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A Troodontid Dinosaur from Ukhaa Tolgod (Late Cretaceous Mongolia)

MARK A. NORELL¹ AND SUNNY H. HWANG²

ABSTRACT

Here we describe a fragmentary troodontid specimen from the sublocality of Grangers Flats at the Late Cretaceous locality of Ukhaa Tolgod, Omnogov, Mongolia. This specimen is provisionally referred to the coeval *Saurornithoides mongoliensis*. IGM 100/1083 displays a pattern of tooth replacement that is like that of basal avialans. The presence of this pattern in avialans has been used by some to refute a theropod origin for this group.

INTRODUCTION

The Late Cretaceous fossil beds of Mongolia are unusual for the diversity and abundance of theropod dinosaurs (Osmólska, 1980; Currie 2000, personal obs.). Yet even with the large number of dinosaur fossils discovered in these formations, troodontid dinosaurs are extremely uncommon. Although they are known from a large species diversity, most of these specimens are known from single individuals (see Makovicky and Norell, in press). Here we report on a fragmentary specimen of a troodontid dinosaur from Ukhaa Tolgod (Dashzeveg et al., 1995).

Although this specimen is extremely fragmentary, it displays some important features of troodontid theropods and documents the occurrence of another troodontid besides *Byronosaurus jaffei* (Norell et al., 2000; Makovicky et al., 2003) at Ukhaa Tolgod.

The specimen (IGM 100/1083) was collected during the 1993 field season of the Mongolian Academy of Sciences–American Museum of Natural History Paleontological Project. It was found as “float” at the Grangers Flats sublocality of Ukhaa Tolgod. It is comprised of a few pieces of the skull and fragments of the axial and appendicular skeleton.

It can be referred to the Troodontidae

¹ Division of Paleontology, American Museum of Natural History (norell@amnh.org).

² Division of Paleontology, American Museum of Natural History (sunny@amnh.org).

based on the presence of an arctometatarsalian pes, closely packed anterior maxillary teeth, a maxillary border to the external nares, and cervical vertebrae with a sharp ventral keel and a low neural spine (Makovicky and Norell, in press).

DESCRIPTION

CRANIUM

A fairly complete right quadrate and a maxillary fragment are associated with IGM 100/1083. The maxillary fragment is from the left side of the skull and shows the presence of erupting teeth and tooth replacement pits similar to those in avialans (fig. 1). The fragment is the segment of the maxilla directly posterior to the premaxilla, anterior to the accessory antorbital fenestra, and ventral to the naris. A finished surface on the anterior corner of the bone indicates that the maxilla formed the posterior border of the nares, as in all troodontids except for *Sinovator changii* (Xu et al., 2002). Numerous neurovascular foramina project ventrally just dorsal to the tooththrow. On the lateral surface of the element, dorsal to the numerous neurovascular foramina, two large superficial canals extend vertically and divide.

The roots of five teeth are preserved within the maxillary fragment. Although no details of the tooth crowns can be observed, their cross sections indicate that the teeth were laterally compressed and blade-like, as is typical of troodontids. The teeth are crowded close together and appear incompletely separated so that the teeth lie in a continuous groove, as in other troodontids (Currie, 1987). However, the posteriormost tooth is completely bounded posteriorly by a thin strip of interdental bone, creating the anterior half of a socket for the sixth tooth, which is unpreserved. This implies that the teeth posterior to the ones preserved would be more widely spaced and placed in distinct sockets, a trend typical in troodontids (Currie, 1987). The ventral margin of the labial maxillary bone extends more ventrally than that of the lingual bone. A thin sulcus lies parallel to the lingual parapet. This sulcus may represent the demarcation between maxilla and interdental bone (Currie, 1987). Tooth replacement pits lie along this sulcus

