A new species of Brontotheriidae from the Middle Eocene of Junggar Basin, Xinjiang, China Postprint

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Abstract

Based on an incomplete skull collected from the Langbulak Formation in the Sangonghe area of the Junggar Basin, Xinjiang Uygur Autonomous Region, a new species of large Irdinmanhan brontothere—Epimanteoceras mae sp. nov. —is described. The new specimen exhibits characteristics including a massive supraorbital process, broad frontal bone, shallow central fossa of the molars, absence of anterolingual cingulum cusp on the molars, and lack of a hypocone on M3, which allow it to be assigned to the genus Epimanteoceras. The features of E. mae include: a zygomatic arch slightly curved laterally, parasagittal crests arched medially, external auditory meatus pseudoorifice inclined posteromedially, and well-developed occipital columnar processes. E. mae is closely related to E. formosus. Phylogenetic analysis indicates that although it is uncertain whether E. mae or E. formosus constitutes the sister group of the Brontotheriinae, both are basal taxa to the latter. They are both similar to the Irdinmanhan brontothere Protitan grangeri from Inner Mongolia, but are much more primitive than Aktautitan hippopotamopus from Kazakhstan. The discovery of E. mae at Sangonghe indicates that the Langbulak Formation is of Middle Eocene age, earlier than the Kyzylbulak Formation that yields A. hippopotamopus in Kazakhstan. Furthermore, the discovery of Epimanteoceras mae in Xinjiang expands the distribution range of this genus, which was previously known only from Inner Mongolia.

Full Text

Preamble

A New Species of Brontotheriidae from the Middle Eocene of Junggar Basin, Xinjiang, China

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Abstract

A new species of large Irdinmanhan brontothere, *Epimanteoceras mae* sp. nov., is described based on an incomplete skull collected from the Üqbulak Formation at the Sangequan site in the Junggar Basin, Xinjiang Uygur Autonomous Region. The specimen can be assigned to the genus *Epimanteoceras* based on its large supraorbital processes, broad frontal bone, shallow central fossae on the molars, and the absence of both the anterolingual cingular cusp on the molars and the hypocone on M3. *E. mae* is characterized by slightly laterally bowed zygomatic arches, medially arched parasagittal ridges, a posteromedially angled external auditory pseudomeatus, and prominent occipital pillar processes. *E. mae* and *E. formosus* are closely related, and while it remains uncertain which of the two forms the sister group to Brontotheriina, both represent the basal group of the latter in phylogenetic analysis.

Both species are close to the Irdinmanhan brontothere *Protitan grangeri* from Inner Mongolia but are considerably more primitive than *Aktautitan hippopotamopus* from Kazakhstan. The discovery of *E. mae* at Sangequan indicates that the Üqbulak Formation is of Middle Eocene age, predating the Kyzylbulak Formation that yields *A. hippopotamopus* in Kazakhstan. Moreover, the discovery of *E. mae* in Xinjiang expands the known distribution of the genus *Epimanteoceras*, which was previously known only from Inner Mongolia.

Key words: Junggar Basin, Sangequan, Middle Eocene, *Epimanteoceras*

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1. Introduction

Brontotheriidae is an extinct family of perissodactyls that represents one of the most diverse ungulate clades, achieving a near-Holarctic distribution during the Middle to Late Eocene (Osborn, 1929; Colbert, 1938; Granger and Gregory, 1943; Wang, 1982; Kumar and Sahni, 1985; Qi and Beard, 1996, 1998; Eberle, 2006; Holroyd and Ciochon, 2000; Mihlbachler et al., 2004a; Mihlbachler, 2008; Kazunori et al., 2011) [Figure 1: see original paper]. Brontotheres first appeared in North America at the beginning of the Bridgerian age (Early Eocene), with the most primitive form being *Eotitanops* (Osborn, 1907). The group underwent rapid radiation, with nearly half of all brontothere genera emerging within approximately two million years during the early Uintan Land Mammal Age (Burger and Tackett, 2014). Brontotheres also dispersed into Asia shortly after the appearance of *Eotitanops* (Missiaen, 2011). By the Late Eocene, they had evolved very large body sizes and conspicuous frontonasal horns, but the entire family went extinct by the end of the period.

