the specimen.

Diagnosis—Small theropod (length of the tibia plus proximal tarsals: 312 mm); fibular condyle of tibia extending farther posteriorly than lateral side of proximal end of this bone; fibula with longitudinal groove on anterior side of proximal end.

Description

The type of *Xinjiangovenator* comprises the tibia, fibula, astragalus, and calcaneum of the right hind limb (Fig. 5). The fibula is currently labeled under the same specimen number as the type of *Tugulusaurus* (IVPP V 4025), but it is clearly derived from the same individual as the tibiotarsus IVPP V 4024–2, since its distal break fits onto the fibular fragment preserved in articulation with this specimen.

The tibia, astragalus, calcaneum, and the distal end of the fibula are closely appressed, but not fused to each other (contra Dong, 1973; Fig. 5A-C, H). The length of the tibia plus proximal tarsals is 312 mm; thus the type of *Xinjiangovenator* represents a slightly larger animal than the type of *Tugulusaurus*.

The cnemial crest is well developed and relatively larger and more slender than in *Tugulusaurus* (Fig. 5A, C, F). Although it is bent laterally over its complete length, it seems to lack the hook-like lateral process anteriorly that is present in *Tugulusaurus* and many other theropods. However, this might be a preservational artifact, since the cnemial crest is slightly eroded anteriorly. The fibular condyle is subrectangular in proximal view and is expanded both transversely and posteriorly (Fig. 5F). Its posterior extension exceeds that of the lateral part of the tibia and is separated from the latter by a step, rather than a notch, as in most theropods. A lateral ridge for the attachment of the fibula was originally present, but is broken. It was clearly offset from the proximal end.

The distal end is strongly flattened antero-posteriorly and expanded transversely. However, in contrast to *Tugulusaurus*, it is more medially than laterally expanded. Not much can be said about the detailed morphology of the distal end of the tibia, since the astragalus, calcaneum, and distal fibula are closely appressed to it (Fig. 5H). However, the outline of the articular facet is most probably broadly triangular and there seems to be no step on the anterior side of the distal tibia. The distal end seems to be slightly medio-proximally inclined.

The proximal end of the fibula (Fig. 5D, E, G) is antero-posteriorly less expanded than that of the tibia (37 mm versus 52 mm). As in most theropods, it is more posteriorly than anteriorly expanded. The proximal articular facet is flat anteriorly, but forms a transversely as well as antero-posteriorly convex condyle posteriorly. The outline of the proximal articular facet is approximately kidney-shaped, with a flattened anterior end that is notched by an anterior groove in the middle (Fig. 5G).

On the medial side of the proximal fibula, a large, deep, and especially posteriorly sharply defined groove is present that covers almost all of the proximal end, with the exception of the basis of the posterior condyle of the articular facet (Fig. 5D). Distally, the groove becomes shallower and ends just above the area of insertion of the M. iliofibularis. On the anterior margin of the groove, a well-developed, elongate, medially directed flange is present at approximately mid-height of the groove. This flange is confluent with the flattened anterior side of the proximal end of the fibula and here marks the end of a narrow longitudinal groove that extends from the proximal articulation distally (Fig. 5E).

The lateral side of the proximal fibula is antero-posteriorly convex. The bone narrows gradually towards the insertion area of the M. iliofibularis, which is developed as a conspicuous, elongate, antero-laterally directed tubercle. Distal to the tubercle, the shaft of the fibula narrows abruptly. Approximately 50 mm distal to the tubercle, the fibula is broken; here, the shaft is narrow antero-posteriorly and transversely flattened.

The distal end of the fibula, which is preserved in articulation with the tibia and tarsus, is of approximately the same width as the fibular shaft at the proximal break, indicating that the shaft was of subequal width throughout its distal half. However, the cross section of the distal end is suboval, with a flattened medio-posterior side. The distal end of the fibula is closely appressed to the latero-anterior side of the tibia and the lateral side of the ascending process of the astragalus over the complete length of the latter (Fig. 5H), as in other coelurosaurs (Osmólska, 1996; Norell and Makovicky, 1999). There is only a very small terminal expansion of the fibular shaft.

As in *Tugulusaurus*, the calcaneum is strongly reduced, and the tarsus is mainly formed by the astragalus (Fig. 5H). However, in contrast to that taxon, the ascending process of the astragalus arises from the complete breadth of the astragalar body and is very high. Its exact height cannot be determined, since the proximal tip of the process is missing, but it seems to have been approximately three times the height of the astragalus body; thus, the total height of the astragalus exceeds 17% of the length of the tibia. The ascending process is offset from the astragalar condyles by a shallow semilunate groove. The facet for the fibula on the astragalus is strongly reduced and faces laterally.

