

A New Brontothere (Brontotheriidae, Perissodactyla, Mammalia) from the Eocene of the Ily Basin of Kazakstan and a Phylogeny of Asian “Horned” Brontotheres

Authors: MIHLBACHLER, MATTHEW C., LUCAS, SPENCER G., EMRY, ROBERT J., and BAYSHASHOV, BOLAT

Source: American Museum Novitates, 2004(3439) : 1-43

Published By: American Museum of Natural History

URL: [https://doi.org/10.1206/0003-0082\(2004\)439<0001:ANBBPM>2.0.CO;2](https://doi.org/10.1206/0003-0082(2004)439<0001:ANBBPM>2.0.CO;2)

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3439, 43 pp., 22 figures, 3 tables May 14, 2004

A New Brontothere (Brontotheriidae, Perissodactyla, Mammalia) from the Eocene of the Ily Basin of Kazakhstan and a Phylogeny of Asian “Horned” Brontotheres

MATTHEW C. MIHLBACHLER,^{1,2} SPENCER G. LUCAS,³ ROBERT J. EMRY,⁴
AND BOLAT BAYSHASHOV⁵

ABSTRACT

A new genus and species of “horned” brontothere, *Aktautitan hippopotamopus*, from the Ily Basin of Kazakhstan is described from three skulls and nearly complete postcranial material. This material occurs in fluvio-lacustrine red beds of the upper part of the Eocene (Irdinmanhan) Kyzylbulak Formation at Aktau Mountain. Trackways occurring in the overlying layers are also attributed to this new brontothere. Additionally, several misleading problems in the taxonomy of Asian horned brontotheres are addressed. We conclude that *Protitan khaitshinus* Yanovskaya, 1980 is a junior objective synonym of *Metatitan relictus* Granger and Gregory, 1943. *Protitan reshetovi* Yanovskaya, 1980 is removed from the genus *Protitan* and possibly belongs within *Metatitan*. *Brachydiastematherium transylvanicum* Böckh and Maty, 1876, the only bona fide European brontothere, known from a single partial mandible, is morphologically consistent with *Metatitan* Granger and Gregory, 1943. Although *B. transylvanicum* is known from very fragmentary material, it is possible that *Metatitan* is a junior synonym of *Brachydiastematherium*. The first cladistic phylogeny of middle and late Eocene Asian horned brontotheres was constructed with 40 characters and 17 taxa. *Aktautitan*, *Metatitan*, *Brachydiastematherium*, and *Embolotherium* form a monophyletic clade, with *Aktautitan hippopotamopus*

¹ Division of Paleontology, American Museum of Natural History. e-mail: mihlbach@amnh.org

² Department of Earth and Environmental Sciences, Columbia University, 2960 Broadway, New York, NY 10027.

³ New Mexico Museum of Natural History, 1801 Mountain Road N.W., Albuquerque, NM 87104. e-mail: slucas@nmmnh.state.nm.us

⁴ Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC. e-mail: emry.robert@nmnh.si.edu

⁵ Institute of Zoology, Kazak Academy of Sciences, Akademgorodok, Almaty 480032, Kazakhstan. e-mail: baybol@nursat.kz

as the most basal member of this clade. Within this clade, there are two monophyletic trichotomies: a *Metatitan relictus*, *M. primus*, *Brachydiastematherium transylvanicum* clade and a “*Metatitan*” *progressus*, *Embolotherium andrewsi*, *E. grangeri* clade. The cladogram topology suggests that the elevated frontonasal horns shared by *Aktautitan* and *Metatitan* represent the ancestral morphology of the bizarre “battering-ram” of *Embolotherium*. We extend the subfamily name Embolotheriinae to include these taxa. The unusually shortened distal limb segments of *A. hippopotamopus* resemble those of a phylogenetically disparate group of large ungulates that have convergently evolved hippolike limb proportions. We conclude that these limb proportions probably do not indicate a semiaquatic lifestyle, as had been previously surmised.