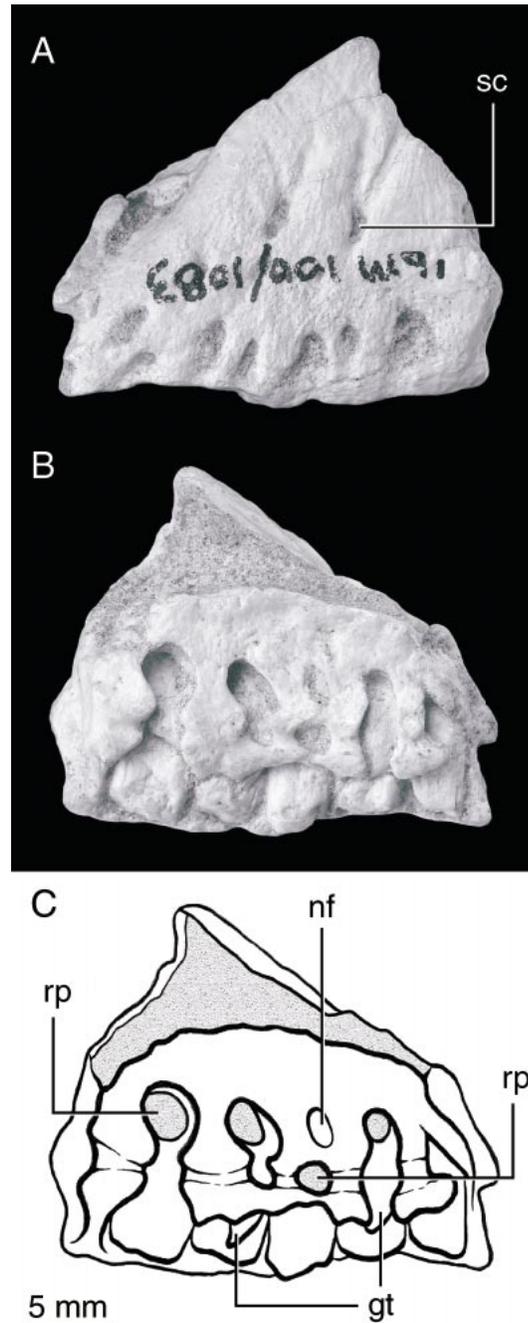


Fig. 1. The left maxilla of IGM 100/1083 in (A) lateral and (B) medial views, and (C) an interpretive drawing of the medial surface.

but are separated from the margin of the parapet by interdental bone; consequently, the replacement pits are completely enclosed by maxillary/interdental bone. Small extensions of the interdental bone protrude ventrally into the spaces between the four anterior teeth. Posterior to the fifth tooth, the interdental bone extends ventrally as a thin ridge, ending just dorsal to the ventrolabial margin of the maxilla.

Each tooth replacement pit is associated with one nutrient foramen that lies dorsal to it. The buccal wall of the maxilla thus accommodates two rows of perforations, the dorsal row of nutrient foramina and the ventral row of tooth replacement pits. The tooth replacement pits excavate the tooth roots as well as piercing the maxilla wall. This is slightly different from the condition seen in birds and crocodylians, in which the replacement pits are restricted to the roots of the teeth being replaced and do not invade the maxilla wall. The teeth that are being replaced have nutrient foramina and replacement pits that are conjoined, with no bone separating the two. Some of the teeth that are not being replaced show conjoined foramina, but this is probably an erosional artifact. The nutrient foramina are larger for the teeth that are being replaced, presumably because the growing teeth required an increased blood supply to fuel their development. Incompletely erupted germ teeth share space in the second and fourth alveoli of the maxillary fragment with mature teeth. The germ teeth in the maxillary fragment are not easily distinguishable from the mature teeth because they are growing within the pulp cavities of the mature teeth. Only a faint line of demarcation differentiates the replacement tooth from the mature tooth. The alternate spacing of the germ teeth is typical of reptilian tooth replacement, in which waves of replacement affect every other tooth (Edmund, 1960). Because the germ teeth are almost fully erupted, the replacement pits in the roots of their respective mature teeth are no longer visible. However, in the fifth tooth preserved, which is not being replaced, the replacement pit is clearly visible in the root of the tooth, although it does not yet have a germ tooth growing within the pit.