As in all tetanurans, the astragalar condyles face antero-distally. A horizontal groove across the condyles is absent.

The ratio between calcaneum width (9 mm) and astragalar width (48 mm) is similar to that of *Tugulusaurus* and other coelurosaurs (5.3). The calcaneum is disc like and has a facet for the fibula anteriorly and another facet for the tibia posteriorly. Nothing can be said about the connection between astragalus and calcaneum, since both elements are closely appressed to each other.

Discussion

As in *Tugulusaurus*, the sparse type material of *Xinjiangovenator* allows a diagnosis of this taxon. Particularly notable is the longitudinal groove on the anterior side of the fibula, a striking difference from all other theropods. The posterior extension of the fibular condyle of the tibia might represent a further autapomorphy of this taxon, although this character varies somewhat between individuals in other theropods, such as *Allosaurus*.

THE PHYLOGENETIC POSITION OF *TUGULUSAURUS* AND *XINJIANGOVENATOR*

In order to determine the phylogenetic position of *Tugulusaurus* and *Xinjiangovenator*, a cladistic analysis was carried out with two outgroup taxa (*Dilophosaurus* and *Ceratosaurus*) and 15 tetanuran ingroup taxa (*Allosaurus*, Aves, *Bagaraatan*, *Coelurus*, Compsognathidae, Dromaeosauridae, *Nqwebasaurus*, *Ornitholestes*, Ornithomimosauria, Oviraptorosauria, Therizinosauroidea, Troodontidae, and Tyrannosauridae), based on 136 osteological characters of all regions of the skeleton (Appendix 1). The matrix was analyzed using the branch-and-bound search algorithm of PAUP 3.1.1 (Swofford, 1992).

The analysis resulted in the recovery of 10 equally parsimonious trees (Fig. 6) with a length of 246 steps (CI: 0.618; RI: 0.719; RC: 0.444; HI: 0.382). The topology of the outgroup (*Dilophosaurus* and *Ceratosaurus* as a monophyletic [e.g., Rowe & Gauthier, 1990; Sereno, 1999], or as a paraphyletic group [Carrano et al., 2002; Rauhut, 2003]) has no effect on tree length or measurements, and does not effect the topology of the ingroup taxa. The trees differ in the detailed relationships of Compsognathidae and *Coelurus* (placed either as sister groups or successively closer outgroups to more advanced coelurosaurs) and in the placement of *Nqwebasaurus*. The uncertainty in the phylogenetic placement of this African taxon might reflect our poor knowledge of coelurosaur evolution on Gondwana.

However, the phylogenetic position of *Tugulusaurus* and *Xinjiangovenator* is stable in all the trees (Fig. 6). *Tugulusaurus* can be referred to the Coelurosauria on the basis of the medial side of metacarpal I forming a sharp edge, the absence of deep extensor pits on the dorsal surface of the metacarpals, the reduced fibular facet on the astragalus, which only faces laterally, the presence of a semilunate groove on the base of the astragalus, and the absence of a horizontal groove across the astragalar condyles. It is more primitive than all other coelurosaurs in that the anterior side of the distal tibia retains a vertical step, and in that the ascending process of the astragalus arises only from the lateral side of the astragalar body and is less than twice the height of the body, and thus represents one of the most basal coelurosaurs known.

Xinjiangovenator shows several characters that identify it as a more derived coelurosaur (high ascending process that arises from the complete breadth of the astragalar body), and shares one derived feature with the enigmatic Late Cretaceous Asian theropod *Bagaraatan* (Osmólska, 1996): the posterior expansion of the fibular condyle and strong reduction of the posterior incision between the fibular condyle and the lateral part of the proximal tibia. Although this might indicate a close relationship between *Xinjiangovenator* and *Bagaraatan*, bootstrap support values are low (41%), and there are significant differences between the tibiae of these two taxa. Thus, the final solution to the