Most Asian brontothere fossils have been recovered from Inner Mongolia and Mongolia (Osborn, 1923, 1925, 1929; Granger and Gregory, 1943; Wang, 1978, 1982, 2000; Ye, 1983; Mihlbachler, 2007). In other regions, brontothere remains are scarce and fragmentary (Wang and Wang, 1997; Mihlbachler et al., 2004a; Emry and Lucas, 2002, 2003; Yanovskaya, 1957; Holroyd and Ciochon, 2000; Thewisse et al., 1987, 2001; West, 1980; Miao, 1982; Wang, 1978; Hu, 1961; Xu and Chiu, 1962; Huang and Zheng, 2004).

In 2012, the Xinjiang exploration team from the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) discovered a brontothere skull in the Junggar Basin, Xinjiang Uygur Autonomous Region [Figure 2: see original paper]. The fossil was preserved in white sandstone beds of the upper Üqbulak Formation at the Sangequan site. Although the facial region anterior to the orbits is missing, this specimen represents the best-preserved brontothere material from Xinjiang. The new species, *Epimanteoceras mae* sp. nov., described herein marks the first record of *Epimanteoceras* from Xinjiang, a genus previously known only from Inner Mongolia. This discovery increases the species diversity of *Epimanteoceras* and significantly expands the geographical range of the genus.

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2. Geological Context

The Sangequan site is located in the central Junggar Basin, approximately 100 km south of the Ulungur River. Both Late Cretaceous and Eocene sections are exposed along the southern cliff, which extends roughly east-west [Figure 2: see original paper]. The total thickness of the section is about 170 m [Figure 3: see original paper]. Based on lithological characteristics, the section can be divided into an upper part (Üqbulak Formation, approximately 86 m thick) and a lower part ("Ulunguhe" Formation?). The Üqbulak Formation disconformably overlies the "Ulunguhe" Formation, and the top of the section is capped by Quaternary conglomerate.

The Üqbulak Formation is of Eocene age (Tong et al., 1990) and consists of beds of grayish-white sandstone, dark yellow siltstone, and reddish-brown mudstone that yield numerous large land mammals. It can be subdivided into six horizons. The "Ulunguhe" Formation comprises brownish-red mudstone and sandstone beds and can be divided into eleven horizons, yielding dinosaur bones and eggshells.

The stratigraphic column of the Sangequan site (measured by Ye and Bi, personal data) is as follows:

Quaternary conglomerate

Üqbulak Formation (86 m) - Horizon 12: Yellow sandstone/grayish-white sandy conglomerate with grayish-white sandstone

"Ulunguhe" Formation? (84 m) - Horizon 10: Well-cemented fine sandstone, gray on concave-convex weathering surface (1 m) - Horizon 7: Brown mudstone, locally green, brownish-red on weathering surface (5 m) - Horizon 6: Grayish-white quartzy fine sandstone with black massive lenses locally (4.5 m) - Horizon 3: Light brown argillaceous cemented sandy conglomerate containing red muddy lenses (1 m) - Horizon 1: Light yellow medium-fine quartzy sandstone containing black lenses locally (7.5 m)

Abbreviations: AMNH, American Museum of Natural History, New York; FMNH, Field Museum of Natural History, Chicago; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing; KAN, Institute of Zoology, Kazakh Academy of Sciences, Almaty, Kazakhstan; TMM, Texas Memorial Museum, University of Texas, Austin; YPM, Yale Peabody Museum of Natural History, Yale University, New Haven, Connecticut.

All measurements were taken in millimeters following the methods of Mihlbachler (2008) and Froehlich (2002), and skull and dental terminology follows Mihlbachler (2008).

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3. Systematic Paleontology

Order Perissodactyla Owen, 1848
Family Brontotheriidae Marsh, 1873
Subfamily Brontotheriinae Marsh, 1873
Tribe Brontotheriina Marsh, 1873
Genus *Epimanteoceras* Gregory and Granger, 1943
***Epimanteoceras mae* sp. nov.** (Figs. 4-8, Tables 1-2)

Etymology: Named in honor of the fossil' s discoverer, Ms. Ma Mei.

Holotype: IVPP V 20713, an incomplete skull (Figs. 4-8) preserving the frontals, parietals, occipital, sphenoids, left M3, detached left M2, and roots of right M3, but lacking the nasals, premaxillae, most of the maxillae, and the right temporal process of the zygomatic bone. Some tooth fragments preserved in the sediment adjacent to the skull undoubtedly belong to the same individual, including upper incisors (labial part of left I1, lingual part of right I1, labial part of left I2, crown of right I2, and labial part of left I3), premolars (partial crowns), and right M1 (ectoloph). The skull is tilted rightward.

