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A Small Derived Theropod from Öösh, Early Cretaceous, Baykhangor Mongolia

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ABSTRACT

A new theropod dinosaur, *Shanag ashile*, from the Early Cretaceous Öösh deposits of Mongolia is described here. The new specimen (IGM 100/1119) comprises a well-preserved right maxilla, dentary, and partial splenial. This specimen exhibits a number of derived theropod features, including a triangular anteriorly tapering maxilla, a large antorbital fossa, and maxillary participation in the caudally elongate external nares. These features resemble the Early Cretaceous dromaeosaurids *Sinornithosaurus millenii* and *Microraptor zhaoianus*, as well as the basal avialan *Archaeopteryx lithographica*. A comprehensive phylogenetic analysis including 58 theropod taxa unambiguously depicts the new Öösh theropod as a member of Dromaeosauridae. Relative to other dromaeosaurids, *Shanag ashile* is autapomorphic in its lack of a promaxillary fenestra and in the presence of interalveolar pneumatic cavities. The discovery of IGM 100/1119 expands our knowledge of Early Cretaceous dromaeosaurids and the faunal similarity between the Öösh and the Jehol biotas.

INTRODUCTION

Theropods were some of the first dinosaur fossils discovered from the Early Cretaceous locality of Öösh (= Ohshih or Oshih), but their described remains are limited to undiagnostic teeth of the large theropod “*Prodeinodon*” (Osborn, 1924a; but see Currie, 2000). Theropod remains are generally much

more rare than the plentiful fossils of *Psittacosaurus mongoliensis* and sauropods at the locality (Osborn, 1923, 1924b). In some places, however, isolated theropod material of a range of sizes is encountered frequently—especially unguals, phalanges, and teeth.

The deposits at Öösh are considered to be Early Cretaceous (Berriasian–Barremian). This is roughly coeval with beds forming the

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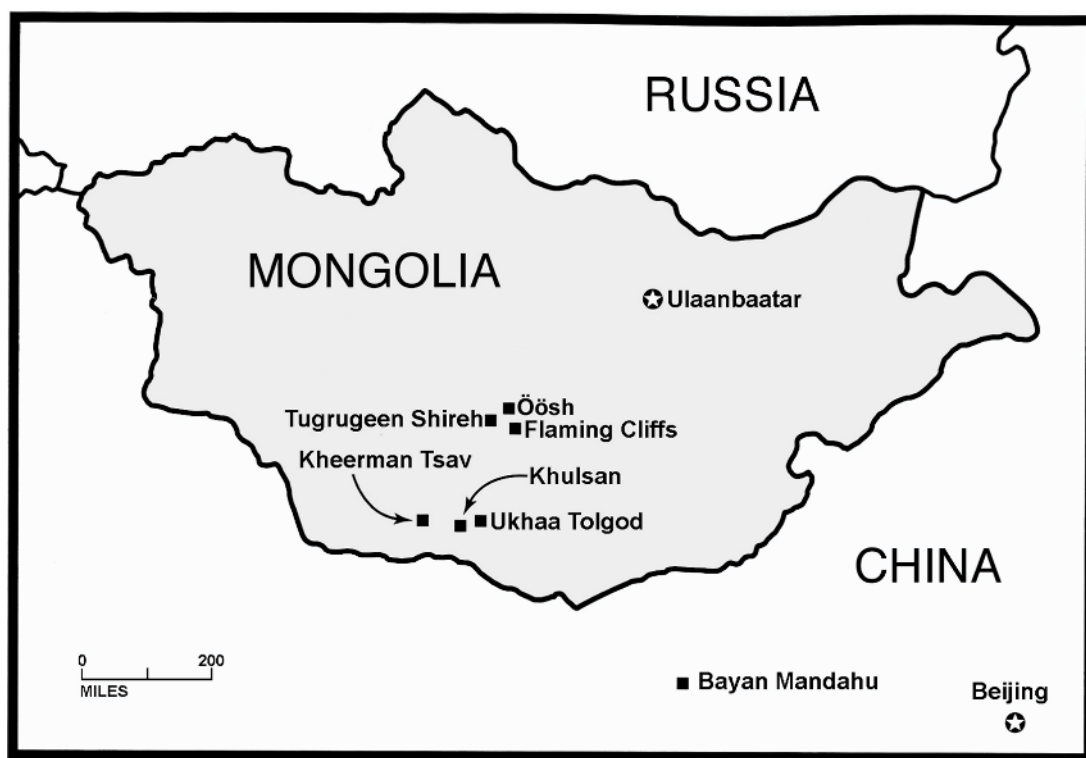


Fig. 1. Map of Mongolia showing geographical relationship of the Öösh locality to other Gobi fossil localities.

Jehol group of northeastern China. The Jehol beds of the Yixian and Jiufotang formations have produced abundant vertebrate fossil remains (reviewed in Zhou et al., 2003). These discoveries include the ubiquitous *Psittacosaurus* (also present in the Öösh beds) as well as avialan and nonavialan dinosaurs, including small feathered theropods (reviewed in Norell and Xu, 2005). Additionally, the Jehol beds contain a diverse mammalian fauna including one of the largest Mesozoic mammals, *Repenomamus* (Li et al., 2001). The Jehol flora is abundant, containing the putative earliest angiosperm *Archaeofructus* (Sun et al., 1998).

The Öösh locality lies in the Altai region of Central Mongolia (see Watabe and Suzuki, 2000; this paper, fig. 1). Fossils were first collected here by American Museum field parties in the 1922 (Andrews, 1932). New collections from the Öösh locality by field parties of the Mongolian Academy of Sciences

and the American Museum of Natural History include a wide array of fossil materials, including gobiconodontids (Rougier et al., 2001), a pterosaur (Andres and Norell, 2005), lizards, large and small sauropods, and psittacosaurus ranging in size from hatchlings to senescent adults.

The Jehol biota and Öösh locality contain some elements in common such as the primitive ceratopsian *Psittacosaurus*. Unfortunately, dates of the Jehol and Öösh faunas are poorly constrained. Despite an abundance of andesitic layers that allow for radiometric dating of rocks that produce Jehol fossils, several different ages have been published. Recent dating efforts agree with previous results (Swisher et al., 1999; Wang et al., 2001) in proposing a Barremian date for the feathered dinosaur beds in Sihetun and bracket the lowermost Yixian beds (one of the most fossiliferous formations in the Jehol group) as being between 128 m.y. and

139 m.y. (Swisher et al., 2002). Older dates have been published that would put much of the Yixian Formation in the Late Jurassic (Lo et al., 1999). These older dates, however, have been criticized on a number of grounds (Zhou et al., 2003).

Similarly, the stratigraphic and temporal divisions for the deposits at Öösh are poorly constrained (Jerzykiewicz and Russell, 1991). According to Shuvalov (2000), rocks that overlie the strata of the Öösh locality examined here have yielded dates of 141 ± 8 m.y. and 126 ± 9 m.y. This indicates a Berriasian–Hauterivian stage for these strata. Correlated exposures have been dated at around 130 m.y. (Samilov et al., 1988; Rougier et al., 2001), and are consistent with the results of Shuvalov (2000). A broader overview of the geology of Öösh is given by Andres and Norell (2005).

COMPONENTS OF THE ÖÖSH LOCALITY

Consistent with previous collecting, Mongolian Academy of Sciences–American Museum of Natural History Mongolian expeditions in 1997, 1999, 2001, and 2005 collected ubiquitous *Psittacosaurus* material and numerous undiagnostic large theropod teeth. In addition to this material, partial vertebrate material was recovered that is referable to varying levels of clade specificity. Isolated squamate vertebrae lacking zygo-phenes/zygantra, exhibiting an unconstricted precondylar region, and nonoblique condyles are insufficient for referral to a specific clade, but these characters do rule out varanoid, cordyliform, lacertiform, or snake affinities. Additional squamate material includes a probable nonvaranoid, nonsnake autarchoglossan (based on the presence of small dorsolateral zygosphenes) and a nonautarchoglossan caudal vertebra with a fracture plane that is on the transverse process. A nearly complete gekkonomorph skull is also known from Öösh (Conrad and Norell, 2006).

A large (~6 cm), heavily rugose postorbital was collected. Its straight frontal process precludes its referral to most coelurosaur clades except ornithomimosaurs or tyrannosauroids. Its size and rugose texture excludes it from ornithomimosaurs. It lacks an anterior

process projecting into the orbit, like that in derived tyrannosaurids. In overall appearance it is similar to the postorbital of *Sinraptor dongi* (Currie and Zhao, 1993) and tentatively considered a noncoelurosaur (allosauroid?) or basal tyrannosauroid postorbital.

A partial pes along with other identified material pertaining to a small theropod was collected and is currently being prepared. Slightly weathered postcranial remains collected as float further indicated the presence of at least one small, derived theropod taxon. This material includes a proximal femur and tibia. The femoral head is weathered but preserves a prominent, moundlike lateral ridge and a well-developed posterior trochanter. The proximal tibia lacks a medial cnemial crest, unlike that seen in *Mononykus olecranus* (Perle et al., 1994) and other alvarezsaurids, and bears a well-developed fibular crest. Unfortunately, the dorsal surface of the femur is poorly preserved, so it is unclear if the lesser and greater trochanters were confluent as in derived avialans. Nonetheless, the moundlike lateral ridge and posterior trochanter indicate this material likely is referable to a small paravian theropod.

In 1999, the Mongolian Academy of Sciences–American Museum of Natural History Mongolian expedition recovered a partial skull of a small theropod dinosaur from Öösh in a coarse, well-sorted sand channel. Although incomplete, this skull (IGM 100/1119; fig. 2) is notable for its possession of several extremely derived coelurosaur characters, clearly distinguishing it as a small dromaeosaurid.

SYSTEMATIC PALEONTOLOGY

THEROPODA MARSH, 1884

COELUROSAURIA VON HUENE, 1914

MANIRAPTORA GAUTHIER, 1986

DROMAEOSAURIDAE MATTHEW AND
BROWN, 1922

Shanag ashile, new taxon

HOLOTYPE: IGM 100/1119, nearly complete right maxilla, dentary, and partial splenial.