INTRODUCTION

The Brontotheriidae is an exclusively Eocene family of perissodactyls, notable for having evolved bony frontonasal protuberances (or “horns”) and body sizes approximating those of extant rhinos and elephants. The bulk of the known brontothere fossil record is from inner and outer Mongolia and western North America (Osborn 1929a, 1929b; Granger and Gregory, 1943; Yanovskaya, 1980; Wang, 1982). Although brontothere records are fewer and more fragmentary in other regions, it is evident that brontotheres had essentially a holarctic distribution, with the exception of western Europe (Pilgrim, 1925; Colbert 1938; Takai, 1939; Gazin, 1942; Dehm and Oettingen-Spielberg, 1958; West, 1980; Kumar and Sahni, 1985; Qi and Beard, 1996; Eberle and Storer, 1999; Holroyd and Ciochon, 2000; Miyata and Tomida, 2003).

Although brontothere taxonomy is widely regarded as being in need of revision (e.g., Prothero, 1994), it is clear that this family was one of the most diverse ungulate clades during the Eocene. A dizzying array of subfamilial names have been given to brontotheres throughout the history of their study, but rigorous testing of brontothere phylogeny has been minimal for North American taxa (Mader, 1989, 1998) and is nonexistent for Asian taxa. For lack of a sound taxonomy or phylogenetic framework for brontotheres, particularly outside of North America, we refer to those brontotheres possessing frontonasal protuberances (horns) as the “horned” brontotheres, and the probable paraphyletic assemblage of more primitive brontotheres that lack frontonasal protuberances as the “hornless” brontotheres.

The new genus and species of horned

brontothere, *Aktautitan hippopotamopus*, described here from eastern Kazakstan, is the first middle Eocene record of a brontothere known from complete skeletons west of the Gobi region.

INSTITUTIONAL ABBREVIATIONS

AMNH	American Museum of Natural History, New York
CM	Carnegie Museum of Natural History, Pittsburgh
FLMNH	Florida Museum of Natural History, Gainesville
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China
KAN	Institute of Zoology, Kazak Academy of Sciences, Almaty, Kazakstan
NMNH	National Museum of Natural History, Washington, DC
PIN	Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia
YPM	Yale Peabody Museum of Natural History, New Haven

GEOLOGICAL CONTEXT

The Ily basin of eastern Kazakstan is the western portion of a paleo-Tien Shan basin that extended into western China (fig. 1). In the Ily basin, the Cenozoic section is best exposed at and around Aktau Mountain in the southern foothills of the Dzhungarian Alatau. At Aktau Mountain, the Cenozoic section is about 2.5 km thick and mostly of Neogene age (Lavrov and Rayushkina, 1983). The lower 150 m or so of this section are of Eocene age and are assigned to the Kyzylbulak Formation (figs. 2, 3A), which is best exposed at Kyzyl Murun, at the core of the Aktau Mountain anticline (Lucas et al., 1997). Here, the Kyzylbulak Formation is siliciclastic red beds of sandstone, conglomerate,



Fig. 1. Map of Kazakhstan showing the location of Aktau Mountain, the collection site of *Aktautitan hippopotamopus*.

erate, mudstone, and shale. The Aktau Formation disconformably overlies the Kyzylbulak Formation and yields late Oligocene (Tabenbulukian) mammals in its lower part, and early Miocene mammals in its middle to upper parts (Lucas et al., 1997).

The brontothere bonebed at Aktau Mountain was discovered in May 1996. It extends over a strike of ~200 m at and around UTM zone 44, 361142E, 4874810N (datum WGS

84) in approximately the middle of the Kyzylbulak Formation exposure at Kyzyl Murun (fig. 2). The bone bed is in a ~0.5-m-thick bed of green, bentonitic shale (figs. 2, 3D). In addition to the brontotheres, the bonebed at Kyzyl Murun yields fossils of a *Teleolophus*-like tapiroid, a new species of the rhinocerotoid *Rhodopagus* and the amyndontid rhinoceros *Sharamynodon mongoliensis* (Lucas and Emry, 2001; Emry and