Type locality: Sangequan site (45°37 39.00 N, 87°58 46.40 E), located in the central Junggar Basin, Xinjiang Uygur Autonomous Region.

Stratigraphic position and age: Upper part of Üqbulak Formation (Tong, 1989), Middle Eocene (Irdinmanhan).

Diagnosis: A medium-sized brontothere. Compared with *Epimanteoceras formosus*, *E. mae* exhibits a more strongly backward-tilting occiput, more distinct occipital pillars with two prominent processes on the upper portion, more severely constricted parasagittal ridges, and an external auditory pseudomeatus that enters the skull in a more oblique posteromedial direction rather than a mediolateral one.

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4. Description

Skull (Figs. 4-7)

The holotype of *Epimanteoceras mae* sp. nov. represents the posterior half of the skull, missing the nasal, premaxillary, and most maxillary bones. The preserved portion measures 50 cm in length, taken on the ventral surface from the occipital condyles to the anterior edge of the specimen.

In dorsal view (Fig. 4), the frontal bones are broad and flat, with the dorsal surface slightly elevated at the frontal suture (fs). Large triangular supraorbital processes are positioned above the M3s. The parasagittal ridges (pr) are constricted posteriorly but remain separated, with the minimum distance between them occurring above the paramastoid process. The zygomatic arches are relatively thin mediolaterally and slightly bowed laterally. The jugals are straight and diverge posteriorly. The dorsal edges of the zygomatic processes of the squamosal (zps) are thinner than the ventral edges. The posterior portions of the zygomatic processes of the temporal bone protrude anterolaterally, forming an angle of approximately 60° with the skull' s midline. The dorsal surfaces of these posterior portions are smooth and slope anteriorly. The anterior portions of the zygomatic processes of the temporal bone run parallel to the skull' s midline with medially angled tips. The frontoparietal suture (fps) is inconspicuous on the dorsal surface, while the surface of the parietal and occipital bones is fragmented, making the lambdoid suture unidentifiable. However, the sutures between the squamosal portion of the temporal bone and the parietal, and between the squamosal portion and the occipital, are clearly visible. The occiput is slightly posteriorly tilted, and the middle portion of the nuchal crest is damaged.

In occipital view (Fig. 5), the nuchal crest is thin and arc-shaped. The dorsal portion of the occiput (at the nuchal crest) is as wide as the ventral portion (at the external auditory pseudomeatus), with the width exceeding the height (ratio = 1.91; height = 11.5 cm). A distinct suture between the exoccipital and supraoccipital bones (so) extends dorsally from the occipital side of the paramastoid process, running parallel to the nuchal crest at the dorsal side of the occipital condyle and curving slightly concave downward above the foramen magnum. The occipital condyles are large (width = 17.5 cm, height = 7.2 cm), compressed hemispherical in shape, with rough surfaces. Prominent occipital pillars (op) rise above the occipital condyles, forming a V-shaped structure on the occiput. Each occipital pillar bears a prominent tongue-shaped process protruding occipitally from its dorsal part, with the distance between these processes (opp) equal to the width of the occipital condyles.

In lateral view (Fig. 6), the remaining portion of the lacrimal bone (l) is small with a smooth surface. The suture between the lacrimal and frontal bones is zigzag-shaped, with only the posterior portion preserved. The orbits (o) are large and elliptical, positioned above the anterior portion of M3 and posterior portion of M2, with the long axis forming an angle of approximately 30–45° with the dorsal surface outline of the skull. The supraorbital processes (sop) extend laterally with slightly downward-angled tips. The zygomatic arches are relatively long (approximately 35 cm from the anterior rim above M3/M2 to the posterior rim at the external auditory pseudomeatus) with smooth surfaces. The squamosal process of the jugal (spj) is slender with a straight ventral edge, lacking the ventral zygomatic flange seen in *Metatelmatherium*. The frontal processes of the jugal (fpj) are small triangular processes positioned above the mesostyle of M3, with relatively long contact surfaces. The angle between the ventral side of the squamosal process of the jugal and the zygomatic process of the squamosal is approximately 135°, giving the zygomatic arches a dorsally angled appearance. The postzygomatic process seen in *Protitan* is absent. The cross-section of the zygomatic process of the temporal bone is triangular, with a rough ventral surface. The postglenoid processes (pgp) are large and oval to long elliptical, with narrower medial than lateral ends. The posttympanic process (ptp) and mastoid process are fused, while the paramastoid processes (pp) are as long as the postglenoid processes, though their apices are somewhat damaged. The postglenoid and posttympanic processes are widely separated, forming a ventrally unconstricted external auditory pseudomeatus. Numerous elliptical nutrient foramina are distributed along the sutures, successively lengthening anteroposteriorly with their long axes parallel to the skull length.