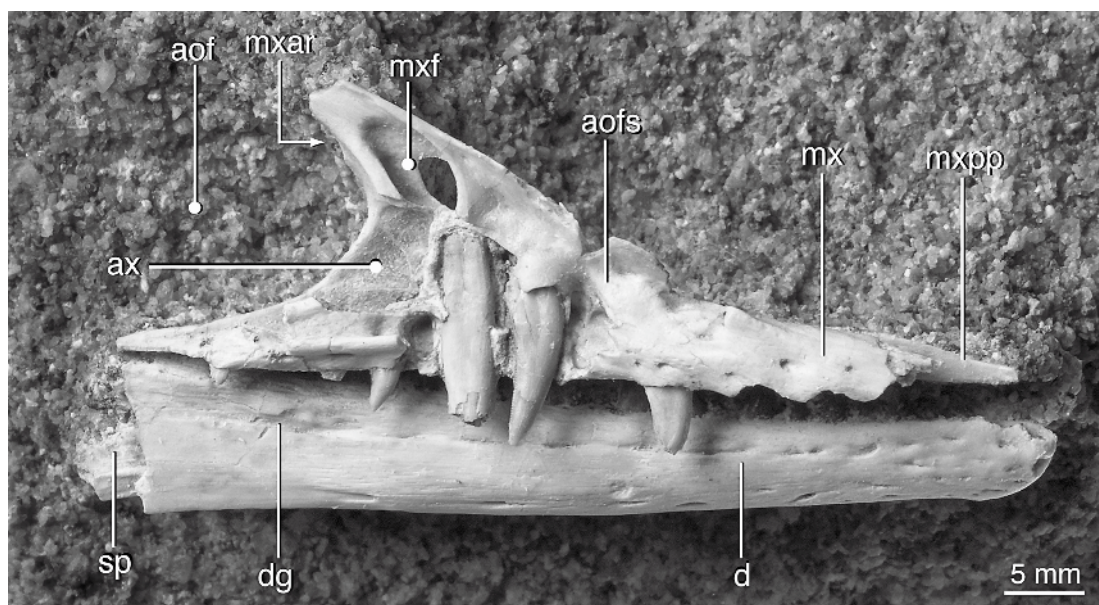


Fig. 2. IGM 100/1119 in right lateral view. Anatomical labels in appendix 3.

ETYMOLOGY: *Shanag*, Black-hatted dancers in the Buddhist Tsam festival, and *ashile*, in reference to the old Öösh locality and formation name used by Dr. Henry F. Osborn.

DIAGNOSIS: Small dromaeosaurid theropod diagnosed by the following combination of characters: triangular, anteriorly tapering maxilla; lateral lamina of nasal process of maxilla reduced to small triangular exposure; absence of a promaxillary fenestra; presence of interalveolar pneumatic cavities; incipient dentary groove on posterolateral surface of dentary.

DESCRIPTION

IGM 100/1119 consists of an almost complete right maxilla and dentary in articulation (fig. 2). The maxilla is eroded laterally, revealing details of its alveoli, pneumatic chambers, and fenestrae. Like most theropods, the maxilla of *Shanag ashile* can be divided into three parts: a posteriorly projecting subantorbital process that contacts the jugal, a dorsally projecting ascending ramus of the nasal process, and an anteriorly projecting ventral ramus of the nasal process (Witmer, 1990, 1997). The maxilla can be further divided into

a medial lamina, or the portion of the maxilla that resides within the antorbital fossa, and a lateral lamina that forms the lateral surface of the maxilla outside the antorbital fossa. These laminae correspond to the lamina lateralis and lamina medialis of Witmer (1997). Nomenclature for the structures of the antorbital cavity follows that used by Witmer (1997).

The maxilla is triangular, tapering anteriorly as in *Archaeopteryx lithographica* (Wellnhofer, 1974: fig. 5; Mayr et al., 2005: fig. 2) and *Sinornithosaurus millenii* (Xu and Wu, 2001). The maxilla contributes to the narial border, as suggested by the slight depression on its dorsal margin near its anterior tip. This is unlike the condition in derived dromaeosaurids, but similar to the basal dromaeosaurids *Microraptor zhaoianus* (Xu et al., 2000) and *Sinornithosaurus millenii* (Xu et al., 1999) and derived troodontids such as *Troodon formosus* (Makovicky and Norell, 2004), *Saurornithoides junior* (IGM 100/1) and *Byronosaurus jaffei* (IGM 100/983). The articulation with the premaxilla is complex. Anteromedially, a thin projection of bone, the surface of which is slightly depressed, extends rostrally past the limit of the dentigerous portion of the maxilla. A complementary

groove separates this process from the lateral lamina of the maxilla. In articulation, a portion of the posterior ramus of the premaxilla would have fit into this groove. A similar construction is present in a disarticulated maxilla of *Velociraptor mongoliensis* (IGM 100/976). Neurovascular foramina are present on the labial surface with each foramen generally corresponds to a single tooth position.

The antorbital fossa is large and occupies much of the lateral surface of the maxilla. Anterior to the fossa, a small triangular lateral lamina is present below the external nares. This is similar to the condition in *Sinornithosaurus millenii* (Xu and Wu, 2001), *Microraptor zhaoianus* (Xu et al., 1999), and *Archaeopteryx lithographica* (Wellnhofer, 1974: fig. 5; Mayr et al., 2005: fig. 2). The rostral boundary of the antorbital fossa is situated approximately 7 mm caudal to the premaxillary contact, above the 3rd maxillary tooth position. The caudal margin of the naris overlaps the rostral border of the antorbital fossa as in *Archaeopteryx lithographica* (Wellnhofer, 1974: fig. 5; Mayr et al., 2005: fig. 2) but unlike dromaeosaurids (Norell and Makovicky, 2004) and troodontids (Makovicky and Norell, 2004). The antorbital fossa is defined shallowly anteriorly, but the dorsal and posteroventral posterior margins are sharply bounded by thin, laterally projecting shelves of bone. Although the proportions of the antorbital fossa and general shape of the maxilla are similar to that of *Archaeopteryx*, the raised dorsal rim of the antorbital fossa differs from the recessed antorbital fossa seen in *Archaeopteryx* (Witmer, 1990). In almost all avialans, the ascending ramus of the maxilla is lost, and as a result, the nasal forms the majority of the dorsal border of the internal antorbital fenestra and antorbital fossa (Cracraft, 1986). *Archaeopteryx lithographica* is the only avialan that retains an extensive ascending ramus of the maxilla, but the ramus is recessed medially so that the nasal forms the dorsal border of the antorbital fossa as in other basal avialans (Witmer, 1990), but not the internal antorbital fenestra unlike other avialans. IGM 100/1119 retains the typical theropod condition in which maxilla excludes the nasal from

the internal antorbital fenestra. Furthermore, there is no indication that the maxilla was recessed medially from the nasal and thus it is unlikely that the nasal formed the dorsal boundary of the antorbital fossa.

The antorbital cavity contains two fenestrae, the antorbital and maxillary fenestrae. There is no sign of a promaxillary (tertiary antorbital) fenestra. *Archaeopteryx lithographica*, which possesses the most plesiomorphic antorbital cavity of any avialan (Witmer, 1997), has both a maxillary and promaxillary fenestra in its recessed antorbital cavity. *Confuciusornis sanctus*, a basal avialan phylogenetically intermediate between *Archaeopteryx lithographica* and Ornithothoraces (*sensu* Chiappe, 1995), has only a small, round accessory antorbital fenestra (Chiappe et al., 1999). Chiappe et al. (1999) tentatively homologized this fenestra with the maxillary fenestra. All other known avialans have complex diverticula extending medially, rostrally, and caudally from one large antorbital cavity (Witmer, 1990), but laterally, the antorbital opening is not subdivided into separate accessory fenestrae. Witmer (1997) suggested that the promaxillary fenestra characterizes Neotheropoda. The lack of a promaxillary fenestra is not, however, entirely unusual among nonavialan theropods. The troodontids *Saurornithoides junior* (Barsbold, 1974; Norell et al., in prep.) and *Byronosaurus jaffei* (IGM 100/983) lack a promaxillary fenestra, while the more basal troodontid *Sinovenator changii* (Xu et al., 2002) retains a promaxillary fenestra. Additionally, the oviraptorosaur *Incisivosaurus gauthieri* (Xu et al., 2002) and the therizinosauroid *Erlikosaurus andrewsi* (Clark et al., 1994) lack a promaxillary fenestra.

The internal antorbital fenestra is large and is defined anteriorly (and probably dorsally) by the ascending process of the maxilla. The antorbital fossa does not extend ventrally beyond the border of the internal antorbital fenestra, as in troodontids (*Saurornithoides junior*, IGM 100/1; *Saurornithoides mongoliensis*, AMNH FR 6515; *Troodon formosus* [Witmer, 1997]). The surface bone is missing from the anterior rim of the internal antorbital fenestra exposing a substantial rostral excavation. Anteriorly, the excavation extends to the

root of the 6th maxillary tooth. The thin lamina of bone forming the anterior wall of the excavation wraps around the entire length of the root. This excavation may correspond to the deep fossa invading the pila postantralis (the strut of bone reinforcing the posteromedial wall of the maxillary antrum) noted by Witmer (1997: 43) in *Ornitholestes hermanni*, *Allosaurus fragilis*, *Marshosaurus bicentesimus*, and *Deinonychus antirrhopus*. The lateral surface of the medial wall of the excavation is not smooth, but crossed by ridges and sculptured with rounded depressions. Ventrally, the dorsal surfaces of the posterior alveoli protrude slightly into the fossa.