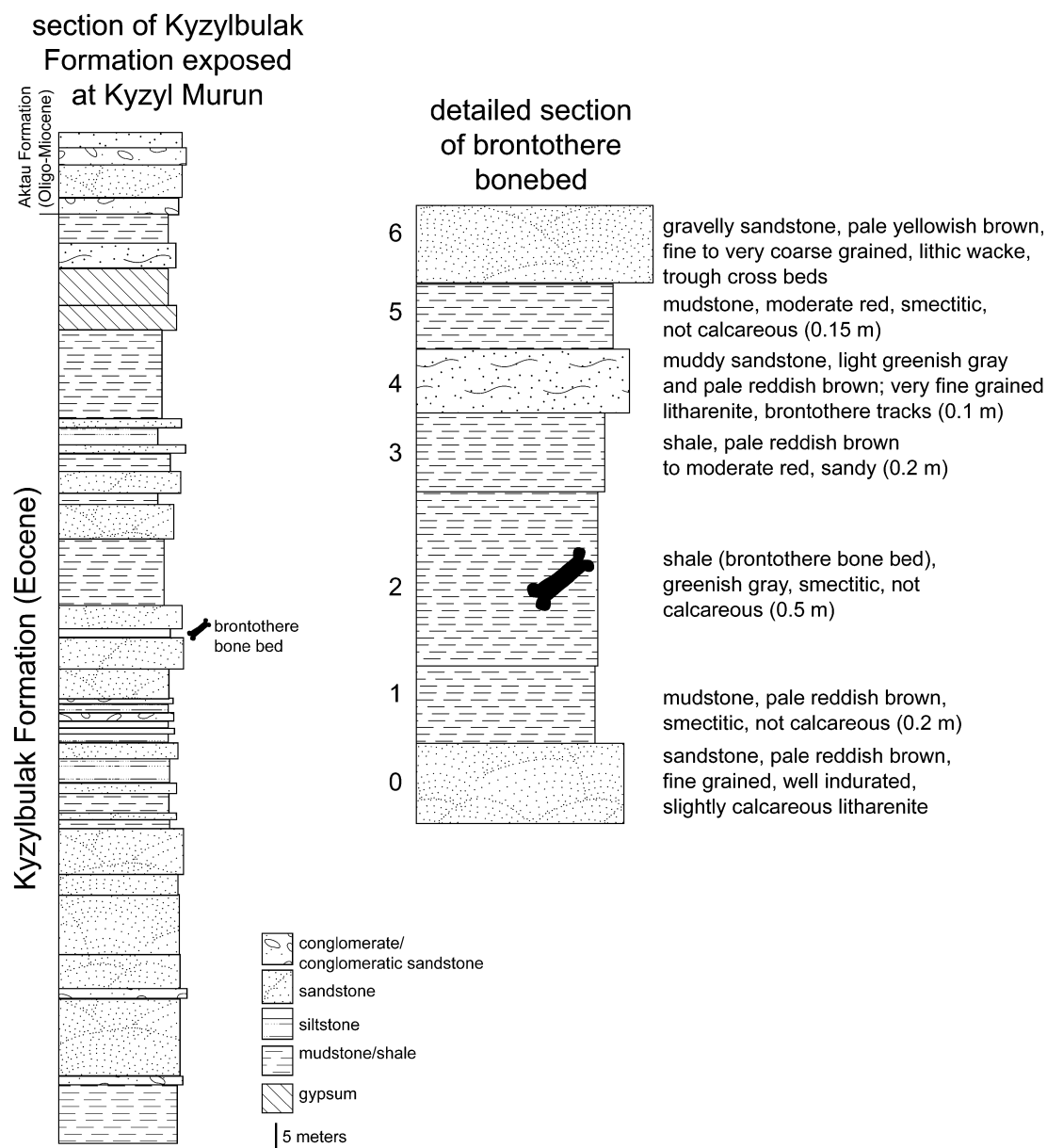


Fig. 2. Measured stratigraphic section of the Kyzylbulak Formation at Kyzyl Murun showing location of brontothere bone bed (after Lucas et al., 1997) and detailed section of bonebed.

Lucas, 2003). These fossils indicate an Irдин-манхан (middle Eocene) age for the brontothere bonebed at Kyzyl Murun.

In the brontothere bonebed at Kyzyl Murun, complete, articulated brontothere skeletons are preserved in green, smectitic shale. In at least two of the excavated brontothere

skeletons, articulated feet were found upright in the shale, with the remaining skeleton lying on its side. The bone-bearing shale has a lenticular geometry, fine laminations, and lacks any evidence of pedogenesis. These features are consistent with a pond or lake deposit, not as floodplain muds in the oth-



Fig. 3. Outcrop photographs of the brontothere bone bed at the Kyzyl Murun. (A) Overview of Kyzyl Murun, an escarpment near the core of the Aktau Mountain anticline, (B) excavation of the brontothere bone bed, and (C) skull and lower jaws of *Aktautitan hippopotamopus* being uncovered in the bone bed. Rock hammer is 28 cm long. (D) detail of brontothere bone bed stratigraphy; numbers correspond to units in detailed section of figure 2.

erwise fluvial deposits of the Kyzylbulak Formation (cf. Lucas et al., 1997). We thus conclude that at least some (or all) of the brontothere remains at Kyzyl Murun were preserved in a lacustrine deposit, and at least some of the animals apparently died while mired in mud.