The fragment of the quadrate is a Y-

shaped bone (fig. 2). The shaft of the quadrate is broken at its dorsal end, so the squamosal articulation is lost. The two ventral articular condyles are separated by a shallow diagonal sulcus. The lateral condyle is smaller than the medial one and is rounded ventrally. The lateral edge of the condyle is anteroposteriorly flattened. The posterior face of this flattened portion is slightly concave where it receives the quadratojugal. The medial condyle, which contacts the articular of the mandible, is roughly oval in ventral view. A low ridge runs diagonally across the ventral surface from the anteromedial corner to the posterolateral corner. The medial edge of the condyle curls dorsally. On the posterior face of the quadrate, a broad, shallow sulcus separates the two condyles and continues dorsally to just below the point of breakage. The ventral base of the pterygoid flange is preserved, but it cannot be determined to what extent the flange extended dorsally and anteriorly because of breakage.

AXIAL SKELETON

An anterior cervical vertebra, an anterior dorsal vertebra, a small sacral fragment, and three isolated posterior caudal vertebrae were found with IGM 100/1083. Aside from the caudals, which are nearly complete, the cervical vertebra is the most well preserved, with the others lacking all or most of their dorsal processes. The sacral fragment is not particularly diagnostic as it consists only of the ventral half of the fused articulation between two consecutive sacral vertebrae. The anterior half of the centrum is missing from one sacral and the posterior half from the other.

The posterior third of the centrum and the lateral extremities of the right apophyses are missing from the anterior cervical (fig. 3). The anterior surface of the centrum is concave, sharply angled posteroventrally, and wider than it is tall, as in most coelurosaurs (Gauthier, 1986). The parapophyses are positioned on the anterolateral corners of the anterior central articulation and extend onto the ventrolateral surface of the centrum. A broad, shallow depression separates the two parapophyses. The anterior end of a midline keel is visible just posterior to the parapop-