The maxillary fenestra in *Shanag ashile* is positioned high on the ascending ramus of the maxilla. This location more generally corresponds to the excavatio pneumatica of other theropods (Witmer, 1997: 43). The plesiomorphic position of the maxillary fenestra is more ventral, such that the center of the maxillary fenestra is aligned with the center of the internal antorbital fenestra. Our interpretation of the structure as the maxillary fenestra is supported, however, by the presence of a maxillary antrum medial to the opening, a similarly positioned maxillary fenestra in *Deinonychus antirrhopus* (Ostrom, 1969; Witmer, 1997), and a generally dorsally displaced maxillary fenestra in dromaeosaurids.

The maxillary fenestra is a relatively large, anteroventrally inclined oval structure with both an internal and external aperture, similar in structure to the well-developed antorbital cavities of *Erlikosaurus andrewsi* (Clark et al., 1994), *Bambiraptor feinbergorum* (AMNH FR 30554), and *Saurornithoides mongoliensis* (AMNH FR 6516). The external aperture is confluent with the lateral surface of the maxilla and defines a fairly deep fossa that is continuous with the maxillary antrum. The internal aperture is positioned at the rostroventral end of this fossa and perforates the maxilla. A somewhat similar arrangement is seen in taxa such as *Marshosaurus bicentesimus* (see Witmer, 1997), *Deinonychus antirrhopus* (Ostrom, 1969), and *Velociraptor mongoliensis* (AMNH FR 6515, IGM 100/982). In these taxa, the maxillary fenestra is contained within a shallow, caudally or

caudodorsally open fossa, both of which are located within the antorbital fossa. The fossa containing the internal aperture of the maxillary fenestra of *Shanag ashile*, however, is much deeper and more sharply defined than those in the previously mentioned taxa. It is, therefore, more similar to *Bambiraptor feinbergorum* (AMNH FR 30554), which has a maxillary fenestra that is nearly continuous with the excavatio pneumatica. In *Bambiraptor feinbergorum* (AMNH FR 30554) both structures are contained within a caudodorsally opening fossa. Thus, it is possible that the oval structure in IGM 100/1119, considered here to be the maxillary fenestra, may in fact represent a maxillary fenestra confluent with an excavatio pneumatica.

Some unusual accessory cavities—interalveolar pneumatic cavities—are present between the pairs of adjacent alveoli separated by a diastema. The interalveolar chambers of IGM 100/1119 would have been closed off from the rest of the craniofacial air sac system in life, surrounded on all sides by a thin layer of bone, and are visible only because of the eroded labial surface of the maxilla. The roots of the teeth that bracket them define the boundaries of the chambers. Thin laminae of bone envelop the roots of the flanking teeth, defining the anterior and posterior limits of the chambers. In addition, the chambers extend dorsally no farther than the dorsal margin of the shorter bounding tooth, no farther ventrally than the crown–root junction of the teeth, and no farther medially than the medial limit of the teeth. The medial walls of the chambers have the same irregular surface as that of the internal antorbital fenestra. These are not the “recessi pneumatici interalveolares” described by Witmer (1997), which are ventrolateral invaginations of the maxillary antrum into the alveolar process. Structures possibly homologous to the pneumatic interalveolar recesses are present within the antorbital fenestra in IGM 100/1119 where the alveoli protrude into the fenestra.

At least nine widely and unevenly spaced alveoli, six of which contain teeth, are present in the maxilla. The number of maxillary teeth is similar to the eight in *Archaeopteryx lithographica* (Wellnhofer, 1988), the nine in *Dromaeosaurus albertensis* (AMNH FR 5356;

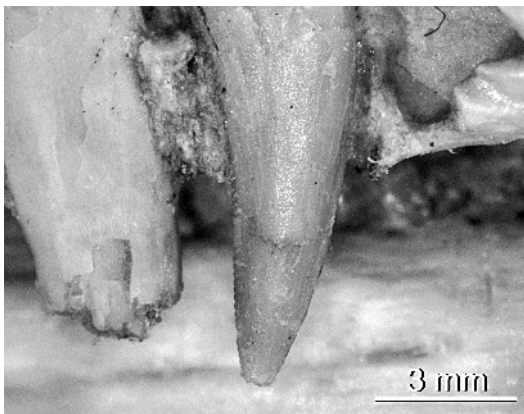


Fig. 3. Detail of posterior tooth morphology in IGM 100/1119. Note serrations on posterior carinae and unconstricted root-crown transition.

Currie, 1995), and the 10 in *Velociraptor mongoliensis* (AMNH FR 6515). The tooth count in IGM 100/1119 is, however, different from the numerous maxillary teeth present in *Jinfengopteryx elegans* (Ji et al., 2005) and troodontids—even basal taxa such as *Sinoovenator changii* (Xu et al., 2002) and *Mei long* (Xu and Norell, 2004). The lateral surface of the maxilla is missing from the central portion of the maxilla so that the roots of two teeth are exposed. Although there are several empty alveoli in the maxillary tooth row, some of the gaps are solid stretches of interdental bone separating adjacent alveoli. The maxillary teeth are laterally compressed, with the carinae positioned lingually. Posterior teeth have serrations on their posterior carinae (fig. 3). The three central maxillary teeth are unusual in that they have long roots constituting approximately 70% of the entire tooth length. Tooth root bulges of these teeth are visible on the medial face of the ascending ramus of the maxilla.

The dentary is long and relatively dorso-ventrally shallow, its height comprising only about 12% of its length, although it is broken posteriorly. The dentary is straight and does not curve medially at the symphysis as in derived troodontids like *Troodon formosus* (Currie, 1985) or *Saurornithoides* (Barsbold, 1974; Norell et al., in prep). It is relatively labiolingually thick, with the tooth row slightly inset from the labial margin and

becoming more inset posteriorly. The ventral and dorsal margins of the dentary are subparallel, as in dromaeosaurids (Currie, 1995) and *Archaeopteryx lithographica* (Wellnhofer, 1992: fig. 6). Two rows of mental foramina are present on the labial surface, although a series of smaller anteriorly directed foramina cluster rostrally. The dorsal row contains a greater number of foramina that are anteroposteriorly elliptical and elongate. The dorsal row of mental foramina does not lie in a deep subalveolar groove as in troodontids (Makovicky et al., 2003) and *Buitreraptor gonzalezorum* (Makovicky et al., 2005). Posteriorly, the dorsal foramina lengthen to form a shallow groove similar to that present in *Archaeopteryx lithographica* (Wellnhofer, 1974: plate 22), the holotype of *Velociraptor mongoliensis* (AMNH FR 6515), and *Tsaagan mangas* (IGM 100/1015; Norell et al., 2006). There are fewer foramina in the lower row, although they are of the same general shape.

A relatively deep Meckelian groove runs along the medial surface of the dentary. Anteriorly, the groove begins just caudal to the rugose symphyseal tip of the dentary. A small fragment of the splenial covers the posterior end of the Meckelian groove, so the posterior extent of the groove cannot be determined. The posterior margin of the dentary is broken, so the posterior articulations are unknown.

There are at least 15 teeth in the dentary. Due to the overhanging maxilla and its teeth, it is difficult to determine the exact number of alveoli present. Like the maxillary tooth count, the dentary tooth count of *Shanag ashile* is comparable to that of some dromaeosaurids, such as the 16 in *Deinonychus antirrhopus* (Ostrom, 1969), 15–16 in *Saurornitholestes langstoni* (Sues, 1978), and 14–15 in *Velociraptor mongoliensis* (AMNH FR 6515; Currie, 1995). The dentary teeth, like the maxillary teeth, are interspersed with diastemata. The anterior teeth are quite small and especially closely packed like in troodontids (Makovicky and Norell, 2004) and *Microraptor zhaoianus* (Xu et al., 2000; this paper, fig. 4). Overall, the dentary teeth are smaller and more closely packed than the maxillary teeth (1.0 versus 1.4 mm basal crown widths and 0.37 versus 0.70 mm gaps



Fig. 4. Detail of the tooth morphology and size variation seen in the dentary of IGM 100/1119. Anatomical labels in appendix 3.

between adjacent teeth not separated by a diastema). The anterior dentary teeth are devoid of serrations, while the posterior teeth have small serrations only on their posterior carinae (12.4 serrations per millimeter). This is the same pattern seen in *Microraptor zhaoianus* (Hwang et al., 2002). Unlike *Microraptor zhaoianus* teeth and the teeth of troodontids and early avialans, the teeth of IGM 100/1119 do not have constrictions between their roots and crowns. This unconstricted root/crown transition is present in *Buitreraptor gonzalezorum* (Makovicky et al., 2005), *Sinornithosaurus millenii* (Xu and Wu, 2001), and other dromaeosaurids.

Only a small sliver of the splenial protrudes past the posterior edge of the dentary, but the anterior portion is nearly intact. It cannot be determined if the splenial was laterally exposed at the contact of the dentary and postdentary bones as in deinonychosaurs, as this region of the mandible is not preserved. It overlaps the posterior third of the dentary, reaching to about the level of the 13th dentary alveolus. The preserved portion of the splenial is thin, long, and sharply triangular, much like the splenial of the dromaeosaurids (Norell and

Makovicky, 2004), *Archaeopteryx lithographica* (Wellnhofer, 1993), and the troodontid *Saurornithoides junior* (Barsbold, 1974; Norell et al., in prep). A long, narrow notch at the posterior of the splenial fragment, corresponding perhaps to the mylohyoid foramen (see Currie, 1995: fig. 7E), is confluent with the Meckelian groove.

DISCUSSION

The taxon preserves an interesting mosaic of avialan and dromaeosaurid characteristics. Like most avialans, *Shanag ashile* possesses a tapering, triangular shaped maxilla, which participates in the narial border and has a large antorbital fossa. Additionally, the caudal margin of the external nares overlaps the rostral border of the antorbital fossa, as in avialans. A number of dromaeosaurid synapomorphies, however, are preserved in IGM 100/1119. These include a straight, parallel-sided dentary and a dorsally displaced maxillary fenestra that is itself recessed in a caudo-dorsally directed depression.