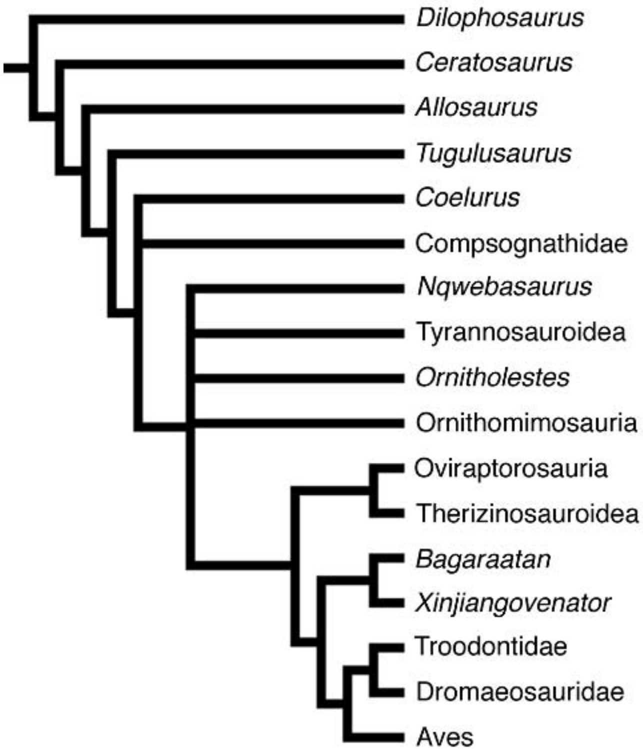

FIGURE 6. Phylogenetic position of *Tugulusaurus* and *Xinjiangovenator*. Strict consensus tree of 10 trees resulting from an analysis of 17 theropod taxa and 136 characters.

phylogenetic position of the former taxon must await the discovery of further material.

CONCLUSIONS

The phylogenetic position of both *Tugulusaurus* and *Xinjiangovenator* does not indicate any close relationships with Early Cretaceous theropods of either Europe or eastern Asia. Since coelurosaur origins reach back to at least the Late Jurassic (e.g., Sereno, 1999), and probably even earlier (Xu et al., 2001), and as more derived coelurosaurs than *Tugulusaurus* are already known from that time, the latter taxon probably represents a relict of an early side branch of coelurosaur evolution. *Xinjiangovenator*, on the other hand, represents a derived coelurosaur, and if the close relationship with *Bagaraatan* can be confirmed, it might be an early member of a, so far, poorly known, Asian lineage of coelurosaurs. In both cases, the relationships might indicate a certain degree of endemism of the theropod fauna in the Lower Cretaceous of central Asian China, rather than a mixture between European and eastern Asian faunas, as might have been suspected. This is also in general accordance with the rest of the dinosaur fauna (e.g., the presence of a stegosaur), although the presence of the ceratopsian genus *Psittacosaurus* indicates at least some faunal exchange with eastern Asian faunas (Sereno and Chao, 1988). Luo (1999) suggested that the Lower Cretaceous eastern Asian fauna also showed a high degree of endemism and contained relicts of groups that are otherwise unknown from this period. However, this view was contested by Manabe et al. (2000) and Barrett et al. (2002), and the biogeographic history of central and eastern Asian Cretaceous dinosaur faunas might be more complex than previously recognized.

ACKNOWLEDGMENTS

The first author would like to thank the staff of the IVPP, especially Zhao Xi-Jin, for his help and hospitality during a visit in 1998. Critical comments by Paul Barrett and two anonymous reviewers greatly improved the manuscript. The first author is grateful for an EU fellowship and DFG-project RA1012/1–1.

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Submitted 26 November 2003; accepted 1 July 2004.

APPENDIX 1

Taxonomic content of operational taxonomic units, and literature used for coding characters. Taxa marked with * have been studied firsthand.

Outgroup: *Dilophosaurus wetherilli** (Welles, 1984); *Ceratosaurus nasicornis** (including *C. dentisulcatus**, *C. magnicornis)* (Gilmore, 1920).

