

A NEW TROODONTID THEROPOD FROM UKHAA TOLGOD, MONGOLIA

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Troodontid theropods, originally described from isolated teeth that were at one time confused with those of pachycephalosaurs (Gilmore, 1924), are represented by only a few taxa known mostly from sparse and fragmentary material (Osmólska and Barsbold, 1990; Russell and Dong, 1994; Varrichio, 1997). Nevertheless, a number of characters have been used to suggest that these dinosaurs are very closely related to Aves (Gauthier, 1986; Currie and Zhao, 1994; Forster et al., 1997), either as part of a group with Dromaeosauridae (e.g., Gauthier, 1986; Sereno, 1997) or alone (e.g., Forster et al., 1998).

Here we describe a new taxon of troodontid dinosaur found at Ukhaa Tolgod, an extremely rich locality in Mongolia's Gobi Desert (Dashzeveg et al., 1994). This taxon is known from two adult individuals, including one of the best preserved troodontid skulls ever collected. These specimens allow us to make preliminary statements on troodontid phylogeny and monophyly and to review the distribution of several characters, such as unserrated teeth and an extensive secondary bony palate, which have implications for maniraptoran phylogeny and the origin of avialans.

SYSTEMATIC PALEONTOLOGY

THEROPODA, Marsh 1881
TETANURAE Gauthier 1986
MANIRAPTORA Gauthier 1986
TROODONTIDAE Gilmore 1924
BYRONOSAURUS JAFFEI sp. nov.
(Figs. 1, 2)

Material—Holotype: IGM (Institute of Geology, Mongolia) 100/983, a fragmentary skull and postcranial bones (Fig. 1). The skull of IGM 100/983 is preserved in two parts. The rostral fragment and the braincase were found in place adjacent to one another in life position separated by a zone of weathering. The anterior section is composed of the muzzle and articulated mandible which have been mediolaterally flattened. The skull is broken at the anterior margin of the orbits and the three dimensionally preserved braincase is separate. The roof of the braincase is missing, exposing an eroded endocast. Postcranial elements were collected as surface float below the skull along with the partial remains of an ornithomimid (see Makovicky and Norell, 1998 for details). Additional remains were collected during the 1994 and 1995 field seasons as float.

Etymology—Named in honor of Byron Jaffe in recognition of his family's support for the Mongolian Academy of Sciences-American Museum of Natural History Paleontological Expeditions.

Locality—The type specimen (IGM 100/983) was collected at Ukhaa Tolgod.

Diagnosis—*Byronosaurus jaffei* can be assigned to the Troodontidae on the basis of the following combination of derived characters: (1) numerous tightly packed teeth on the anterior part of the tooth row (Currie, 1987); (2) maxillary participation in the posterior margin of the nares (Barsbold and Osmólska, 1990) (also present in therizinosaurs [e.g., *Erlikosaurus*]); (3) otosphenoidal crest large and prominent (Currie and Zhao, 1994); (4) dentaries that are roughly triangular in side view with mental foramina in a deep groove (Currie, 1987); and (5) a lacrimal with an elongate anterior process dorsal to the antorbital fossa.

Byronosaurus jaffei can be differentiated from all other troodontid species reported to date on the basis of the following derived characters: (6) teeth devoid of serrations on the anterior and posterior carinae (also found in Spinosauridae, *Pelacanimitus* and some basal Avialae); (7) the presence of a large interfenestral bar that is not inset medially from the lateral surface of the maxilla; (8) the presence of a connection between the nasal passage and the antorbital fenestra through the interfenestral bar; and (9) a horizontal groove on the maxilla adjacent, and parallel to the tooth row, containing small foramina.

Referred Specimen—A second specimen (IGM 100/984), collected July 15, 1996 at a locality called Bolor's Hill, approximately 5 km away from the main Ukhaa Tolgod exposure, can be referred to *Byronosaurus jaffei*. The fragmentary rostrum preserves some important features not preserved on the type, including a secondary bony palate formed by both the premaxillary and maxillary shelves and the vomer. It is referred to *Byronosaurus jaffei* on the basis of the derived characters 6, 7, and 8.

Description—This description is a composite based on both the type and referred specimens.