To test the phylogenetic placement of *Shanag ashile* we have expanded the Norell

et al. (2006) study by including the new taxon and 15 additional characters, several of which are novel and pertain to the maxilla morphology of dromaeosaurids and avialans. A total of 56 coelurosaurian taxa and 251 characters (19 ordered) were used in the analysis, with *Allosaurus fragilis* and *Sinraptor dongi* used to root the most parsimonious trees. The dataset was treated with equally weighted parsimony analysis implemented in TNT v. 1.0 (Goloboff et al., 2003). A heuristic tree search strategy was conducted performing 1000 replicates of Wagner trees (using random addition sequences) followed by TBR branch swapping (holding 10 trees per replicate). The best trees obtained at the end of the replicates were subjected to a final round of TBR branch swapping. Zero length branches were collapsed if they lack support under any of the most parsimonious reconstructions (i.e., rule 1 of Coddington and Scharff, 1994). This analysis resulted in 552 most parsimonious trees of 764 steps (CI = 0.381, RI = 0.709) found in 625 out of the 1000 replicates.

Shanag ashile was found to be a member of a dromaeosaurid clade less inclusive than Unenlagiinae (i.e., *Buitreraptor gonzalezorum*, *Unenlagia comahuensis*, and *Rahonavis ostromi*) in all of the most parsimonious reconstructions (fig. 5). This placement is supported by the presence in *Shanag ashile* of three of the clade's six unambiguous synapomorphies: a solid quadrate (char. 52.0—unknown in *Shanag ashile*); dentary with subparallel dorsal and ventral edges (char. 70.1); large maxillary and dentary teeth, less than 25 in dentary (char. 84.0); anterior cervical centra level with or shorter than posterior extent of neural arch (char. 96.0—unknown in *Shanag ashile*); extremely long extension of the prezygapophyses of the distal caudal vertebrae (char. 120.1—unknown in *Shanag ashile*); and dorsal displacement of maxillary fenestra (char. 237.1). Given the large percentage of missing data for IGM 100/1119, *Shanag ashile* was recovered in numerous placements within the large clade more derived than Unenlagiinae (i.e., *Sinornithosaurus* + *Velociraptor*), resulting in an unresolved strict consensus. The Adams consensus depicted in figure 5 shows this lack of resolution is due to the labile position of IGM 100/1119 and to a lesser extent,

Saurornitholestes langstoni. The Adams consensus demonstrates that consistent structure exists within the large non-unenlagiine dromaeosaurid clade. This phylogenetic structure is nearly identical to that recovered in the analysis of Norell et al. (2006). In the present analysis, an Adams consensus shows the consistent presence of a *Deinonychus* + *Velociraptor* sister group relationship when the position of *Saurornitholestes* is not considered as well as the consistent presence of an *Achillobator* + *Utahraptor* clade. However, in the latter case, both *Adasaurus* and *Dromaeosaurus* are depicted closer to *Achillobator* than *Utahraptor* or closer to *Utahraptor* than *Achillobator* in some of the fundamental trees. The largely incomplete nature of *Dromaeosaurus albertensis* and *Adasaurus mongoliensis* reduced the resolution within this subclade of large-bodied dromaeosaurids.

Although the exact sister taxon of *Shanag ashile* is currently ambiguous, it is most similar in general shape and morphology to *Sinornithosaurus millenii* (Xu et al., 1999). Both taxa possess a triangle-shaped, anteriorly tapering maxilla as well as maxillary participation in the external nares. In the most parsimonious trees that recover *Shanag ashile* closely related to *Sinornithosaurus millenii*, the topology is supported by a single synapomorphy—the lateral lamina of the ventral ramus of the maxilla reduced to a small triangular exposure (char. 244.1). *Shanag ashile* remains distinguishable from *Sinornithosaurus millenii* due to its lack of a promaxillary fenestra.

Prior to the discovery of IGM 100/1119, the only theropod material from the Early Cretaceous Öösh deposits were undiagnostic. *Shanag ashile* marks the first theropod taxon from the deposits referable to a specific theropod clade—the Dromaeosauridae. The discovery of IGM 100/1119 is important as it extends our knowledge of Early Cretaceous dromaeosaurids. The best known Early Cretaceous dromaeosaurids—*Sinornithosaurus* and *Microaptor*—are known from the Jehol beds of China. The presence *Shanag ashile* in the Jehol-contemporaneous Öösh deposits of Mongolia suggests a wider diversity of Early Cretaceous dromaeosaurids that show a broader distribution of character states and avianlike cranial features.

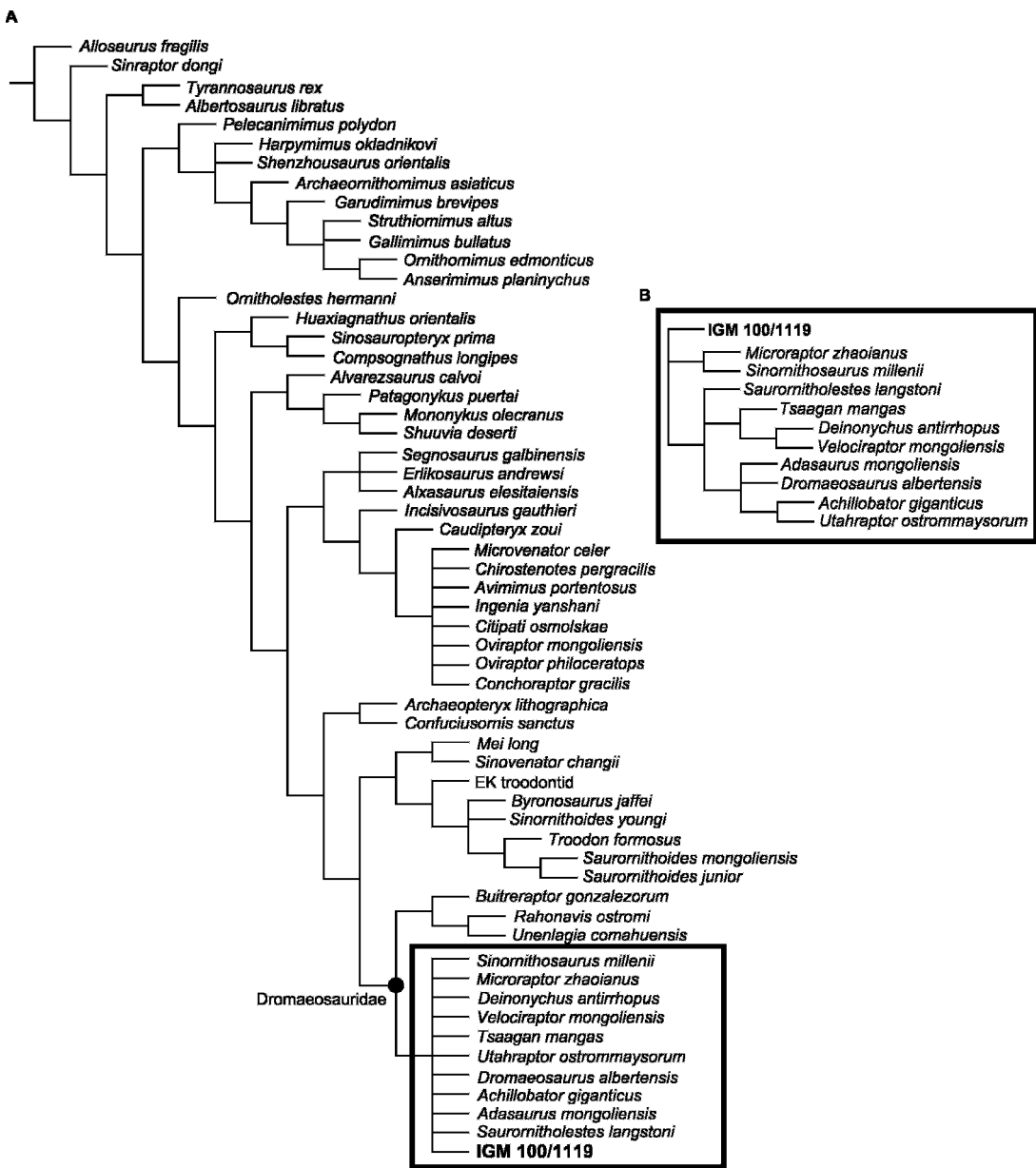


Fig. 5. Phylogenetic placement of IGM 100/1119. A. Strict consensus of 552 most parsimonious reconstructions of coelurosaurian interrelationships found in our phylogenetic analysis of 251 characters and 56 coelurosaurian taxa. The new taxon is indicated in bold. B. Adams consensus topology of non-unenlagiine dromaeosaurids recovered from this analysis.

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APPENDIX 1

CHARACTER LIST CORRESPONDING TO DATA MATRIX USED IN PHYLOGENETIC ANALYSIS

Characters are derived from the Theropod Working Group Matrix. This matrix is *matrix 2007.1* and is available at <http://research.amnh.org/users/turner.html> or <http://research.amnh.org/vertpaleo/norell.html>. Character definitions 1–236 follow from Norell et al. (2006) and are in turn based largely on the recent work of Makovicky and Sues (1998), Norell et al. (2001), Xu et al. (2002), Makovicky et al. (2003), Hwang et al. (2004), and Makovicky et al. (2005). The added characters are listed and examples of the differing character states are figured here (figs. 6–17). When applicable, the respective sources are cited along with the character numbers of the character's original publication. Characters 9, 16, 17, 18, 27, 37, 39, 40, 68, 76, 113, 157, 164, 169, 174, 182, 184, 220, and 241 were set as ordered characters (also marked “+” in the list). These characters were ordered because they represent potentially nested sets of character states or include presence/absence states. Ordering of these characters affects the tree length and has limited effects on tree topology of the most parsimonious trees. In the unordered analysis more resolution

was found in derived members of the oviraptorosaurian clade: an *Avimimus* + *Chirostenotes* + *Microvenator* clade was recovered as well as a *Conchoraptor* + *Citipati* sister relationship. Similar topology is found in the Adams consensus of the ordered analysis.