Ingroup: *Allosaurus*: *A. fragilis**, *A. maximus**, *Allosaurus* n. sp.* (Gilmore, 1920; Madsen, 1976); Aves: *Archaeopteryx**, *Rahonavis**, Confuciusornithidae*, Ornithothoraces* (Wellnhofer, 1974, 1992, 1993; Elzanowski and Wellnhofer, 1996; Forster et al., 1998); *Bagaraatan ostromi* (Osmólska, 1996); *Coelurus fragilis**; Compsognathidae: *Aristosuchus pusillus**, *Compsognathus longipes**, *Sinosauropteryx prima**, unnamed compsognathid from the Early Cretaceous of Brazil* (Ostrom, 1978; Chen et al., 1998; Martill et al., 2000); Dromaeosauridae: *Adasaurus mongoliensis*, *Deinonychus antirrhopus**, *Dromaeosaurus albertensis**, *Microraptor zhaoianus**, *Saurornitholestes langstoni**, *Sinornithosaurus millenii**, *Utahraptor ostrommaysorum*, *Velociraptor mongoliensis** (Ostrom, 1969, 1976; Norell and Makovicky, 1997, 1999; Barsbold and Osmólska, 1999; Xu, Wang, and Wu, 1999); *Nqwebasaurus thwazi* (De Klerk et al., 2000); *Ornitholestes hermanni** (Osborn, 1916); Ornithomimosauria: *Harpyimimus okladnikovi*, *Pelecanimimus polyodon*, *Deinocheirus mirificus*, *Garudimimus brevipes*, Ornithomimidae* (Osborn, 1916; Osmólska et al., 1972; Barsbold and Perle, 1984; Barsbold and Osmólska, 1990; Pérez-Moreno et al., 1994); Oviraptorosauria: *Microvenator celer**, *Caenagnathasia martinsoni*, *Chirostenotes elegans**, *Chirostenotes pergracilis**, *Elmisaurus rarus*, Oviraptoridae* (Barsbold et al., 1990; Currie, 1990; Sues, 1997; Makovicky and Sues, 1998; Clark et al., 1999); Therizinosauroidea: *Alxasaurus elesitaiensis*, *Beipiaosaurus inexpectus**, Therizinosauridae (Barsbold and Maryanska, 1990; Russell and Dong, 1993a; Clark et al., 1994; Makovicky, 1995; Xu, Tang and Wang, 1999); Troodontidae: *Borogovia gracilicrus*, *Byronosaurus jaffei*, *Saurornithoides junior*, *Saurornithoides mongoliensis*, *Sinornithoides youngi**, *Sinovenator changii**, *Troodon formosus**, unnamed troodontid from the Early Cretaceous of Mongolia (Barsbold, 1974; Currie, 1985; Barsbold et al., 1987; Osmólska and Barsbold, 1990; Currie and Zhao, 1993; Russell and Dong, 1993b); Tyrannosauridae: *Albertosaurus sarcophagus*, *Alectrosaurus olseni**, *Alioramus remotus*, *Aublysodon mirandus*, *Daspletosaurus torosus**, *Gorgosaurus libratus**, *Maleevosaurus novojilovi*, *Tarbosaurus bataar*, *Tyrannosaurus rex** (Osborn, 1916; Lambe, 1917; Russell, 1970; Maleev, 1974; Molnar, 1991).

APPENDIX 2

Characters used in the phylogenetic analysis carried out to determine the relationships of *Tugulusaurus* and *Xinjiangovenator*. Although character state "0" usually represents the plesiomorphic condition, this is not true for all characters, since character polarity was determined by rooting the tree (Nixon and Carpenter, 1993). Most characters are taken (sometimes modified) from Xu, Wang, and Wu (1999) and Rauhut (2003). Characters 66, 86, 87, and 120 are new; character 95 is taken from Holtz (2000).