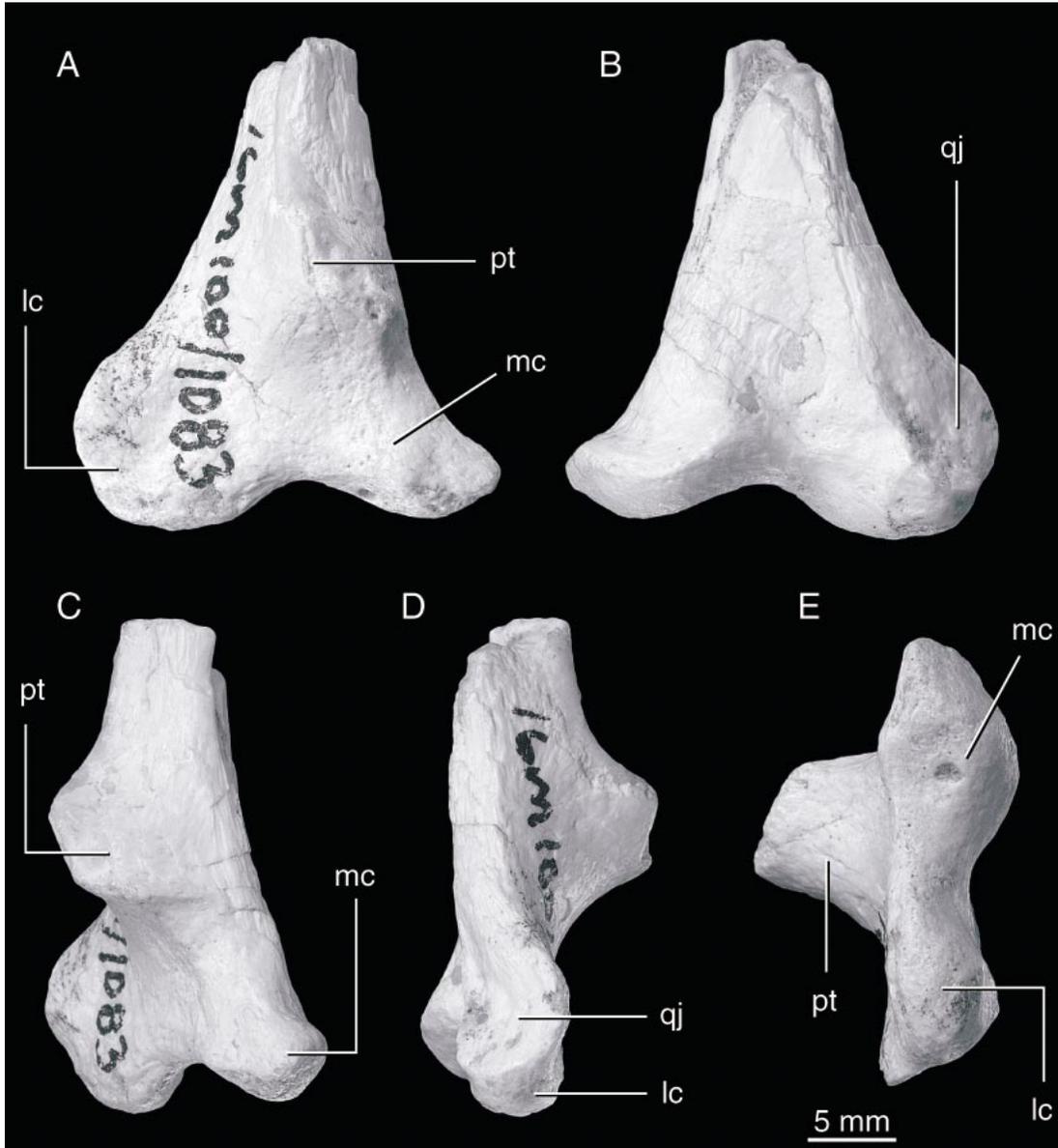


Fig. 2. The right quadrate of IGM 100/1083 in (A) anterior, (B) posterior, (C) medial, (D) lateral, and (E) ventral views.

physes; the posterior end is lost due to breakage. The sharp ventral keel and low neural spine on the anterior cervical vertebra are diagnostic of troodontids (Makovicky, 1995). Two small elliptical foramina lie on the lateral surface of the cervical vertebra. One, probably a nutrient foramen, lies on the lateral surface of the centrum just posteroven-

tral to the diapophysis. A pneumatic opening lies in the infrapostzygapophyseal fossa. On the right side of the vertebra, where the transverse process has broken away, this foramen can be seen opening into an air space that pneumatizes the transverse process and neural arch. The pneumatic foramina are substantially larger and more rounded than the