NEWLY ADDED CHARACTERS

Character 237: Dorsal displacement of accessory (maxillary) fenestra: absent (0) or present (1). *In all dromaeosaurids with known cranial material except Buitreraptor gonzalezorum, the maxillary fenestra is displaced dorsally within the antorbital fossa (fig. 6). In other theropods, this displacement is absent with the fenestra positioned more ventrally or central on the medial lamina of the maxilla. (Modified from Senter et al., 2004: char. 5).*

Character 238: Jugal process of maxilla, ventral to the external antorbital fenestra dorsoventrally narrow (0) or dorsoventrally wide (1). *In some dromaeosaurids, such as Tsagan mangas (IGM*

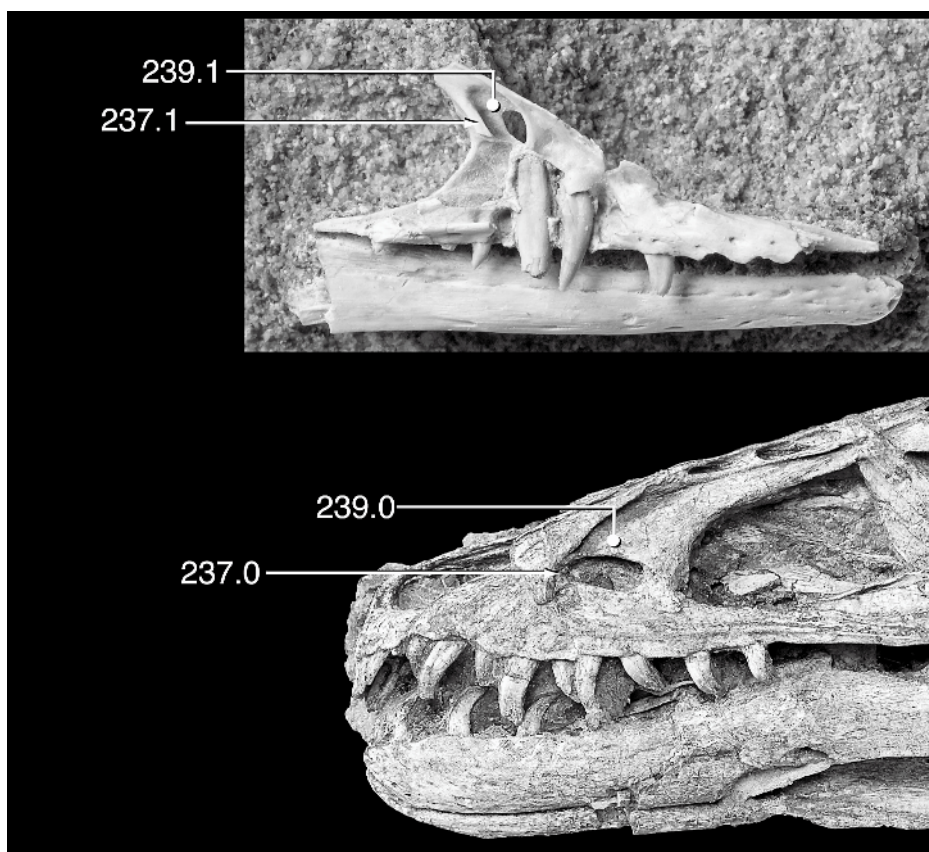


Fig. 6. Systematic variation in maxillary fenestra morphology among coelurosaur theropods. *Shanag ashile* (IGM 100/1119), top, illustrating a dorsally displaced maxillary fenestra (character 237.1) and a maxillary fenestra recessed within a shallow caudal or caudodorsally open fossa (character 239.1). *Dilong paradoxus* (IVPP V14243), bottom, illustrating the absence of the above character states (character 237.0 and 239.0).

100/1015) the jugal process of the maxilla is dorsoventrally wide. In other dromaeosaurids, such as *Velociraptor mongoliensis* (AMNH FR 6515) the jugal process of the maxilla is dorsoventrally narrow (fig. 7). (Modified from Senter et al., 2004: char. 14).

Character 239: Accessory antorbital (maxillary) fenestra recessed within a shallow, caudally or caudodorsally open fossa, which is itself located within the maxillary antorbital fossa: absent (0) or present (1). (NEW). All dromaeosaurids with known cranial material except perhaps *Sinornithosaurus millenii* exhibit state 1 (fig. 6). Witmer (1997: 43) discusses this morphology in detail.

Character 240: Nasal process of maxilla, dorsal ramus (ascending ramus of maxilla): prominent, exposed medially and laterally (0) or absent or reduced to slight medial, and no lateral exposure

(1). Most theropods, including *Velociraptor mongoliensis*, have a prominent ascending ramus of the maxilla. In derived avialans this lamina becomes reduced or absent (fig. 8). (Modified from Gauthier, 1986 and Cracraft, 1986 by Chiappe, 1996: char. 6 by Clarke and Norell, 2002: char. 10).

Character 241: + In lateral view, participation of the ventral ramus of the nasal process of the maxilla in the anterior margin of the internal antorbital fenestra: present extensively (0) or small dorsal projection of the maxilla participates in the anterior margin (1) or no dorsal projection of maxilla participates in the anterior margin (2). In most theropods, the ventral ramus of the nasal process of the maxilla forms the anterior margin of the internal antorbital fenestra. A reduction and loss of this ramus is a trend within avialans (fig. 8). (Modified from Clarke and Norell, 2002: char. 11).

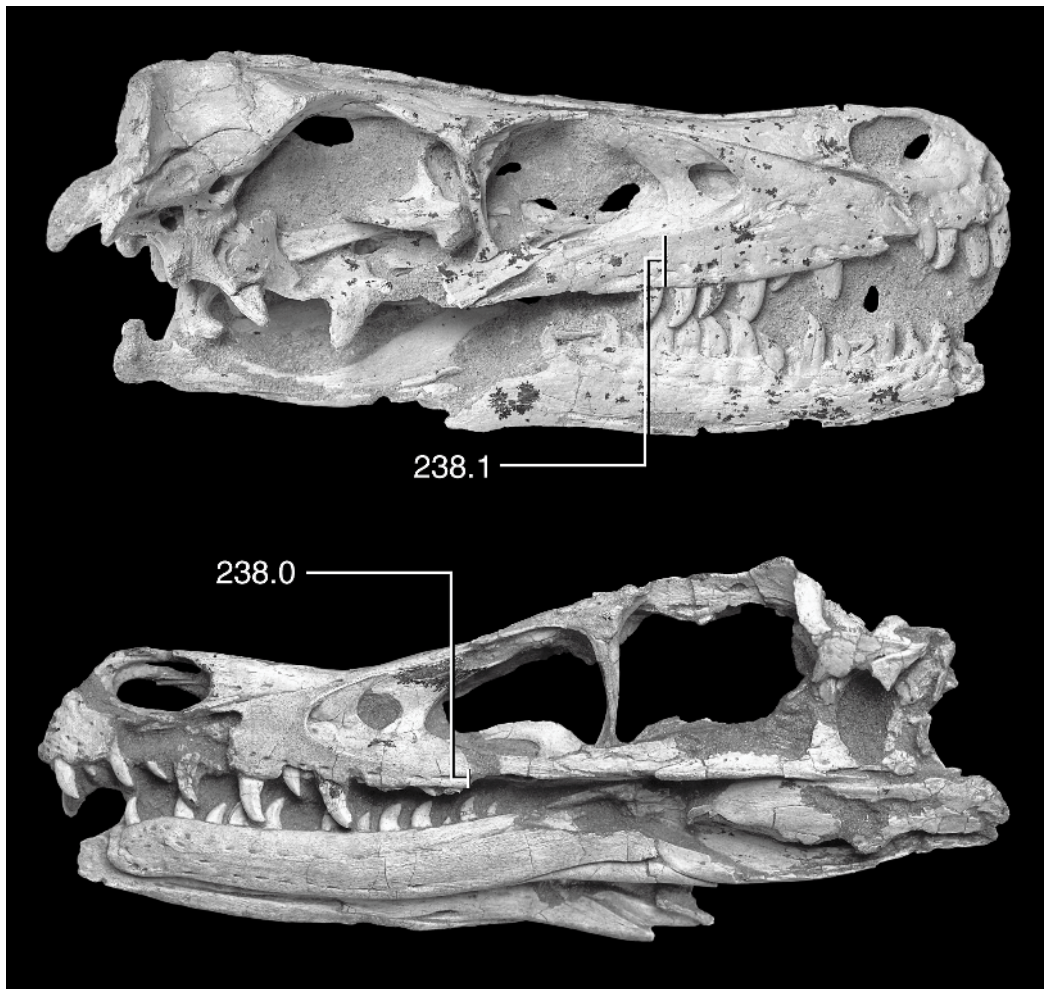


Fig. 7. Systematic variation in jugal morphology among dromaeosaurid theropods. *Tsaagan mangas* (IGM 100/1015), top, illustrating a wide jugal process of the maxilla below the external antorbital fenestra (character 238.1). *Velociraptor mongoliensis* (AMNH FR 6515), bottom, illustrating a narrow jugal process of the maxilla below the external antorbital fenestra (character 238.0). Images not to scale.

Character 242: In lateral view, dorsal border of the internal antorbital fenestra formed by lacrimal and maxilla (0) or by lacrimal and nasal (1). (*NEW*). In all basal avialans, except *Archaeopteryx lithographica*, the nasal forms the dorsal border of the internal antorbital fenestra. In non-avialan theropods, including *Archaeopteryx lithographica*, the dorsal border is formed from the medial lamina of the ascending process of the maxilla (fig. 9).

Character 243: In lateral view, dorsal border of the antorbital fossa formed by the lacrimal and maxilla (0) or by the lacrimal and nasal (1) or by

maxilla, premaxilla, and lacrimal (2). (*NEW*). In all basal avialans, including *Archaeopteryx lithographica*, the nasal forms the dorsal border of the antorbital fossa. This is because the ascending process of the maxilla in *Archaeopteryx lithographica* is recessed medially slightly (fig. 10).