1. Premaxillary palatal shelf: absent (0); present (1)
2. Contact between subnarial process of premaxilla and nasal: present (0); absent (1)
3. Maxillary antorbital fossa: shallow (0); deep, with sharp margins (1)
4. Maxillary antorbital fossa: 25% or less of length of internal antorbital fenestra (0); more than 40% of length of antorbital fenestra (1)
5. Maxillary fenestra: absent (0); present (1)
6. Pneumatic foramen in nasals: absent (0); present (1)
7. Shape of nasals: expanding posteriorly (0); of subequal width throughout their length (1)
8. Sublacrimal part of jugal: expanded (0); not expanded (1)
9. Jugal antorbital fossa: absent or poorly developed (0); large, crescentic depression (1)
10. Jugal: broad, plate like (0); very slender, rod like (1)
11. Lateral surface of vertical strut of lacrimal depressed below level of surrounding bones: no (0); yes (1)
12. Lacrimal fenestra: present (0); absent (1)
13. Lacrimal: inverted L-shaped (0); T-shaped (1)
14. Lacrimal–frontal contact: absent (0); present (1)
15. Frontal: rectangular (0); elongated triangular (1)
16. Frontal length relative to parietal: smaller or sub equal (0); nearly two times as long (1)
17. Pronounced rim for eyeballs on ventral side of frontals: absent (0); present (1)
18. Supratemporal fenestrae: widely separated (0); contacting each other posteriorly, but separated anteriorly (1); confluent, parietals forming saggital crest (2)
19. Postorbital part of skull roof: as high as orbital region (0); deflected ventrally (1)
20. Quadratojugal process of squamosal: broad (0); tapering (1)
21. Squamosal–quadratojugal contact: present (0); absent (1)
22. Posterior process of quadratojugal: absent (0); present (1)
23. Pneumatisation of quadrate: absent (0); present (1)
24. Mandibular joint: below quadrate head (0); posterior to quadrate head (1); anterior to quadrate head (2)
25. Base of paroccipital processes: solid (0); hollowed (1)
26. Shape of paroccipital process: straight and vertically oriented (0); distal end with distinct twist as to face caudodorsally (1)
27. Basisphenoid recess: deep and open ventrally (0); basisphenoid pneumatized, but without ventral opening (1)
28. Basipterygoid processes: approximately as long as wide (0); longer than wide (1); shortened, broad, and narrow (2)
29. Parasphenoid: forming thin bony plate (0); expanded, cone-shaped, and pneumatized (1)
30. Endocranium: small (EQ < 2.5) (0); enlarged (EQ >2.5) (1)
31. Forebrain shape: small and narrow (0); enlarged and triangular (1)
32. Palatine–ectopterygoid contact: absent (0); present (1)
33. Ectopterygoid: posterior to palatine (0); lateral to palatine (1)
34. Ectopterygoid: not pneumatized (0); with a deep ventral depression medially (1); with a foramen ventrally (2)
35. Tooth row: extending posteriorly to orbit (0); completely antorbital (1)
36. Dentary in occlusal view: straight (0); anterior portion curved medially (1)
37. Anterior myliohyoid foramen: completely enclosed in splenial (0); opened antero-ventrally (1); absent (2)
38. Coronoid: present (0); absent (1)
39. Premaxillary teeth: present (0); absent (1)
40. Serrations on premaxillary teeth: present (0); absent (1)
41. Serrations on maxillary and dentary teeth: present (0); absent (1)
42. Constriction between tooth crown and root: absent (0); present (1)
43. Number of pleurocoels in cervicals: two (0); one (1)
44. Axial neural spine: sheet like (0); antero-posteriorly reduced and rod like (1)
45. Large groove excavated into posterior base of axis: present (0); absent (1)
46. Ventral keel in anterior cervicals: present (0); absent (1)
47. Anterior cervical prezygapophyses: transverse distance less than width of neural canal (0); situated lateral to neural canal (1)
48. Prezygapophyses in anterior postaxial cervicals: straight (0); flexed (1)
49. Anterior articular facet of anterior cervical vertebrae: oval, as high as wide (0); kidney-shaped (1)
50. Cervical neural spines: exceeding height of neural arch (0); lower than neural arch (1)
51. Antero-posterior length of mid-cervical neural spines: less than half length of centrum (0); more than half length of centrum (1)
52. Hyposphene: single sheet of bone (0); wide, formed by ventrally flexed medial parts of postzygapophyses, and only connected by thin horizontal lamina of bone (1)
53. Pleurocoels in posterior dorsal vertebrae: absent (0); present (1)
54. Hypapophyses in anterior dorsals: absent or poorly developed (0); strongly pronounced (1)
55. Ventral keel in anterior dorsals: absent or very poorly developed (0); pronounced (1)
56. Neural spine of posterior dorsals: significantly higher than long (0); approximately as high as long (1)
57. Number of sacral vertebrae: four to five (0); more than five (1)
58. Sacral centra: rounded or keeled ventrally (0); flattened ventrally (1)
59. Pleurocoels in sacral vertebrae: absent (0); present (1)
60. Number of caudal vertebrae: 41 or more (0); fewer than 41 (1); fewer than 35 (2) (ordered)