In ventral view (Fig. 7), the ventral surface of the skull is rather crushed, making the suture between the sphenoid and temporal bones unidentifiable. The posterior narial canal (pn) is relatively long, with its anterior margin positioned between the protocones of the M3s and its posterior margin between the postglenoid processes. The anterior portion of the posterior nares is rimmed by a moderately wide U-shaped emargination (e). The pterygoid process is long, extending posteriorly to the suture between the sphenoid and occipital bones, with a smooth inner wall surface. The maxilloturbinates are exposed in the choanae and extend beyond the anterior rim of the posterior nares, but are combined into a wavy bony layer in the thin posterior narial pouches. The vomer (v) is thin, with its posterior part showing a short Y-shaped divarication and a tiny fossa between the two branches. The ventral sphenoidal fossae (large pits on the ventral sphenoid surface seen in *Protitan*, *Metatitan*, and *Diplacodon*), which are continuous with the ventral narial canal, are absent. The posterior opening of the alisphenoid canal (ac) is positioned at the posterior end of the vomer, opening posteriorly. The foramen ovale (fo) lies on the posterior part of the sphenoid bone behind the pterygoid canal, with its aperture opening anteriorly. The foramina lacerum (fl) are positioned medial to the external auditory pseudomeatus (eap), widely separated from the foramen ovale, where the sphenoid and basioccipital bones connect. The external auditory pseudomeatus lies anterior to the foramen magnum, separated by 6 cm, and enters the skull in a more oblique posteromedial direction at approximately 60° to the skull' s long axis. The small hypoglossal canals (hc) are positioned between the occipital condyles and foramina lacerum, medial to the paramastoid process, with their apertures opening ventrolaterally.

Upper dentition (Fig. 8)

The remaining teeth of specimen V 20713 include left M3, an incomplete left M2, fragmentary incisors, and fragmentary premolars. The left M3 is the only tooth preserved in the maxilla, while the left M2 lacks its mesiolabial portion (parastyle and paracone).

The incisors are relatively large and successively enlarge from I1 to I3 (Fig. 8A–E, Table 2). I1 is subcaniniform or quadrihedron-shaped, but only the labial portion of the left I1 (Fig. 8A) and lingual portion of the right I1 (Fig. 8B) are preserved and rather worn. The lingual cingulum is V-shaped, with a short robust distal branch and a long slender mesial branch; no labial cingulum is present. I2 is subcaniniform, with only the labial portion of the left I2 (Fig. 8C) and crown of the right I2 (Fig. 8D) preserved, showing less wear than the I1s. Two ridges divide the crown into labial and lingual sides, with a flat lingual surface and swollen labial surface; the labial cingulum is absent. I3 is subcaniniform, with half of the left I3 preserved (Fig. 8E), and its crown is higher than that of I2. Due to the missing rostral portion, the shape of the incisor row and diastemata between incisors, I3 and canine, canine and P1, and P1 and P2 are unknown.

Only the ectoloph of the right M1 is preserved (Fig. 8F). The left M2 lacks the parastyle and half of the mesostyle and paracone. The right M3 is broken off, retaining only roots in the maxilla, while the left M3 is the only complete molar remaining in the maxilla (Fig. 7).

M2 is quadrangular (Fig. 8G) and moderately worn. The ectoloph is W-shaped, tall, and lingually tilted, with very weak ribs on the distal labial surface. The metacone incorporated in the ectoloph is wedge-shaped. The mesostyle is well developed, but the metastyle is weak. The protocone and hypocone are conical; the protocone is positioned near the midpoint of the lingual edge, leaving only a round wear surface, while the hypocone, situated at the distolingual corner, is much smaller than the protocone with a long elliptical wear surface. The protoconule and metaconule are absent. The central fossa is shallow and triangular. The labial cingulum is weak but slightly developed near the metastyle. The mesial cingulum is thin with a strip-shaped wear surface. The lingual cingulum is developed anterior to the protocone but absent posterior to it. The distal cingulum is very weak or absent.