Each premaxilla contains four teeth. Large nasal processes of the premaxillae divide the nasals anteriorly. The premaxilla lacks a posterior process, and consequently the maxilla forms the posterior margin of the naris, a derived character for troodontids (Osmólska and Barsbold, 1990). A foramen opening into the supra-alveolar canal is present in the maxilla, below the posteroventral corner of the naris and just posterior to the premaxilla-maxilla suture. Both the premaxillae and the maxillae contribute to an extensive secondary bony palate. Posteriorly, the vomer also participated in this feature.

The maxilla is perforated laterally by two large openings, the accessory antorbital fenestra anteriorly and the antorbital fenestra posteriorly, which are separated by a wide interfenestral bar that is confluent with the side of the rostrum (Fig. 1). The accessory antorbital fenestra has an osseous medial wall, whereas the posterior fenestra is lacking a floor. Posteriorly, two passages run through the interfenestral bar. A ventral passage

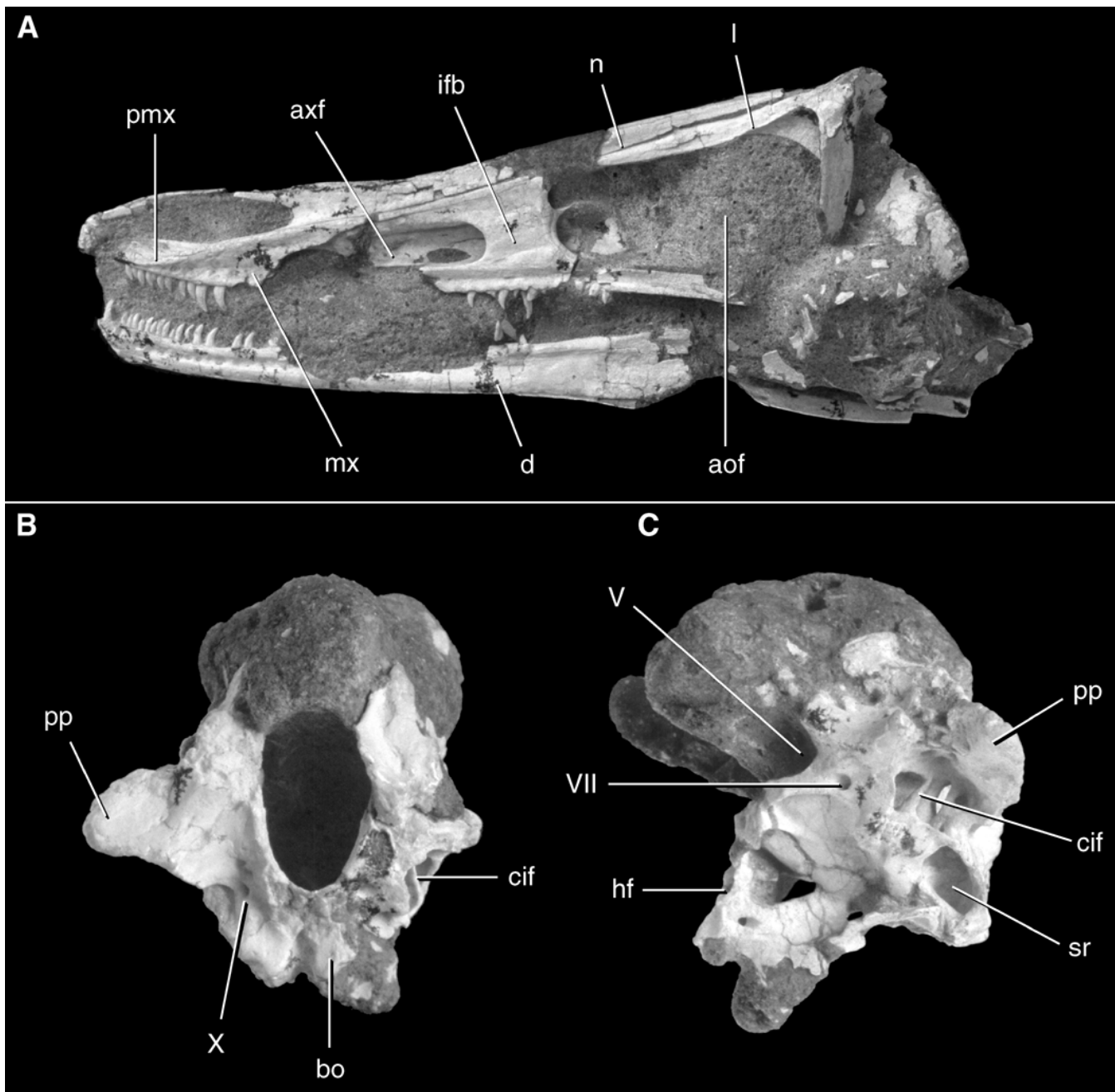


FIGURE 1. The rostrum (A) and braincase (B,C) of IGM 100/983. A), left lateral view (scale bar equals 2 cm.), B) posterior view, and C), left lateral view (scale bar equals 1 cm). **Abbreviations:** aof, antorbital fenestra; axf, accessory antorbital fenestra; bo, basioccipital; cif, crista interfenestralis; d, dentary; hf, hypophyseal fossa; ifb, interfenestral bar; l, lacrimal; n, nasal; pmx, premaxilla; pp, paroccipital process; sr, subotic recess; V, trigeminal, VII, facial, X, vagus.

allows communication between the accessory and antorbital fenestrae. Dorsally, a passage travels through the bar between the antorbital fenestra and the nasal passage, the floor of which bulges into the dorsal part of the accessory antorbital fenestra. The accessory antorbital sinus is enclosed completely within the maxilla, whereas the antorbital fenestra is