Character 244: In lateral view, lateral lamina of the ventral ramus of nasal process of maxilla: present, large broad exposure (0), or present, reduced to small triangular exposure (1). (*NEW*). The derived state is found in basal dromaeosaurids such as *Sinornithosaurus millenii*, basal troodontids like *Mei long*, and in the new taxon *Shanag ashile* (fig. 11).

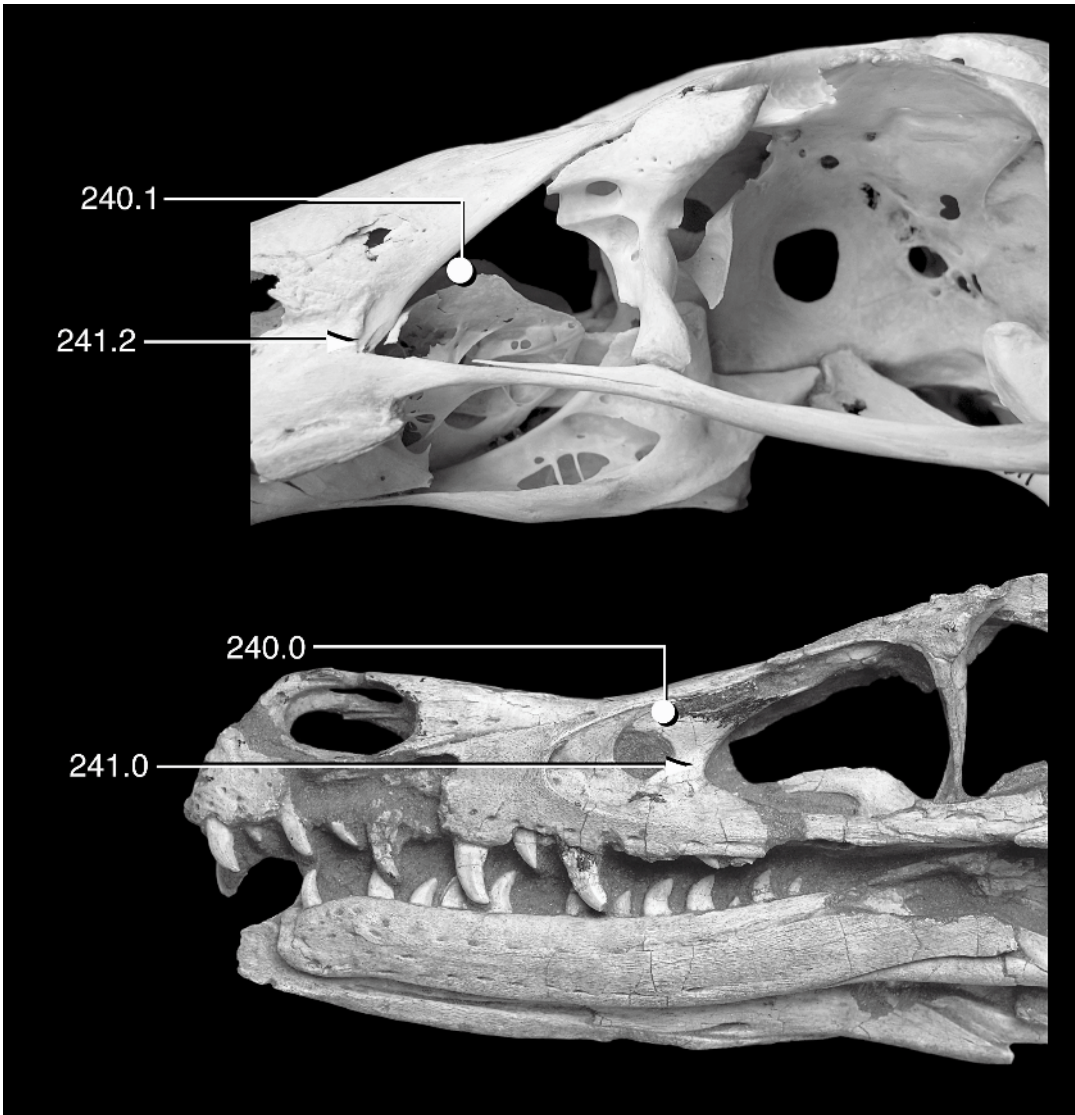


Fig. 8. Systematic variation in antorbital fenestra morphology among paravian theropods. *Diomedea epomophora* (AMNH 5311), top, illustrating a reduced dorsal ramus of the nasal process of maxilla (character 240.1) and a ventral ramus of the maxilla with no dorsal projection participating in the anterior margin of the antorbital fenestra (character 241.2). *Velociraptor mongoliensis* (AMNH FR 6515), bottom, illustrating a prominent dorsal ramus of the nasal process of maxilla that is exposed medially and laterally (character 240.0) and extensive participation of the ventral ramus of the nasal process of the maxilla in the anterior margin of the antorbital fenestra (character 241.0). Images not to scale.

Character 245: Supratemporal fossa with limited extension onto dorsal surfaces of frontal and postorbital (0) or covers most of frontal process of the postorbital and extends anteriorly onto dorsal surface of frontal (1). A number of large theropods, dromaeosaurids, and some oviraptorosaurians exhibit state 1 (fig. 12). This character is

distinguished from character 42, which codes for the shape of the fossa on the frontal and postorbital. (Modified from Currie 1995, by Currie and Varricchio, 2004: char. 14).

Character 246: Jugal does not participate in margin of antorbital fenestra (0) or participates in antorbital fenestra (1). In *Allosaurus fragilis* and

Oviraptor philoceratops the jugal does not participate in the margin of the antorbital fenestra (fig. 13).

Character 247: Anterior and posterior denticles of teeth not significantly different in size (0) or anterior denticles, when present, significantly smaller than posterior denticles (1). *The anterior and posterior denticles in most theropods as well as Dromaeosaurus albertensis exhibit state 0. Most dromaeosaurids exhibit state 1 (fig. 14). (See Ostrom, 1969).*

Character 248: Maxillary teeth almost perpendicular to jaw margin (0) or inclined strongly posteroventrally (1). *Bambiraptor feinbergorum and Atrociraptor marshalli exhibit state 1 (fig. 15). (Modified from Currie and Varricchio, 2004: char. 40).*

Character 249: Maxillary tooth height highly variable with gaps evident for replacement (0) or almost isodont with no replacement gaps (1). *State 1 usually depicts no more than a 30% difference in height between adjacent teeth (fig. 15). (Currie and Varricchio, 2004: char. 41).*

Character 250: Splenial forms notched anterior margin of internal mandibular fenestra: absent (0) or present (1). *State 1 is present in Allosaurus fragilis and Tyrannosaurus rex (fig. 16). (Currie and Varricchio, 2004: char. 35).*

Character 251: First premaxillary tooth size compared with crowns of premaxillary teeth 2 and 3: slightly smaller or same size (0) or much smaller (1) or much larger (2) (fig. 17). *(Modified from Currie, 1995; Currie and Varricchio, 2004: char. 42).*

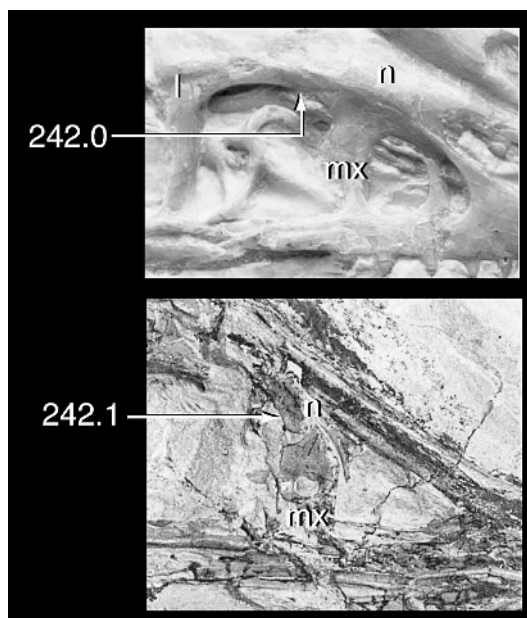


Fig. 9. Systematic variation in internal antorbital fenestra morphology among paravian theropods. *Archaeopteryx lithographica* (WDC-CSG-100), top, illustrating a dorsal border of the internal antorbital fenestra formed by the lacrimal and maxilla (character 242.0). From Mayr et al. (2005). Reprinted with permission from AAAS. *Confuciusornis sanctus* (GMV 2131), bottom, illustrating a dorsal border of the internal antorbital fenestra formed by the lacrimal and/or nasal (character 242.1). Images not to scale.