SYSTEMATIC PALEONTOLOGY

ORDER PERISSODACTYLA OWEN, 1848

FAMILY BRONTOTHERIIDAE MARSH, 1873

SUBFAMILY EMBOLOTHERIINAE OSBORN, 1929B

Aktautitan hippopotamopus, new genus and species

HOLOTYPE: KAN N2/875, a complete skull, mandible and skeleton lacking only parts of the right tarsus and pes.

TYPE LOCALITY: Kyzylbulak Formation, Kyzyl Murun near Aktau Mountain, Ily Basin, Kazakhstan.

AGE: Middle Eocene (Irdinmanhan land-mammal “age”)

ETYMOLOGY: *Aktautitan*, Aktau (in reference to the name of the mountain where the fossils were found); titan, giant; *hippopotamopus*, Greek, “hippopotamus foot” (in reference to the hippopotamus-like limb proportions of this species).

REFERRED SPECIMEN: KAN N2/873, a complete skull and articulated mandible, complete dentition, a fully articulated right forelimb with radius, ulna, and manus and a partial left manus. (An anterior portion of a third cranium [KAN N/2 639] was not directly examined by Mhiblachler, but is considered referable to *Aktautitan hippopotamopus* by Lucas and Emry.)

DIAGNOSIS: *Aktautitan hippopotamopus* can generally be characterized as a large brontothere with a relatively elongate skull; unbowed zygomatic arches; unreduced dental formula (3/3 1/1 4/4 3/3); small elliptical frontonasal horns; relatively tall upper molar

ectolph with a very thin inner band of enamel; small third anterolingual cusp on the mesial cingulum of the upper molars; shallow central fossa in the upper molars; large pointed hypocone on the M3; i2 larger than i3; metaconid absent on p2, present but small on p3, present and molariform on p4; and m3 very elongate. *A. hippopotamopus* is similar to *Metatitan*, *Protambolotherium*, and *Embolotherium* in having frontonasal protuberances that are situated close together and are elevated on tall superorbital pillars, creating a single frontonasal process. *A. hippopotamopus*, like *Metatitan*, retains a large, elevated nasal process, with downfolded lateral margins, that extends forward from the peak of the frontonasal process. *A. hippopotamopus* differs from *Metatitan* in the following characteristics: dorsal surface of the skull forms a continuously concave surface; posterior zygomatic processes absent; orbit more anterior, positioned directly above the M2; larger incisors that arch anteriorly from the canines; upper incisors grade from subglobular (I1) to caninform (I3); lower incisors short and conical with blunt points; postcanine diastema present; and p3 metaconid smaller and less lingually positioned. The distal limb segments of *A. hippopotamopus* are proportionally much shorter than those of other brontotheres, resulting in remarkably shortened limbs that are more similar in proportion to those of *Hippopotamus* and a number of short-limbed rhinocerotoids such as *Teleoceras* and *Metamynodon*.

DESCRIPTION

The completeness and position of the brontothere skeletons in the sediment suggest that the animals were trapped in deep mud and preserved completely (although some of the specimens had been eroded away). All of the feet were preserved deepest in the mudstone (30 cm or more below the level of the thorax). The digits of the feet were hyperflexed, extending outward and upward from the distal ends of the metapodials (see figs. 12, 16). Some of the longbones, especially those of the lower limbs, were preserved vertically in the sediment, with the remainders of the skeletons collapsed directly over the limbs and feet. Compression of the mudstone

bed has resulted in deformation of the bones within it, and those longbones preserved more or less vertically are substantially shorter than their counterparts that were preserved more or less horizontally.

The skull of the holotype (KAN N2/875) is essentially complete, although it was lying on its side and is somewhat compressed laterally. The referred skull (KAN N2/873) is compressed obliquely (more laterally than vertically). This distortion compromises the measurement of various cranial dimensions. The postcranial material belonging to the holotype, KAN N2/875, consists of the entire skeleton, missing only some parts of the right tarsus and proximal metatarsus (the right ankle was the only part of this individual exposed at the surface). Much of the thorax and forelimbs remain articulated in a large block, preventing detailed study of some of the individual bones.