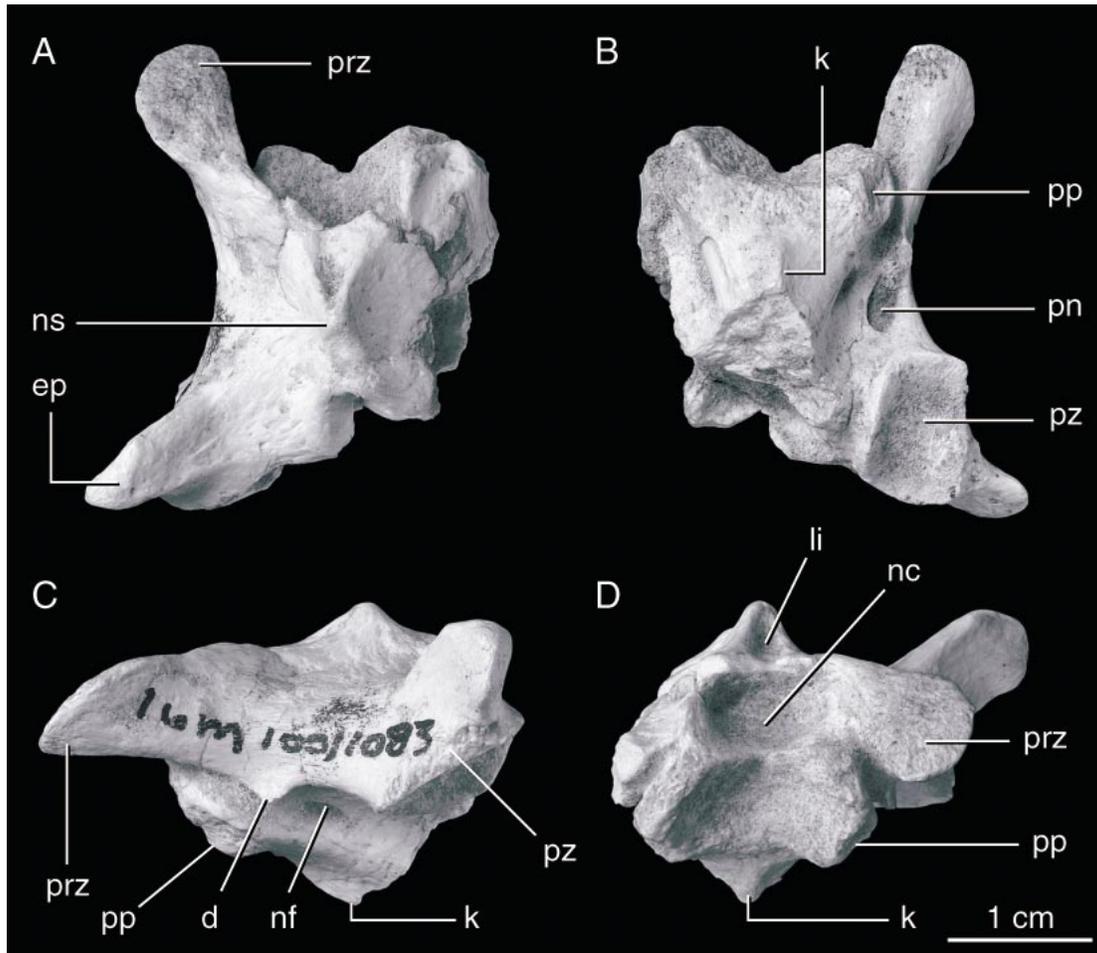


Fig. 3. The anterior cervical of IGM 100/1083 in (A) anterior, (B) left lateral, (C) ventral, and (D) dorsal views.

nutrient foramina. On the broken surface of the centrum, the cross section of one small pneumatic chamber is visible.

The prezygapophysis is long and diverges slightly laterally from the midline of the cervical. The articulating facet slopes anteroventrally and is oval in dorsal view. The diapophysis is triangular and points posteroventrally. Its ventral apex is level with the posterior margin of the parapophysis. The postzygapophysis diverges strongly posterolaterally from the midline and is almost perpendicular to the posterior surface of the centrum. The dorsally curving epiphysis is large and laterally flat. The articular facet of the postzygapophysis is round and concave,

with sharp edges. The neural spine is short and slopes posteroventrally. The arch widens caudally, and the ligament scars are small and shallow.

All of the apophyses of the anterior dorsal vertebra are missing, but the centrum is distinctive enough to characterize the vertebra as an anterior dorsal. The anterior face of the centrum is concave while the posterior face is flat, a characteristic of troodontid and avimimid dorsal vertebrae (Makovicky, 1995). The anterior face is subcircular, while the posterior surface is shaped roughly like an inverted triangle. The constricted centrum bears a well-developed hypapophysis that extends over the anterior half of the ventral sur-

face and projects 6 mm ventrally from the ventral surface of the centrum. The ventral extension of the hypapophysis is equal to half the height of the anterior surface of the centrum. Hypapophyses are present only on anterior troodontid dorsals (Makovicky, 1995). Posteriorly, the hypapophysis grades into a ventral midline keel that runs along the remainder of the centrum. The lateral surfaces of the centrum are deeply concave, giving the centrum a pinched appearance. The floor of the neural canal is broad and moderately curved. The dorsal centrum lacks pneumatic foramina, as in *Sinovenator changii* (Xu et al., 2002).