APPENDIX 2

DATA MATRIX USED IN PHYLOGENETIC ANALYSIS

Character states enclosed between brackets represent conditions found to be variable within a terminal taxon (i.e., polymorphic scorings). Multiple states enclosed in braces indicate uncertainty or ambiguity in the condition of a terminal taxon (among these states, but not among the remaining character states). Following Makovicky et al. (2005), we considered *Neuquenraptor argentinus* a junior synonym of *Unenlagia comahuensis*. An electronic version of this dataset can be downloaded from <https://research.amnh.org/users/turner.html>

Allosaurus fragilis

?11000?00000001000110010001000001110110010??
000000000010001000000000010001000000000010
1010010000000100100000000000001000000?01????
00000000000000?0000010000001000000010000000

0000?10000011000000100000000000000000010000
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Sinraptor dongi

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?0000000000010000?00000100?10?0000000001010
1001000000010010000000000000?????????1?00?0?0
??00?0?????000010000?010?000001000000000?001
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?0?000?00010000111100010

Ingenia yanshani

?01?0????????????1?1????1????????????????????
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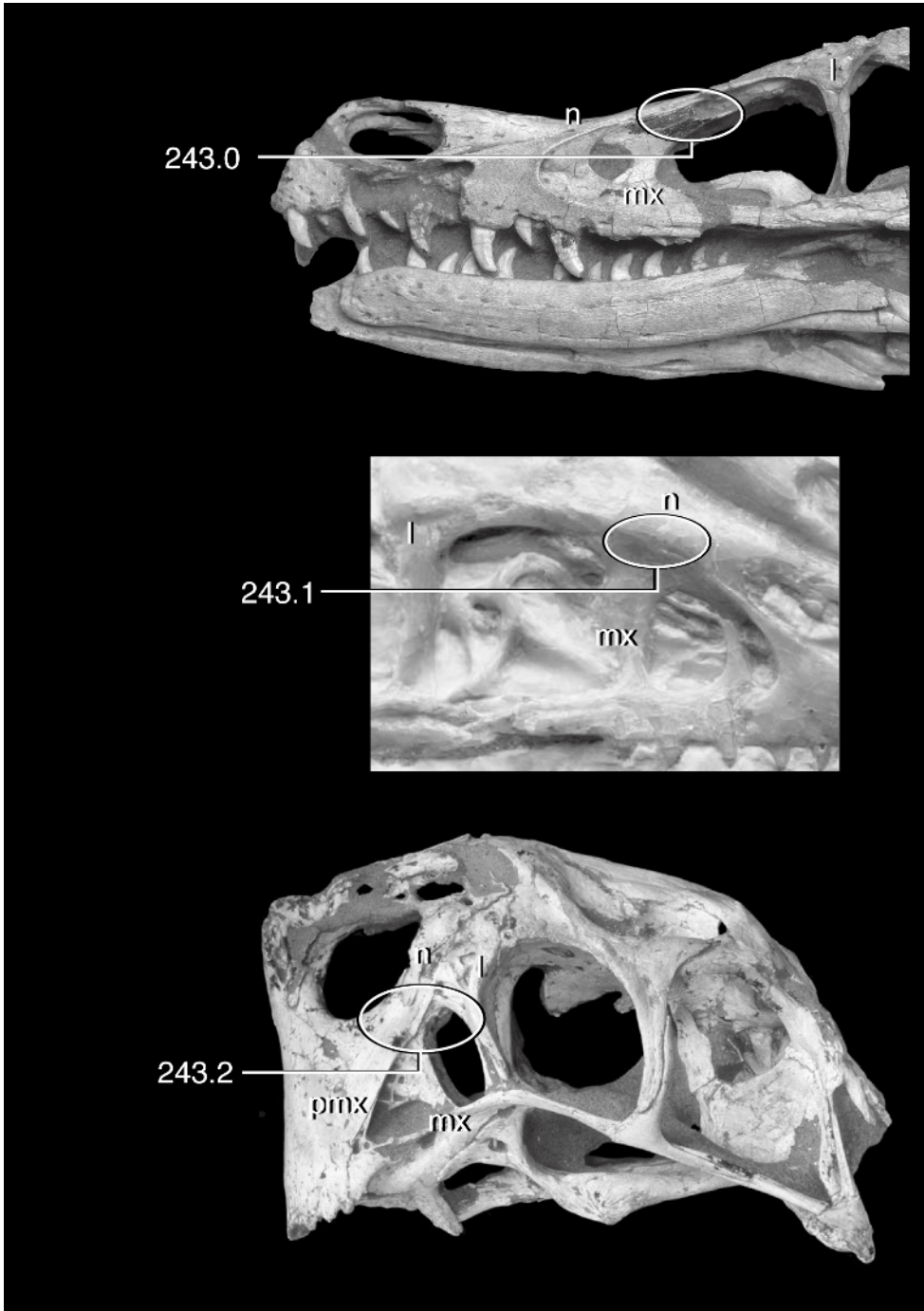


Fig. 10. Systematic variation in antorbital fossa morphology among coelurosaur theropods. *Velociraptor mongoliensis* (AMNH FR 6515), top, illustrating a dorsal border of the antorbital fossa formed by the lacrimal and maxilla (character 243.0). *Archaeopteryx lithographica* (WDC-CSG-100), middle, illustrating a dorsal border of the antorbital fossa formed by the lacrimal and nasal (character 243.1). From Mayr et al. (2005). Reprinted with permission from AAAS. *Citipati osmolskae* (IGM 100/978), bottom, illustrating a dorsal border of the antorbital fossa formed by the maxilla, premaxilla, and lacrimal (character 243.2). Images not to scale.

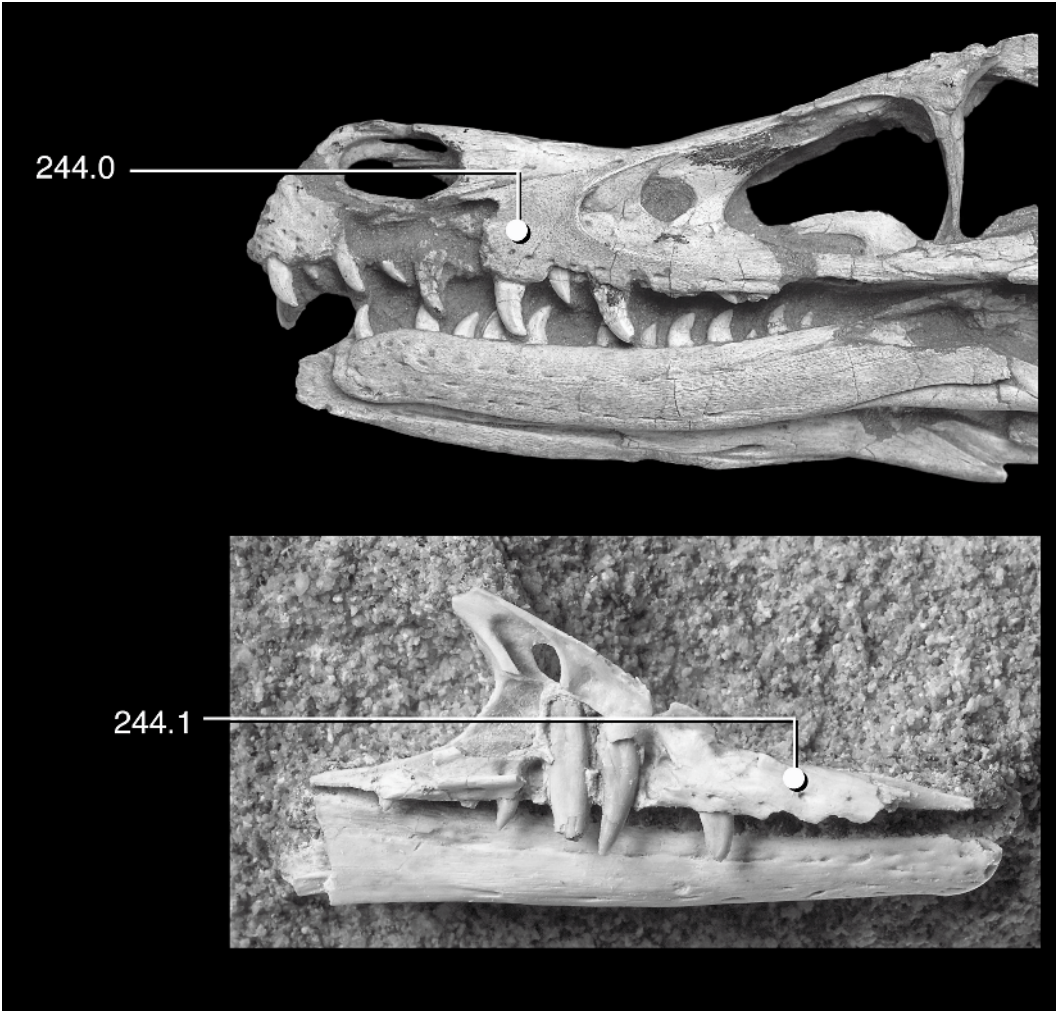


Fig. 11. Systematic variation in maxilla morphology among paravian theropods. *Velociraptor mongoliensis* (AMNH FR 6515), top, illustrating a large, prominent lateral lamina of the ventral ramus of nasal process of maxilla (character 244.0). *Shanag ashile* (IGM 100/1119), bottom, illustrating a reduced, small triangular exposure of the lateral lamina of the ventral ramus of nasal process of maxilla (character 244.1). Images not to scale.

Citipati osmolskae

?011001001001??221000101111?01011?00010210001
100000110001000110121120?0100010111?1???????
1011101100101111001??201?002100111?011110011
0100100?110000001000211001?01012010?0101011
1?210100000000?0000000000000000000110200000
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Oviraptor mongoliensis

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Oviraptor philoceratops

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Conchoraptor gracilis

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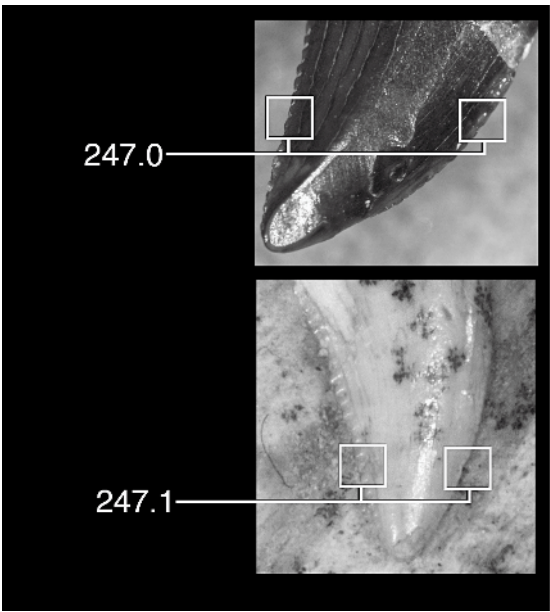


Fig. 14. Systematic variation in tooth denticle size among theropod dinosaurs. *Dromaeosaurus albertensis* (AMNH FR 5356), top, illustrating anterior and posterior denticles not significantly different in size (character 247.0). *Velociraptor mongoliensis* (IGM 100/1252), bottom, illustrating anterior denticles that are significantly smaller than posterior denticles (character 247.1). Images not to scale.