61. Number of caudal vertebrae bearing transverse processes: 16 or more (0); fewer than 16 (1); ten or fewer (2)
62. Number of caudal vertebrae with well-developed neural spines: 11 or more (0); fewer than 11 (1)
63. Ventral surface of anterior caudals: rounded (0); with distinct keel, bearing narrow, shallow groove on its midline (1)
64. Prezygapophyses of distal caudal vertebrae: short (0); overhanging at least one fourth of length of preceding centrum (1)
65. Neural spines of mid-caudals: rod-like (0); subrectangular and sheet-like (1)
66. Mid-caudal vertebral centra: approximately as broad as high (0); significantly broader than high (1)
67. Relative length of distal caudal centra: greater than in proximal caudals (0); short (1)
68. Shape of anterior caudal centra: oval (0); subrectangular and box like (1)
69. Distal chevrons: rod-like or L-shaped (0); skid like (1)
70. Scapula: short and broad (ratio length / minimal height of shaft ‹ 9) (0); slender and elongate (ratio › 10) (1)
71. Distal end of scapula: expanded (0); not expanded (1)
72. Acromion process of scapula: abruptly expanded dorsally (0); small, dorsal rim of proximal scapula slopes gently downwards (1)
73. Anterior projection of acromion process: absent (0); present, extends anterior to glenoid fossa (1)
74. Glenoid facet on scapula: facing ventrally (0); facing ventrolaterally (1)
75. Tapering ventral process on coracoid: absent (0); present (1)
76. Coracoid: higher than long (0); longer than high (1)
77. Shape of coracoid: semicircular (0); subrectangular (1)
78. Ratio femur / humerus: more than 2.5 (0); between 1.2 and 2.2 (1); less than 1 (2)
79. Shape of internal tuberosity on humerus: triangular, often rounded (0); rectangular (1)
80. Deltopectoral crest: well developed (0); strongly reduced, small, triangular eminence (1)
81. Humerus in lateral view: sigmoidal (0); straight (1)
82. Distal condyles of humerus: located mainly on distal surface (0); located on cranial surface (1)
83. Olecranon process of ulna: well developed (0); strongly reduced or absent (1)
84. True semilunate carpal: absent (0); present (1)
85. Metacarpus (Mc I–III only): short and broad (ratio length/width < 2) (0); slender and elongated (ratio > 2.2) (1)
86. Outline of proximal end of metacarpal I: trapezoidal or medially rounded (0); triangular, with dorso-medial point (1)
87. Medial side of metacarpal I: rounded (0); forming sharp edge (1)
88. Contact between Mc I and Mc II: only proximally (0); Mc I closely appressed to proximal half of Mc II (1)
89. Medial side of Mc II: with medial expansion proximally (0); straight (1)
90. Proximal articular end of Mc III: similar in width to Mc I and II (0); very slender as compared with Mc I and II (1)
91. Number of manual digits: four or more (0); three or less (1)
92. Extensor pits on dorsal surface of distal end of metacarpals: deep, well developed (0); absent or poorly developed (1)
93. Shaft of Mc III: straight (0); bowed laterally (1)
94. Penultimate phalanx of third finger: shorter (0) or longer than both proximal phalanges taken together (1)
95. Manual ungual cross section: broad, less than three times as deep as wide (0); blade-like, more than three times as deep as wide (1)
96. Dorsal lip at proximal articular end of manual unguals: absent (0); present (1)
97. Flexor tubercle on manual unguals: less than half height of articular facet (0); more than half height of articular facet (1)
98. Pelvis: propubic (0); opisthopubic (1)
99. Preacetabular part of ilium: significantly shorter (0), subequal in length to (1), or significantly longer than postacetabular process (2)
100. Articulation of iliac blades with sacrum: vertical, separated above sacrum (0); inclined medio-dorsally, contacting each other or sacral neural spines at midline (1)
101. Posterior end of ilium: rectangular (0); sloping downwards (1)
102. Pubic peduncle of ilium: transversely broad, triangular in outline (0); antero-posteriorly elongated and narrow (1)
103. Pubic peduncle: subequal in antero-posterior length to ischial peduncle (0); significantly longer than ischial peduncle (1)
104. Anterior margin of pubic peduncle: straight or convex (0); concave (1)
105. Obturator foramen in pubis: completely enclosed (0); open ventrally (1); absent (2)
106. Pubic boot in ventral view: broadly triangular (0); narrow, with subparallel margins (1)
107. Pubic boot: with distinct anterior expansion (0); only expanded posteriorly (1)
108. Obturator process on ischium: confluent with pubic peduncle (0); offset from pubic peduncle by distinct notch (1)
109. Obturator process: proximally placed (0); distally placed (1)
110. Ventral notch between obturator-process or -flange on ischium: present (0); absent (1)
111. Ischium at least three fourths length of pubis (0); ischium two thirds or less length of pubis (1)
112. Distal end of ischium: slightly expanded (0); strongly expanded, forming ischial "boot" (1); tapering (2)
113. Femoral head: confluent with greater trochanter (0); separated from greater trochanter by distinct cleft (1)
114. Femoral head: directed antero-medially (0); directed strictly medially (1)
115. Greater trochanter: narrowing from medial to lateral (0); expanded, forming trochanteric crest (1)
116. Lesser trochanter: spike-like or developed as trochanteric shelf (0); broadened ("winglike") (1); fused with greater trochanter (2)
117. Placement of lesser trochanter: at distal end of femoral head (0); more proximally, but below greater trochanter (1); as high as or higher than greater trochanter (2)
118. Posterolateral trochanter on proximal femur: absent or poorly developed (0); well developed (1)
119. Fourth trochanter on femur: well developed (0); reduced to low ridge or absent (1)
120. Fibular condyle on lateral side of proximal tibia: offset from medial part posteriorly by deep incision and not extending to level of medial part posteriorly (0); incision reduced or absent, fibular condyle extending as far posteriorly as medial part of proximal tibia, or even farther (1)
121. Fibular crest of tibia: extending from proximal articular surface downwards (0); separated from proximal articular surface (1)
122. Anterior side of distal tibia: with distinct "step", running obliquely from medio-distal to latero-proximal (0); flat (1)
123. Distal articular surface of tibia: subrectangular with small lateral process (0); narrow triangular in outline and medio-laterally expanded (1); rectangular and more than 3 times wider than long (2)
124. Groove on medial side of proximal end of fibula: present, but narrow (0); present and wide (1); absent (2)
125. Fibular shaft: gradually narrowing from proximal end to mid-shaft (0); abruptly narrowing below insertion of M. iliofibularis (1)
126. Fibular facet on astragalus: large and facing partially proximally (0); reduced and facing laterally or absent (1)
127. Ascending process of astragalus: arising out of lateral part of astragalar body (0); arising out of complete breadth of astragalar body (1)
128. Ascending process of astragalus: lower than astragalar body (0); higher than astragalar body (1); more than twice height of astragalar body (2)
129. Semilunate groove at basis of ascending process of astragalus: absent (0); present (1)
130. Astragalar condyles: facing distally (0); facing antero-distally (1)
131. Horizontal groove across astragalar condyles anteriorly: absent (0); present (1)
132. Arctometatarsalian pes: absent (0); present (1)
133. Pedal digit IV: shorter than III and subequal in length to II (0); longer than II and only slightly shorter than III (1)
134. Metatarsal I: contacting ankle joint (0); splint-like and attached to proximal shaft of Mt II (1); broadly triangular and attached to distal part of Mt II (2)
135. Metatarsal V: transversely flattened and bowed anteriorly distally (0); straight, very slender and splint-like (1)
136. Raptorial claw on pedal digit II: absent (0); present (1)