Asian brontotheres are rarely known from associated skulls and postcrania. The entire skeleton of *Rhinotitan mongoliensis* (Wang, 1982) and parts of the skeletons of *Metatitan relictus* (= *Protitan khatishinus* Yanovskaya, 1980, see below), cf. *Parabrontops gobiensis* (PIN 3109, mistakenly referred to *Metatitan relictus* by Yanovskaya, 1980; see below for explanation), and *Embolotherium andrewsi* (Yanovskaya, 1980) have been described. The skeletons of many North American taxa are better known. They include essentially complete skeletons of *Brontops*, *Dolichorhinus*, and *Palaeosyops* and partial postcranial material from several other North American taxa (Peterson, 1924; Osborn, 1929a). The postcranial remains of *Aktaititan hippopotamopus* are compared to Asian taxa when possible, but due to the lack of abundant comparative material, observations of the skeletons of North American species have been included as points of reference.

SKULL

The bony protuberances that characterize horned brontotheres are formed by a pair of triangular processes of the frontal bone that project anteriorly and overlap a pair of nasal swellings that are plesiomorphically situated superior to and somewhat anterior to the orbits (Osborn, 1929a; Mader, 1989). A ridge

of bone, probably indicating the contact of the frontal and nasal bones, is clearly visible in *A. hippopotamopus* and forms the expected configuration with the frontal bone overlapping the nasal bone and forming the peak of the frontonasal horns (fig. 4B). There are many derived aspects of the frontonasal region in *A. hippopotamopus* that resemble *Metatitan* (sensu Granger and Gregory, 1943). The use of *Metatitan* as a point of comparison in the following cranial description refers primarily to *M. relictus* and *M. primus*. "*Metatitan*" *progressus* shares many characteristics of the frontonasal region, but other aspects of its skull are unknown. In both *A. hippopotamopus* and *Metatitan*, the frontonasal protuberances and the free-hanging nasal processes are elevated on tall superorbital pillars formed inferiorly by the nasal bone and superiorly by the overlying frontal bone (figs. 4, 5, 19). These pillars are joined at the midline (though they have become separated in the more obliquely distorted specimens such as KAN N2/873), forming a single frontonasal process that originates above the orbits and projects superiorly and anteriorly at about a 45° angle. The frontonasal horns of other brontotheres such as *Protitan*, *Rhinotitan*, and North American horned brontotheres are positioned farther apart, remain separate, and most often project somewhat laterally. In contrast, the frontonasal process of *A. hippopotamopus* and *Metatitan* converge medially, and the bony protuberances that form the peak of the frontonasal process are placed close together near the midline of the skull.

In both skulls of *Aktautitan hippopotamopus* the distance from the anterior rim of the orbit to the peak of the frontonasal process is 22 cm. The bony frontal protuberance at the peak of this structure is positioned over the nasal incision. The nasal incision itself extends posteriorly to the level of the P4. The nasal process extends anteriorly from the peak of the frontonasal process and is angled slightly downward. This orientation creates a sharp bend in the nasal bone underneath the frontonasal protuberances. The free-hanging nasal process of *A. hippopotamopus* is relatively thin, and its lateral margins are folded downward. This morphology is also essentially the same as that of *Metatitan*.

The orbit of *Aktautitan hippopotamopus* is positioned anterior to the midway point between the anterior and posterior ends of the skull, a condition common to all but the most primitive brontotheres such as *Lambdaotherium* and *Eotitanops*, where the orbits are more posteriorly located (Osborn, 1929a; Mader, 1989). The floor of the orbit of *A. hippopotamopus* is positioned directly above the M2 (fig. 4B). The posterior lateral root of M1 is situated directly below the anterior orbital rim, and the M3 is positioned completely posterior to the orbit. This orbital position is shared by the Asian taxa, *Embolotherium* and *Rhinotitan*, and is more anterior than that of *Protitan*, *Metatitan relictus*, and, *M. primus*, where the anterior lateral root of M3 and the posterior lateral root of M2 rest directly below the orbit, but the anterior root of M2 is anterior to the floor of the orbit.