1100000000010001101001000?000001100000?00010
?001000101000001111011

Velociraptor mongoliensis

?011001001000012011200001011100011100012111?
10?01000100001110100000001001111100010100101
00001100011001111101111100011011012111001110
1111110010011100000010022111011101022010111
2112011111?000000000101011010010000000001100
000000011?001000101000001110011

Utahraptor ostrommaysorum

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Adasaurus mongoliensis

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Achillobator giganticus

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Tsaagan mangas

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Saurornitholestes langstoni

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Sinornithosaurus millenii

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?01????????00?00100?1???010100?100?00000?1?

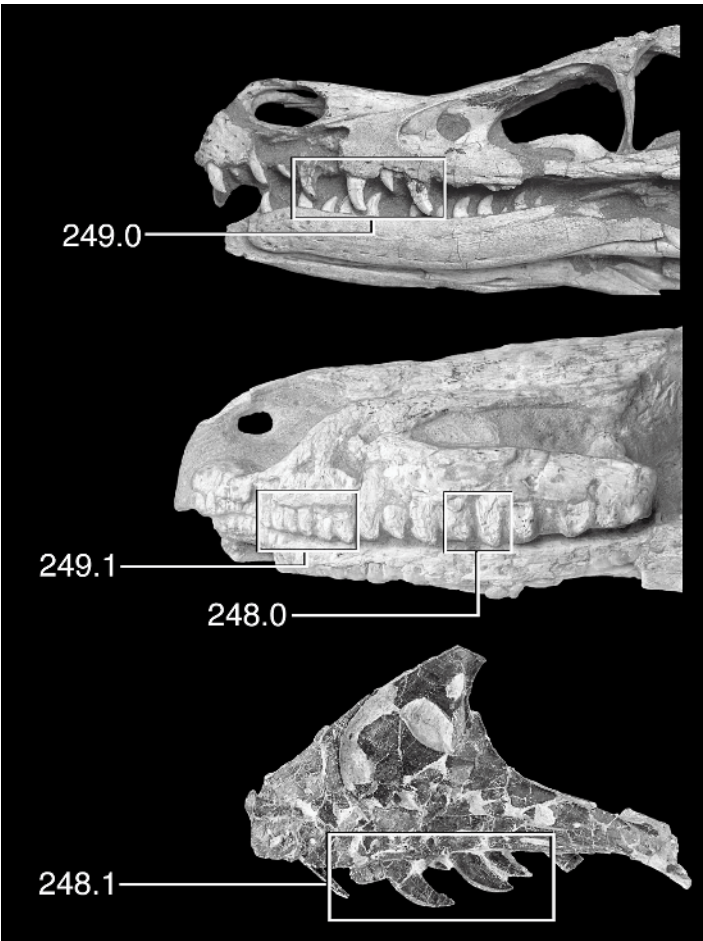


Fig. 15. Systematic variation in maxillary tooth orientation and height in deinonychosaurian theropods. *Saurornithoides mongoliensis* (AMNH FR 6516), middle, illustrating maxillary teeth perpendicular to the jaw margin (character 248.0) and isodont teeth with no replacement gaps (character 249.1). *Bambiraptor feinbergorum* (AMNH FR 30554), bottom, illustrating maxillary teeth strongly inclined posterioventrally (character 248.1). *Velociraptor mongoliensis* (AMNH FR 6515), top, illustrating maxillary teeth with variable height and tooth replacement gaps (character 249.0). Images not to scale.

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Microaptor zhaoianus

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Rahonavis ostromi

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Mononykus olecranus

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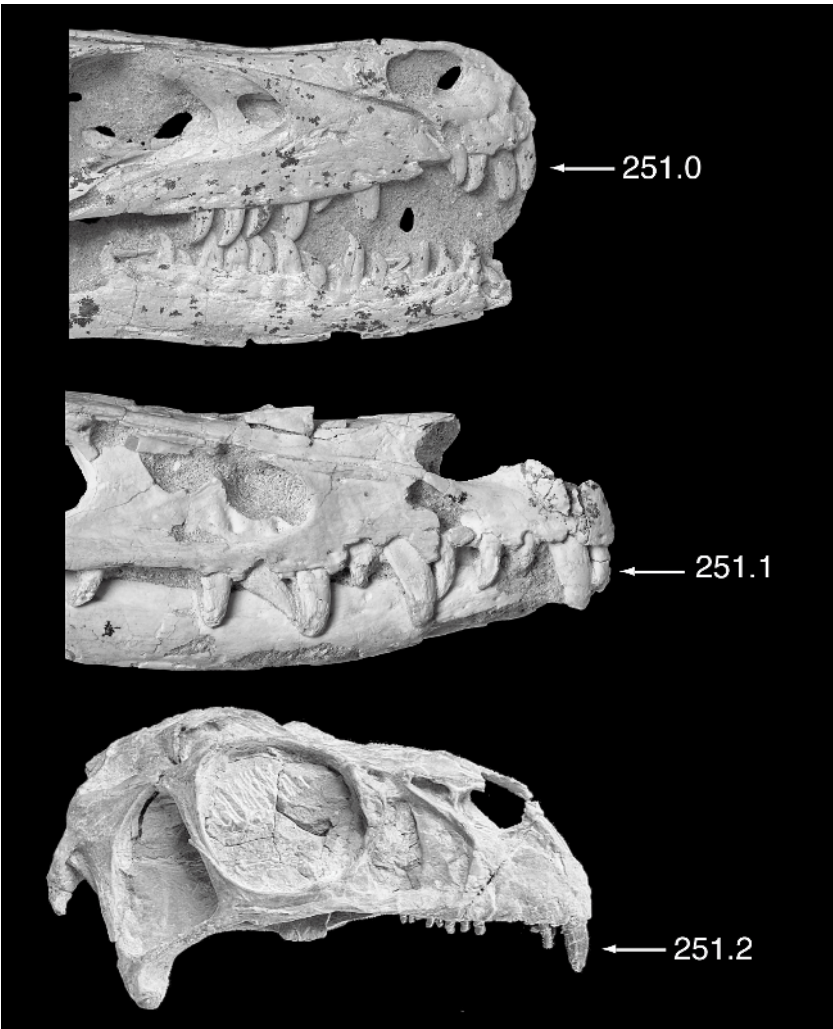


Fig. 17. Systematic variation in first premaxillary tooth size among coelurosaur theropods. *Tsaagan mangas* (IGM 100/1015), top, illustrating a first premaxillary tooth similar in size to premaxillary teeth 2 and 3 (character 251.0). *Velociraptor mongoliensis* (IGM 100/982), middle, illustrating a first premaxillary tooth much smaller than premaxillary teeth 2 and 3 (character 251.1). *Incisivosaurus gauthieri* (IVPP V13326), bottom, illustrating a first premaxillary tooth much larger than premaxillary teeth 2 and 3 (character 251.2). Images not to scale.

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Garudimimus brevipes

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Pelecanimimus polydon

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Harpymimus okladnikovi

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Troodon formosus

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Saurornithoides mongoliensis

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Saurornithoides junior

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Byronosaurus jaffei

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Sinornithoides youngi

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Sinovenator changii

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0000000?1?011??

Mei long

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EK troodontid (IGM 100/44)

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Segnosaurus galbinensis

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Erlikosaurus andrewsi

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Alxasaurus elesitaiensis

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21?00?01010?211?021?2?????01????00???????000002
10000?00?01?00?0?00?0?00?00?00?00?00?00?00?

Tyrannosaurus rex

?10000?0110000100210000010101000000011000010
211000010010001?0000000001001100100000000101
0110100000?000010100000010000?001000??1?????
00000010000?0?0?1000100100010000000101101100
00001?010010000?0001000002000000010000000000
000000?0?0010000100000011000?0

Albertosaurus libratus

?10000?00?0?0????100000101?10000000110000??21
100?010010001????0000000100?100100000000101011
0100000?0001010000001000000010000?100010000
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0001001000000010001000002000000010000000000
00?000?0?001000?000000000000000000000000000000

Shenzhousaurus orientalis

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Ornithomimus edmonticus

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001?10110000100000101000000001001001?????0112
00020000000?10200100000011000010100100000010
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Archaeornithomimus asiaticus

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Anserimimus planinychus

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Huaxiagnathus orientalis

7010707777777777770001777177077770070777777777777
77777777700700107777777000107101070070777177777
777077777007707100010777700000000070070010000
000020707000000100700001170777077777077070100
00000707011700077700707007070010700000007771
70077

Sinosauropteryx prima

001?0????????????0001???1???0????0000?????00??1
10??????????00?01????????0001001010?00?01??100

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1000000000?011?0000?0?000?0?00?0?000??0000000
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Compsognathus longipes

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 ???0?0????000??0010001?????0?000000?10??0??0
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 00000001100?00??0?0????00?0?001000000000?0??
 0?0

Buitreraptor gonzalorum

20110????????????0000101100????????100?10??
011?0????????00?001????????0210??100?00101111
00111?1010??100011012?121?????01101111010?1?1
0?0?????11?101??11[02]2???01??1?120???1?0?0??
1?011?0?1110000????????1????????1101000110000?00
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Neuquenraptor + Unenlagia

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IGM 100/1119

[illegible]

APPENDIX 3

INSTITUTIONAL ABBREVIATIONS

AMNH	American Museum of Natural History, New York, USA	ANATOMICAL ABBREVIATIONS	
FMNH	Field Museum of Natural History, Chicago, USA	aof	antorbital fenestra
IGM	Mongolian Institute of Geology, Ulaan Bataar, Mongolia	aofs	antorbital fossa
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China	ax	anterior excavation
GMV	National Geological Museum of China, Beijing, China	d	dentary
PIN	Paleontological Institute Moscow, Russia	dg	dentary groove
WDC	Wyoming Dinosaur Center, Thermopolis, USA	l	lacrimal
ZPAL	Instytut Paleobiologii PAN, Warszawa, Poland	mx	maxilla
		mxar	ascending ramus of maxilla
		mxr	maxillary fenestra
		mxpp	premaxillary process of maxilla
		n	nasal
		pmx	premaxilla
		sp	splénial

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