All three posterior caudal vertebrae have elongated centra and low pre- and postzygapophyses. The caudal vertebrae are identical in all aspects except for size and degree of preservation. The caudals are posterior to the transition point as determined by their lack of transverse processes. They also lack neural spines, instead having only a shallow midline sulcus along their entire dorsal length. This, in addition to their small size, indicates that these vertebrae were near the caudal terminus of the tail. Small chevron facets are located on the ventrolateral corners of both the anterior and posterior ends of the centra. Pre- and postzygapophyses slightly overlap the centra of the preceding and succeeding vertebrae. The prezygapophyses diverge dorsolaterally from the anterior part of the centrum. The slightly shorter postzygapophyses parallel each other. When articulated, the postzygapophyses fit into the curved surface between the two prezygapophyses of the following vertebra.

PES

The proximal end of the right fourth metatarsal and its associated distal tarsal are preserved in IGM 100/1083 (fig. 4). The plate-like distal tarsal is fused to metatarsal IV, as in other adult troodontids (Makovicky and Norell, in press). The medial edge of the distal tarsal overhangs the medial surface of metatarsal IV, and the anterior edge of the tarsal is flush with the anterior margin of the metatarsal. Medially, the distal tarsal probably contacted another distal tarsal covering metatarsal II.



Fig. 4. Oblique anteromedial view of the left metatarsal IV showing the fused distal tarsal.

A small, dorsoventrally elongate, rugose concavity is present at the posterolateral corner of the proximal end of metatarsal IV for the articulation of metatarsal V. The proximomedial surface of metatarsal IV is flattened where it articulates with metatarsal II. The shaft of metatarsal IV is suboval in cross section just below the proximal articular surface, but becomes triangular distally. A rugose ridge runs down the posterolateral edge of metatarsal IV, starting 3 cm distal to

the proximal surface and continuing to the broken end of the metatarsal fragment.

Only the distal end of the left third metatarsal is preserved, and the bone is extremely weathered. Metatarsal IV is much more robust than metatarsal III, as in all troodontids (Makovicky and Norell, in press). The posteroproximal extension of the distal articular surface of metatarsal III, a feature of many troodontids (Makovicky and Norell, in press), still exists in outline, even though the surface itself is eroded away. The anterior surface of the fragment is flat. The medial and lateral edges are slightly concave where they would be appressed to metatarsals II and IV, and meet in a long, sharp ridge that runs along the posterior face from the proximal end of the fragment to slightly past its midpoint. The portion of the medial surface distal to this ridge is bowed slightly outwards while the distal lateral face is slightly concave, as in other troodontids. The fragment is triangular in cross section throughout its existing length.

Five isolated phalanges were found with IGM 100/1083, including a hypertrophied digit II ungual. The digit II ungual is strongly recurved and laterally compressed, as in most troodontids (Makovicky and Norell, in press). Proximally, the lateral and medial grooves for the claw sheath fork into two grooves that flank the dorsal and ventral margins of the proximal articular facet. The articular facet is deep and tall and is bisected by a sharp ridge. A large flexor tubercle is positioned below the ventral margin of the facet. The phalanges are unremarkable.