The parasagittal ridges of *Aktautitan hippopotamopus* (fig. 4A) originate from above the postorbital processes of the frontal bone and converge somewhat medially as they run posteriorly toward the nuchal crest. Although the posteriormost regions of both skulls, including the nuchal crests, are not well preserved, it appears as if the parasagittal ridges remained separate throughout their length from the orbits to the nuchal crest. However, it is not possible to determine the degree of constriction of the parasagittal ridges over the parietal region, but they do not appear to have converged into a single sagittal crest. The entire dorsal surface of the skull of *A. hippopotamopus*, from the peaks of the frontonasal horns to the parietal, appears to have been a continuously concave surface, forming the distinctly "saddle-shaped" cranium that is common to many horned brontotheres (Osborn, 1929a). *Rhinotitan* and *Metatitan* are notable exceptions to this generality. In these taxa, the dorsal surface of the frontal is concave, but over the parietal region the dorsal surface of their crania becomes convex. In this respect, *Metatitan* and *Rhinotitan* resemble some "hornless" brontotheres. The condition of a convex parietal bone is more extreme in *Metatitan*, however, because the parietal and squamosal sinuses are greatly expanded and the occiput is widened, giving the posterior half of the skull a swollen ap-

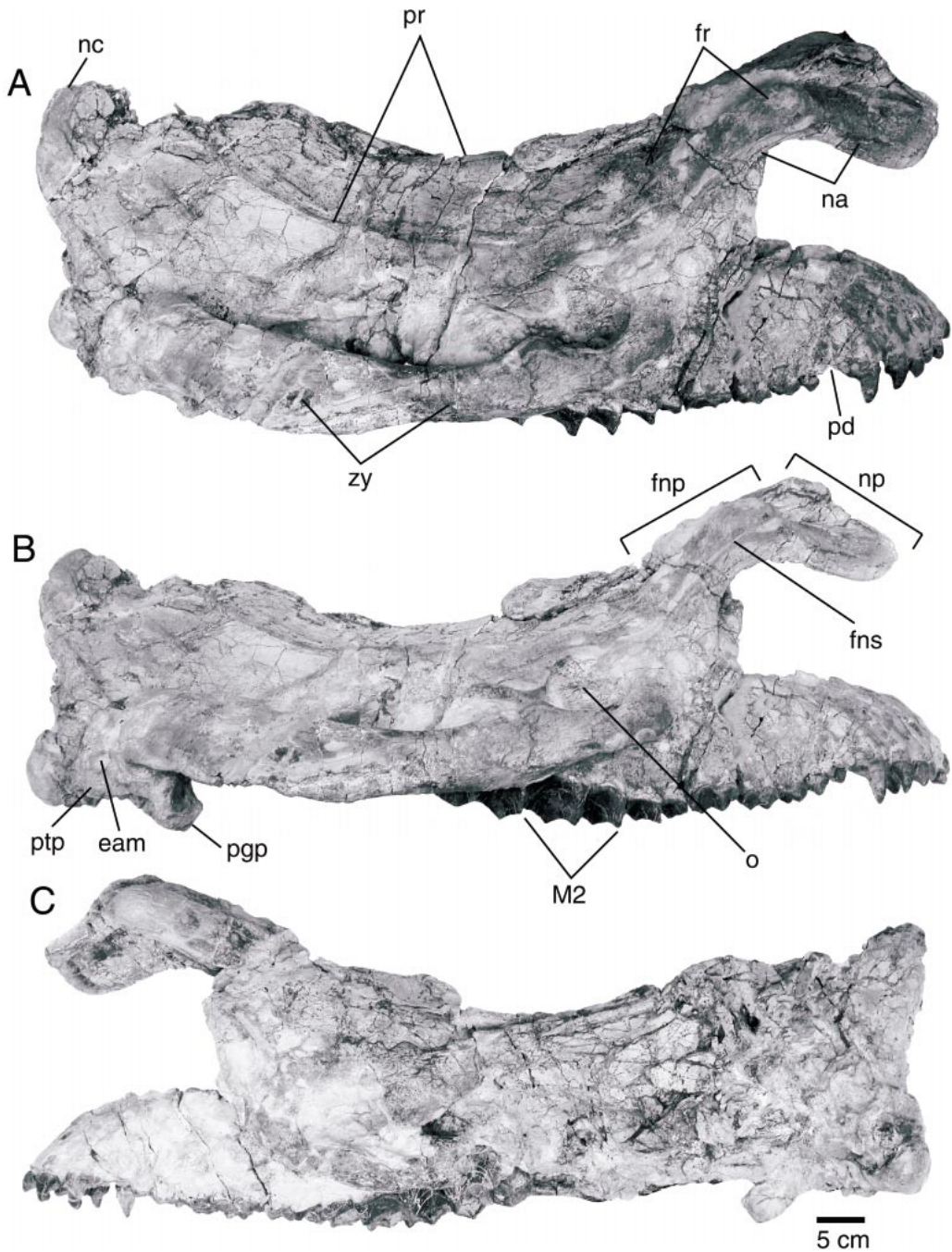


Fig. 4. Holotype skull of *Aktautitan hippopotamopus* (KAN N2/875). (A) Right lateral view tilted slightly so that the dorsal surface of the skull can be seen, (B) right view, and (C) left view.

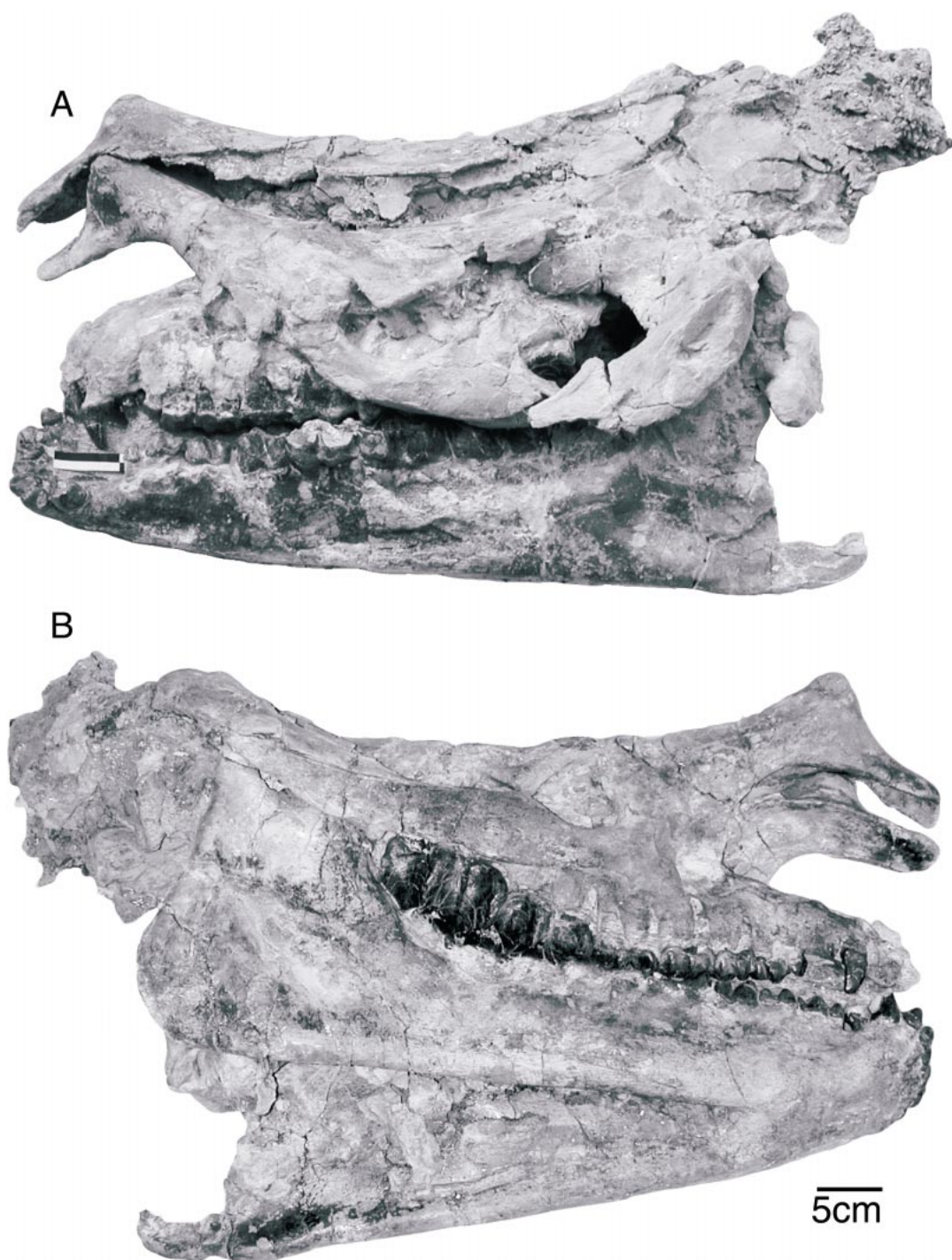


Fig. 5. Skull referred to *Aktautitan hippopotamopus* (KAN N2/873). (A) Left view, (B) right view.

pearance. *A. hippopotamopus* lacks these derived *Metatitan* features.