bordered posteriorly and dorsally by the "T"-shaped lacrimal that has an extensive anterior process between the nasal and the maxilla. Posterior to the postorbital bar on the skull roof, the lacrimal extensively overhangs the orbit. On both the maxilla and dentary, just dorsal and ventral to the corresponding tooth rows, a shall-

low groove filled with small foramina extends the length of the tooth row.

Like other troodontids, *Byronosaurus jaffei* displays numerous and heterodont teeth. The most anterior teeth are small and tightly packed. More posterior teeth are larger and more widely spaced, but the posteriormost teeth are tiny. The teeth of *Byronosaurus jaffei* are similar to other troodontids in having a constriction between the root and the tooth crown, but are atypical of theropods, and similar to avialans and *Pelecanimimus*, in lacking anterior and posterior serrations (Fig. 2).

The braincase is typical of troodontids in having extensive

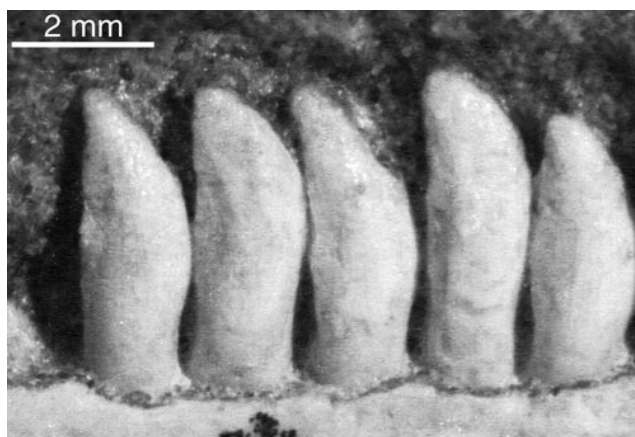


FIGURE 2. Teeth of IGM 100/983. Scale bar equals 2 mm.

pneumatic spaces that lie both ventral and anteroventral to the braincase. Like in other troodontids these are delimited by an expanded otosphenoidal crest that creates the “lateral depression” (see Currie and Zhao, 1994). The trigeminal and facial foramina lie on a continuous sulcus dorsal to the otosphenoidal crest, rather than being separated by a raised mound as in *Troodon formosus* (pers. obs.: TMP [Royal Tyrrell Museum of Palaeontology] 86.36.457). The middle ear region is extremely well preserved (Fig. 1C), and conclusively shows that *Byronosaurus jaffei* had a fully ossified crista interfenestralis formed exclusively of the prootic. The base of the crista interfenestralis is level with the braincase wall, unlike in *Troodon formosus* (Currie and Zhao, 1994) and *Saurornithoides junior* (pers. obs.), where the crista interfenestralis is inset in a deep middle ear cavity.