DISCUSSION

Although very fragmentary, IGM 100/1083 is very similar to the holotype specimen of *Saurornithoides mongoliensis* (AMNH 6516) from the roughly coeval Djadokhta beds at Bayn Dzak. Similarities include the packing of teeth and pattern of sculpture on the anterior maxillary fragment and the general shape and conformation of the preserved parts of metatarsal III. The only significant difference between the two specimens is size; IGM 100/1083 is the larger of the two (pedal digit II ungual length: AMNH 6516 = 29.3 mm, IGM 100/1083 =

34.7 mm). Provisionally we refer IGM 100/1083 to this taxon as cf. *Saurornithoides mongoliensis*. Aside from the holotype, only a single other specimen has been referred to *Saurornithoides mongoliensis*, a hindlimb from the Chinese Djadokhta locality of Bayan Mandahu (Currie and Peng, 1993). However, referral of this specimen to *Saurornithoides mongoliensis* is somewhat questionable (see Norell et al., ms).

The quadrate of IGM 100/1083 is unusual among known troodontid quadrates. All other described troodontid quadrates possess a single pneumatic foramen that opens into an extension of the middle ear sac (Barsbold et al., 1987; Currie and Zhao, 1993; Xu et al., 2002). The quadrate of IGM 100/1083 is solid, with no sign of a pneumatic opening, and the broken shaft does not reveal a pneumatic interior.

The putative interdental bone forming the buccal parapet on the maxillary fragment of IGM 100/1083 is formed into thin stalklike structures that are expanded distally into knobs. These knobs would have fit into the constrictions between the roots and crowns of adjacent teeth. This avialanlike characteristic was previously noted by Currie (1987) in another troodontid specimen (TMP 82.16.138). Most other theropods have well-developed interdental plates that taper to a point at their distal extremities, extend to the ventral margin of the maxilla, and meet the labial wall of the maxilla to form sockets (Currie, 1987).

Also like avialans, IGM 100/1083 has a vertical tooth family. The germ teeth are erupting vertically into the mature tooth, as they do in crocodylians and avialans. In other theropods, the replacement teeth erupt lingually to the mature tooth row, so that different generations of teeth exist side by side (Martin and Stewart, 1999). Only a thin line of demarcation differentiates a mature tooth from the replacement tooth directly beneath it in IGM 100/1083, which is very different from the distinct, easily discernable replacement teeth observed in other theropods. Vertically erupting teeth have not been described in any other nonavialan theropod.

Martin and Stewart (1999) argued that the lack of similarity between avialan and other theropod tooth morphology and replacement

disallows a theropod origin for avialans. These authors claimed that unserrated teeth, constrictions between the crowns and expanded roots of the teeth, vertical tooth replacement, and tooth replacement pits closed at their bases are unique features of avialans. However, IGM 100/1083 possesses both vertical tooth families and tooth replacement pits closed at their bases. Constriction between the crown and root of the teeth is present in troodontids (Currie, 1987), therizinosaurids (Clark et al., 1994), alvarezsaurids (Perle et al., 1993), and *Microraptor zhaoianus*, a dromaeosaurid (Xu et al., 2000; Hwang et al., 2002), although these constrictions are not necessarily homologous. *Byronosaurus jaffei*, a troodontid (Norell et al., 2000), and the dromaeosaurids *Sinornithosaurus milleni* and *Microraptor zhaoianus* (Xu et al., 1999, 2000; Hwang et al., 2002) have teeth that are devoid of serrations. Appearance of these supposedly unique avialan dental characters in nonavian conclusively demonstrates that features considered by Martin and Stewart (1999) to be restricted to avialans and crocodylians actually have a broader distribution.

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APPENDIX 1

INSTITUTIONAL ABBREVIATIONS

AMNH American Museum of Natural History,
New York

IGM

Institute of Geology Mongolia, Ulaan-
baatar

TMP

Royal Tyrell Museum of Paleontology,
Drumheller

APPENDIX 2

ANATOMICAL ABBREVIATIONS

d diapophysis
ep epipophysis
gt germ tooth
k ventral keel
lc lateral condyle
li ligament scar
mc medial condyle
nc neural canal

nf nutrient foramen
ns neural spine
pn pneumatic foramen
pp parapophysis
prz prezygapophysis
pt pterygoid flange of the quadrate
pz postzygapophysis
qj articulation point for the quadratojugal
rp tooth replacement pit
sc superficial canal