M3 is morphologically similar to M2 (Fig. 8H) but slightly larger (Table 2) and less worn. The paracone and metacone are comparable in size. The mesostyle is more developed than in M2, while the metastyle is weaker than both parastyle and mesostyle. The protocone is a tall conical cusp positioned as in M2, with almost unworn enamel. The hypocone is absent on M3, but a shallow triangular central fossa is present. The mesial cingulum is weaker than in M2, while the distal cingulum is relatively thick. The labial cingulum is very weak and disappears beneath the mesostyle, and the lingual cingulum is absent. The anterolingual cingular cusp is absent.

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5. Comparison

Specimen V 20713 is assigned to *Epimanteoceras* based on the following characters: (1) flat, broadened frontal bone with large supraorbital processes; (2) occiput that tilts backward beyond the occipital condyles in lateral view (Fig. 6); (3) parasagittal ridges that strongly constrict on the dorsal cranial surface but remain separate posteriorly without merging into a true sagittal crest; (4) orbits positioned above the posterior portion of M2 and anterior portion of M3; (5) temporal process of the zygomatic bone that is horizontal while the zygomatic process of the temporal bone slopes posterodorsally, giving the zygomatic arches a curved appearance; (6) postglenoid and mastoid processes that are ventrally unconstricted, forming broad, ventrally opened external auditory pseudomeatus; (7) subcaniniform incisors; (8) absence of anterolingual cingular cusps on molars; and (9) absence of hypocone on M3. Additionally, the material is comparable in size to *E. formosus* (AMNH 21613), the only previously known species of this genus (Table 2).

The specimen represents a new species of *Epimanteoceras*. Differences between *E. mae* sp. nov. and *E. formosus* include: (1) posterior portions of parasagittal ridges that are medially bowed in the new species versus nearly parallel in *E. formosus*; (2) temporal ridge that is absent or weaker than in *E. formosus*; (3) more strongly arched zygomatic arches in dorsal view; (4) more robust occipital pillars with tongue-shaped processes; (5) larger occipital condyles; and (6) external auditory pseudomeatus that enters the skull in a posteromedial direction versus a mediolateral direction in *E. formosus*.

Protitan is an Irdinmanhan brontothere genus from Inner Mongolia (Osborn, 1923) similar to *E. mae* in overall profile and dentition. *Protitan* includes two valid species (Mihlbachler, 2008): *P. grangeri* (Osborn, 1925) and *P. minor* (Granger and Gregory, 1943). *E. mae* differs from both *P. grangeri* (AMNH 20103) and *P. minor* (AMNH 26416) in its smaller size, broad frontal bone, large supraorbital processes, more curved zygomatic arches, and absence of postzygomatic processes and ventral sphenoidal fossae. Additionally, *E. mae* differs from *P. grangeri* in having a more posteromedially angled external auditory pseudomeatus. The curved zygomatic arch represents a plesiomorphic character for all *Protitan* species.

Aktautitan hippopotamopus (Mihlbachler et al., 2004) is an Irdinmanhan brontothere from the Ily Basin of Kazakhstan, geographically close to *E. mae* but morphologically quite distinct. *E. mae* differs from *A. hippopotamopus* (KAN N2/875) in having posteriorly strongly constricted parasagittal ridges, more posteriorly positioned orbits (positioned above M2 in *A. hippopotamopus*), large supraorbital processes, curved zygomatic arches, a ventrally opened and more posteromedially angled external auditory pseudomeatus (ventrally closed and tubular in *A. hippopotamopus*), caniniform incisors (globular I1 and I2 in *A. hippopotamopus*), and presence of hypocone in M3. All but the more posteriorly positioned orbits and presence of hypocone in M3 are plesiomorphic characters.

The Late Bridgerian *Telmatherium validus* (Marsh, 1872) from North America has been widely regarded as the ancestor or sister taxon of horned brontotheres in North America and Asia (Granger and Gregory, 1943; Mader, 1989, 1998). It resembles *E. mae* in profile but is smaller (Tables 1, 2). The new species is more derived than *T. validus* (YPM 11120, AMNH 12678, AMNH 1570) in having posteriorly weakly constricted parasagittal ridges (compared to primitive genera such as *Eotitanops* and *Palaeosyops*), a more posteriorly positioned anterior margin of the posterior nares (anterior to the protocones of M3s and near the posterior margin of M2 in *T. validus*), and presence of central molar fossae. Additionally, *E. mae* differs from *T. validus* in its broadened frontal bone, large supraorbital processes, more posteriorly positioned orbits (also positioned above M2 in *T. validus*), and more posteromedially angled external auditory pseudomeatus.