APPENDIX 3

Data matrix of 17 terminal taxa and 136 characters. Missing and inapplicable characters are coded as "?". Uncertainties (due to polymorphism in higher level taxa or intermediate or slightly transformed character states) are marked with letters: P = 0/1; Q = 1/2; R = 0/2.

	Character						
Taxon	5	10	15	20	25	30	35_
Allosaurus	00001	10010	00000	00000	00010	00100	00011
Aves	?1011	01101	11111	11?11	11121	10101	1?0?1
Bagaraatan	?????	?????	?????	?????	?????	?????	?????
Ceratosaurus	01000	11??0	00000	0?100	0001?	00000	0?000
Coelurus	?????	?????	?????	?????	?????	?????	?????
Compsognathidae	01011	?01?0	0?000	1?00?	???0?	00?0?	????1
Dilophosaurus	00000	0?000	0?0?0	00000	10000	00000	0???0
Dromaeosauridae	00011	01100	1P11P	112P1	01001	10101	11021
Nqwebasaurus	?????	?????	?????	1????	?????	?????	?????
Ornitholestes	00011	???10	?00??	1?201	??00?	0??0?	???Q1
Ornithomimosauria	10111	01100	11101	11011	01121	00111	11021
Oviraptorosauria	1011P	1P101	?0110	0?201	11101	00201	?110?
Therizinosauroidea	11110	0?100	0100P	11001	01?01	0120?	1?1?1
Troodontidae	01011	01100	11111	11211	??1R1	01111	1?021
Tugulusaurus	?????	?????	?????	?????	?????	?????	?????
Tyrannosauridae	0P011	01010	00010	00200	01101	00100	00021
Xinjiangovenator	?????	?????	?????	?????	?????	?????	?????