The paroccipital processes are short and their ends are round in posterior view (Fig. 1B). They are nearly vertical and are solid as in other troodontids. A group of small depressions at the posterodorsal corner of the middle ear cavity above the crista interfenestralis may represent vestiges of the posterior tympanic recess. A depression is also apparent in this region in the London specimen of *Archaeopteryx lithographica* (pers. obs.), where it is separate from a secondary opening of the posterior tympanic recess, posterior to the fenestra pseudorotundum (Witmer, 1990). A well developed subotic recess is present and extends below the braincase floor. A concave depression filled with small pockets lies dorsal and medial to the middle ear cavity on the dorsolateral surface of the braincase. This feature has been called the dorsal tympanic recess in other non-avian theropods (Currie and Zhao, 1994; Witmer, 1997; Makovicky and Norell, 1998). However, the homology of this depression with the avian dorsal tympanic recess has not been established. In posterior view, the occiput is higher than wide (as in *Troodon formosus* and both species of *Saurornithoides*) and the basal tubera are separated by a small “V”-shaped notch.

Vertebrae include the axis, two other anterior cervicals, dorsals, a sacral and four caudals. None of the preserved vertebrae is complete. The cervicals, which represent the axis and probably the third and fourth cervicals, have elongate centra with significantly wider than tall anterior intercentral faces as in most coelurosaurs (Gauthier, 1986). The postzygapophyses of the axis and following vertebra are capped by robust epipophyses. The best preserved of the dorsal centra bears a deep rounded hypapophysis, similar to that of *Mononykus olecranus*, on the anterior end of the centrum. The diameter of the neural canal is more than half the diameter of the centrum as in *Velociraptor*

mongoliensis (Norell and Makovicky, 1999) and basal Avialae (Chiappe et al., 1996). Four fragments of distal caudals are preserved. The centra of the distal caudals are long and laterally constricted. The neural canal is diminutive and a distinct sulcus extends above it along the roof of the neural arch. Such a sulcus is also present in other troodontids (Russell, 1969; Russell and Dong, 1994; Varrichio, 1997).

Preserved portions of the hindlimb include part of the femoral shaft, the right knee, the distal end of metatarsal III, and three phalanges, among them the penultimate phalanx of digit II. This phalanx bears an elongate heel proximally. As in other troodontids, but in contrast to dromaeosaurids, the shaft between the articular ends is not foreshortened (Currie and Peng, 1994). The medial face is vertical whereas the lateral one is convex, a feature that identifies the phalanx as being from the right foot. Erosion has destroyed much of the distal ginglymus. In profile, the phalanx resembles the corresponding bone in *Troodon formosus* (Currie and Peng, 1994) and an indeterminate troodontid from Mongolia (Barsbold et al., 1987).

Discussion

The discovery of *Byronosaurus jaffei* underscores the extensive Asian diversity of the Troodontidae. To this point, eight species of troodontids have been described, and seven of these are from Central Asia. *Byronosaurus jaffei* also displays a number of character states that are interesting for non-avian theropods. Among these the teeth require special note.

As described above, the unserrated teeth of *Byronosaurus jaffei* (Fig. 2) are very similar to those found in basal avialans like *Archaeopteryx lithographica*. This is particularly noteworthy in light of claims that serrated teeth are “characteristic of theropod dinosaurs” (Feduccia, 1996:77). A second feature of *Byronosaurus jaffei* is the presence of a secondary palate formed by extensive palatal shelves that meet the vomer on the midline. Such a condition has also been reported in the dromaeosaur *Velociraptor mongoliensis* (Norell and Makovicky, 1998) and the ornithomimosaur *Garudimimus brevipes* (Barsbold, 1983).