Metatelmatherium ultimum (Granger and Gregory, 1938) is a genus known from both North America and Asia (Granger and Gregory, 1943). The Asian specimen was discovered near Camp Margetts from Arshantan strata (Wang et al., 2010). Despite its primitive evolutionary status, *M. ultimum* is the only certain species predating *Epimanteoceras* in Asia. *E. mae* is more derived than *M. ultimum* (AMNH 2060) in its widened occiput, posteriorly weakly constricted parasagittal ridges (compared to primitive genera such as *Eotitanops* and *Palaeosyops*), and presence of central fossae on molars. It also differs in its larger body size, broadened frontal bone, large supraorbital processes, more posteromedially angled external auditory pseudomeatus, absence of zygomatic ventral flange, and absence of molar anterolingual cingular cusps.

The North American late Uintan *Protitanotherium emarginatum* (Hatcher, 1895) resembles *E. mae* in profile except for the nasal region. *E. mae* is more primitive than *Pr. emarginatum* (TMM 41723) in its curved zygomatic arches, ventrally opened external auditory pseudomeatus (ventrally closed and tubular in *Pr. emarginatum*), and caniniform incisors (all globular in *Pr. emarginatum*). It also differs in having large supraorbital processes and more posteriorly positioned orbits (also positioned above M2 in *Pr. emarginatum*).

Another North American late Uintan form, *Diplacodon elatus* (FMNH P14632, P14633) (Marsh, 1875), also resembles *E. mae* in profile except for the nasal region. *E. mae* is more primitive than *D. elatus* in its curved zygomatic arches, ventrally opened external auditory pseudomeatus (ventrally closed and tubular in *D. elatus*), and all caniniform incisors (only I3 is caniniform in *D. elatus*). It also differs in having somewhat strongly constricted parasagittal ridges, more posteriorly positioned orbits (also positioned above M2 in *D. elatus*), and absence of ventral sphenoidal fossae.

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6. Phylogenetic Analysis

To assess the phylogenetic position of *Epimanteoceras mae*, a phylogenetic analysis was performed using the data matrix of Mihlbachler (2008) with the new species added (Appendix I). The matrix included 52 taxa and 87 characters, with *Hyracotherium*, *Pachynolophus*, *Danjiangia*, and *Lambdotherium* designated as outgroups.

The analysis was conducted using traditional search in TNT (version 1.1) with equal weighting of all characters. All characters were ordered except characters 26 and 73. The analysis generated 72 parsimonious trees with a tree length of 311 steps, consistency index of 0.450, and retention index of 0.813.

The strict consensus tree of the 72 most parsimonious trees (Fig. 9) is nearly identical to that of Mihlbachler (2008). *E. mae* is deeply nested within Brontotheriini and shares with other members the following optimized apomorphies (Mihlbachler, 2008): a pair of triangular frontal processes that overlap or intrude into the nasal bone, and reduced occipital condyles. In the strict consensus tree (Fig. 9), *E. mae* nests within the polytomic construction (*Nanotitanops shanghuangensis* (*E. formosus*)) also exhibited by Mihlbachler (2008).

Due to collapse of the polytomic construction (*Nanotitanops shanghuangensis*–*E. mae*), the precise phylogenetic position of *E. mae* within Brontotheriini cannot be resolved. To identify problematic taxa within the polytomy, the "IterPCR" script was run in TNT. The result, identical to Mihlbachler (2008), identified the problematic taxon within the polytomic construction *N. shanghuangensis*-*E. mae* as *N. shanghuangensis* (Fig. 10) (the other problematic taxon, *N. mississippiensis* within Brontotheriita (node 5 in Fig. 10), is irrelevant to the new species). The Jiangsu brontothere *N. shanghuangensis* lacks skull material and is known only from a few isolated teeth. Its teeth are smaller than those of *Eotitanops* and *Palaeosyops* but much more derived in dental morphology (Mihlbachler, 2008), resembling *Epimanteoceras* or even *Rhinotitan.* As a possible sister taxon to *E. formosus* or Brontotheriina, *N. shanghuangensis* occupies an uncertain position within or outside Brontotheriina, generating a polytomic construction near the Brontotheriina node (node 4 in Fig. 10).