	Character						
Taxon	40	45	50	55	60	65	70_
Allosaurus	00000	00110	01000	10001	00000	00110	00001
Aves	00101	11101	11111	01?11	0P1?2	210P?	00111
Bagaraatan	0????	?????	?????	?????	?????	10?11	?0?1?
Ceratosaurus	00?00	00000	00000	00000	00000	00000	00000
Coelurus	?????	??1??	11101	10001	1????	?0?01	?0???
Compsognathidae	0??01	0010?	0???1	1?0??	10000	00?1P	00011
Dilophosaurus	0?000	00000	00?01	00000	00000	00000	000?0
Dromaeosauridae	01000	00111	11110	01P11	0P1P2	2101?	?0111
Nqwebasaurus	?????	?????	??111	?????	?????	?????	????1
Ornitholestes	00?01	001??	11111	??011	?010?	?011?	?00??
Ornithomimosauria	12101	11101	11111	10000	?1111	10011	10011
Oviraptorosauria	1211?	??0??	11111	0?111	0111Q	0000?	010??
Therizinosauroidea	1011?	010??	1?0?1	?00??	0P1??	1??0?	?10?1
Troodontidae	11?00	01111	11?11	01011	01102	2101?	0011?
Tugulusaurus	?????	?????	?????	?????	?????	???1?	10???
Tyrannosauridae	0000P	00110	?1000	00101	00001	10011	00011
Xinjiangovenator	?????	?????	?????	?????	?????	?????	?????

	Character						
Taxon	75	80	85	90	95	100	105_
Allosaurus	00001	00000	00000	00100	10000	00000	00101
Aves	11111	11210	01111	??111	1?111	11121	11102
Bagaraatan	?????	?????	?????	?????	?????	??0??	1?1?2
Ceratosaurus	10000	00100	100?0	??000	000??	??000	?0000
Coelurus	???0?	??100	000P?	???0?	?????	?????	????1
Compsognathidae	000?1	00P00	000?0	???00	1?0P0	0001?	0111P
Dilophosaurus	00000	00100	00000	00000	00000	000?0	0000?
Dromaeosauridae	11111	11110	01111	11111	11111	11120	11112
Nqwebasaurus	00?01	0?1?0	00?00	??100	110?1	?0???	?????
Ornitholestes	?????	??100	0???1	??111	1?01?	0001?	11112
Ornithomimosauria	1P001	00101	10P00	11110	11010	00011	01112
Oviraptorosauria	?00?1	11110	00111	??111	1100P	10011	11102
Therizinosauroidea	10?01	1P110	0?110	??010	110?0	?01Q0	10002
Troodontidae	11111	11110	01111	??111	11111	110?1	1???2
Tugulusaurus	?????	?????	?????	111??	?1??0	?0???	?????
Tyrannosauridae	00001	00001	100?0	0111?	110?0	00011	01112
Xinjiangovenator	?????	?????	?????	?????	?????	?????	?????

	Character						
Taxon	110	115	120	125	130	135	___
Allosaurus	00100	00010	11000	10100	00101	10020	0
Aves	11111	12111	22110	11221	11211	00021	P
Bagaraatan	?????	??111	220?1	11Q?1	?1211	0????	?
Ceratosaurus	??000	01000	10000	00P00	00000	10???	?
Coelurus	10???	??0?0	1100?	1120?	?????	?????	?
Compsognathidae	11101	P0010	11?10	1?100	?12?1	?0020	0
Dilophosaurus	00000	??000	0000P	00000	00000	00010	0
Dromaeosauridae	11111	12111	221P0	112Q1	11211	0P121	1
Nqwebasaurus	?0???	??11P	1Q0?0	???11	?121?	0002?	0
Ornitholestes	??101	?2???	???1?	???00	?????	?0???	?
Ornithomimosauria	10101	0P110	12010	11110	11211	0P020	0
Oviraptorosauria	?0111	02111	12?1?	11Q?1	11211	?P021	0
Therizinosauroidea	?0111	0?111	12???	1????	112??	?0?P?	0
Troodontidae	??111	12111	2211?	11221	11211	01121	1
Tugulusaurus	?????	??000	1Q000	101??	10P11	0????	?
Tyrannosauridae	10101	02110	12000	11110	11211	01020	0
Xinjiangovenator	?????	?????	????1	1?Q11	11211	0????	?