To evaluate the phylogenetic position of *Byronosaurus jaffei* within the Troodontidae, we conducted a cladistic analysis of 38 characters (Appendices 1, 2). The ingroup includes *Byronosaurus jaffei*, *Troodon formosus*, *Saurornithoides mongoliensis*, *Saurornithoides junior*, *Sinornithoides youngi*, and an unnamed Early Cretaceous troodontid (IGM [Institute of Geology, Mongolia] 100/44) (Barsbold et al., 1987) from Mongolia. *Tochisaurus nemegtensis*, *Borogovia gracilicrus*, and *Koparion douglassi* were excluded from the analysis because their codings are redundant with a number of other taxa. Additionally, *Tochisaurus nemegtensis* and *Koparion douglassi* cannot be diagnosed by autapomorphies. Other taxa erroneously referred to the Troodontidae including *Ornithodesmus cluniculus* (Howse and Milner, 1993) and *Bradycnema draculai* have been shown to have affinities with other theropod groups (Norell and Makovicky, 1997; G. Dyke, pers. comm.), and were omitted from the analysis.

In developing a phylogenetic analysis of these taxa, consideration was given to the lack of consensus in current hypotheses of maniraptoriform relationships when choosing a root. Dromaeosauridae, Oviraptoridae, Avialae and Ornithomimosauria were included as outgroup taxa. Analyses were conducted with constrained outgroup configurations that reflect current, conflicting hypotheses of maniraptoran relationships (Gauthier, 1986; Holtz, 1994; Forster et al., 1998), as well as an unconstrained analysis rooted on ornithomimosaur. In no case did any recombination of the outgroup taxon configurations have an effect on the topology within Troodontidae, and the outgroup taxa did not fall into the ingroup in the unconstrained analysis.

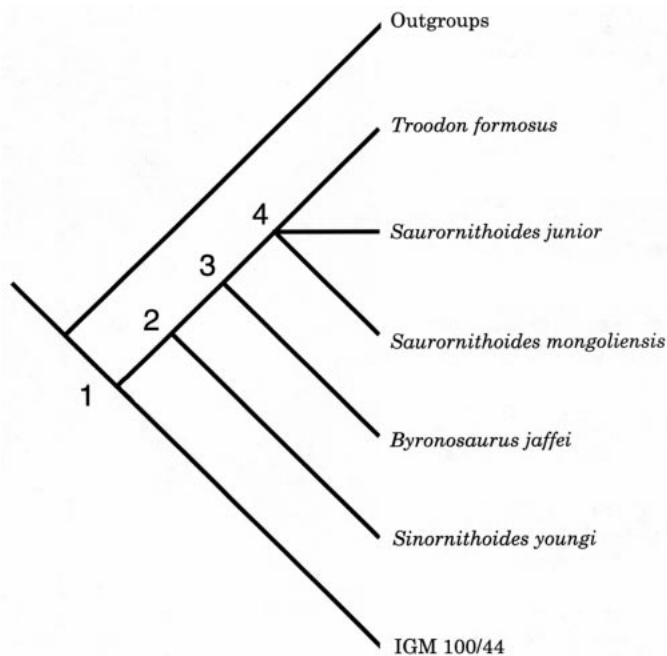


FIGURE 3. Strict consensus tree for phylogenetic relationships among troodontids. Unambiguous diagnoses for nodes under all outgroup topologies: 1 (7, 36), 2 (15), 3 (26, 30), 4 (24). Numbers refer to character list; all numbered apomorphies represent state 1 of characters.

All analyses yield three identical trees with lengths varying from 44 to 50 steps depending on outgroup configuration. A strict consensus of troodontid relationships is shown in Figure 3.

As can be determined from this analysis, *Byronosaurus jaffei* lies in a clade including both described species of *Saurornithoides* and the North American *Troodon formosus*. The sister-taxon of this clade is the Central Asian Early Cretaceous *Sinornithoides youngi*. The unnamed Mongolian taxon (IGM 100/44) occupies the base of the troodontid tree. Due to large amounts of missing data, branch support is low, ranging from three steps for Troodontidae (four with dromaeosaurs as nearest outgroup) to one step for two of the three internal nodes.

In summary, Troodontidae can be diagnosed by two unambiguous synapomorphies under all applied outgroup topologies: presence of a groove along the dentary for the mental foramina, and a slender Mt II that is distinctly shorter than Mt IV. In each analysis a third and occasionally a fourth, separate character supports troodontid monophyly (characters 1, 17, 21, 35, and/or 38), but these are dependent on outgroup topology. The distribution of other characters such as a long anterior ramus of the lacrimal (character 11) await discovery of additional cranial material.

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