The summary tree (Fig. 10) is derived from strict reduced consensus trees with problematic taxa (*N. shanghuangensis* and *N. mississippiensis*) removed, and is identical to that of Mihlbachler (2008). In this tree, the positions of taxa within the polytomic construction are resolved. *E. mae* forms a trifurcated branch with *E. formosus* and the monophyletic clade Brontotheriina (node 4 in Fig. 10). *E. mae* and *E. formosus* are primitive to Brontotheriina in lacking conspicuous frontonasal protuberances (Mihlbachler, 2008).

Although *E. mae* does not form a monophyletic clade with *E. formosus*, morphological evidence (the combination of features such as larger supraorbital processes, broadened frontal bone, strongly constricted parasagittal ridges, posteriorly dorsally curved zygomatic arches, absence of anterolingual cingular cusps on molars, and absence of hypocone on M3) and phylogenetic analysis are sufficient to justify its assignment to *Epimanteoceras*. The failure of the two *Epimanteoceras* species to form a monophyletic clade likely results from missing important synapomorphic features due to the absence of the facial skull portion: (1) inconspicuous frontonasal protuberances (character 3: state 2); (2) more complex P1 with distinct paracone and metacone (character 47: state 1); and (3) premolar hypocones and protocones situated closely and connected by lingual crests (character 53: state 2). Furthermore, the genus-level feature of *Epimanteoceras*—large supraorbital processes (Granger and Gregory, 1943)—was not included in Mihlbachler' s (2008) matrix. Large supraorbital processes are only observed in *E. formosus*, being small or inconspicuous in other brontotheres. Unfortunately, only two *E. formosus* specimens are known, and the supraorbital processes are missing in one (AMNH 21607), preventing inclusion of this character in the matrix. However, it would be a valuable character if more *Epimanteoceras* specimens were available.

Beyond morphological differences between *E. mae* and *E. formosus*, the considerable geographic distance between their collection sites provides additional justification for erecting a new species.

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7. Discussion on the Age of Strata

Fossils from the Sangequan area were previously recovered primarily from the Huashigou ("fossil gully") site, located west of the brontothere bone bed (Tong, 1989a, b; Tong et al., 1990; Wei and Tong, 1992; Li et al., 2009). Tong (1989a) used "Üqbulak Formation" for the upper strata, which are relatively lighter in color than the lower strata. Three fossil sites were identified at Huashigou (Tong, 1989a): 82507A, 82507B, and 82507C (from bottom to top). The Irdinmanhan tapir *Rhodopagus* was found at 82507C (Tong, 1989a). The fauna from the lower site 82507B includes *Breviodon minutus*, *Schlosseria magister*, *Uintatherium* cf. *insperatus*, *Metacoryphodon* sp., *Pantolamddodon* sp., and cf. *Mesonyx uqbulakensis* (Tong, 1989a)—all large Middle Eocene land mammals. Fossils from the lowest site 82507A are fragmentary, with only *Hyopsodus* confirmed (Tong, 1989a).

The brontothere fossiliferous layer lies approximately 13 km west of Huashigou and can be easily correlated with the Huashigou site. *Epimanteoceras mae* was excavated from the top layer of the Üqbulak Formation, comparable to the horizon containing site 82507C. The Sangequan brontothere is somewhat plesiomorphic relative to the Irdinmanhan brontothere *Protitan* from Inner Mongolia, as is *E. formosus*. Together with *Rhodopagus* from site 82507C (Tong, 1989a), the discovery of *E. mae* at Sangequan indicates an Irdinmanhan (Middle Eocene) age for the Üqbulak Formation, supporting previous conclusions (Tong, 1989a). Additionally, the Kazakhstan Irdinmanhan brontothere *Aktautitan hippopotamopus* is more derived than *E. mae*, indicating that the strata yielding *A. hippopotamopus* are younger than the Üqbulak Formation at Sangequan.

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Appendix 1: Character codes of *Epimanteoceras mae* according to Mihlbachler (2008)

Epimanteoceras mae (IVPP V 20713)
1????????? ??10? ????2 0120100111 0100000000 1011?????? ???1111121 113214302? ?????????? ???????

Note: Figure translations are in progress. See original paper for figures.