The zygomatic arches of *A. hippopotamopus* are relatively slender (figs. 4, 6A) and lack the large lateral expansions that have been observed in *Embolotherium* and North American late Eocene brontotheres such as *Brontops* (Osborn, 1929a, 1929b). The zygomata of *A. hippopotamopus* also lack the posterior zygomatic process, a small projection rising superiorly from the posterior end of the zygomatic arch found in *Metatitan relictus* and *Protitan* (Granger and Gregory, 1943).

Unfortunately, the basicranium and occipital regions of both *Aktautitan hippopotamopus* skulls are badly damaged, but some phylogenetically informative details of the basicranium can be discerned in the holotype. For instance, the posterior nares appear to have been positioned between the M3s (fig. 6A). The posttympanic processes and postglenoid processes are close together, forming a constricted space for the external auditory meatus (fig. 4B). The posttympanic process is much shorter than the postglenoid process, and it curves anteriorly toward the postglenoid process, nearly making contact with it. A thin sliver of sediment can be seen in the constricted space between these two processes. Consequently, the external auditory meatus nearly forms a tube. This condition is common to all horned brontotheres with known basicrania, except *Protitan* (fig. 19A), where the posttympanic process and postglenoid process are spaced farther apart, creating a wide space for the external auditory meatus.

UPPER DENTITION

In KAN N2/875 the jaw has been separated from the skull, allowing for a complete description of the upper and lower dentition. The jaw of KAN N2/873 remains cemented to the cranium, limiting inspection of the teeth. *Aktautitan hippopotamopus* retains an unreduced dental formula $3/3 \ 1/1 \ 4/4 \ 3/3$ (fig. 6). The incisors are quite large and packed tightly together without diastemata between them, except for a narrow gap between the central incisors (I1) (fig. 6D, E). The incisor row is arched anterior to the ca-

nines. The crown morphology of the upper incisors grades mesiodistally from a blunt, subglobular I1 to a much sharper and taller caniniform I3. A short diastema separates the I3 and the canine. The size and appearance of the upper incisors strongly resemble *Rhinotitan*. In *Metatitan* the I1 and I2 are much smaller and are fully globular in appearance, whereas the I3 is of similar size and morphology as that of *Aktautitan*. There is some evidence of dimorphism in the canines of *A. hippopotamopus*. The canines of KAN N2/875 are larger than those of KAN N2/873 by a greater magnitude than the size differences of most other dental dimensions (appendix 1).

There is a short postcanine diastema with a length slightly less than the mesiodistal length of the P2. The labial enamel wall of the P1 is rounded. There is a large paracone and smaller, more lingually positioned metacone (fig. 6C). The P1 crown is expanded lingually, creating a small platform upon which there may have been a protocone or a small crest on the lingual side of the tooth, but the tooth is too worn to discern these details. The P2, P3, and P4 are about as broad as long and become progressively less oblique posteriorly. In other words, in occlusal view, P2 is somewhat rhomboidal, P3 is less rhomboidal, and P4 is essentially rectangular. The distal and mesial sides of the P2–P4 are essentially parallel. The P2, P3, and P4 possess straight ectolophs (mesostyle absent), labially oriented parastyles, and large rounded protocones. Hypocones are distinctly absent on all premolars. Vestigial paraconules and preprotocristas are evident on P2–P3, but are lacking on P4.

The upper molars of *A. hippopotamopus* possess W-shaped ectolophs and isolated conical lingual cusps that characterize advanced brontothere molars (fig. 6B). The nearly unworn M3 indicates that the ectoloph was rather tall (paracone height ~65 mm). A crown height ratio (paracone height/tooth length) yields a value of 0.67. This value falls among indexes calculated on (nearly) unworn M3s of *Protitan robustus* (0.64), *Rhinotitan mongoliensis* (0.60), and *Embolotherium andrewsi* (0.73). An unworn *Metatitan* M3 is not available.

The inner (lingual) band of enamel of the

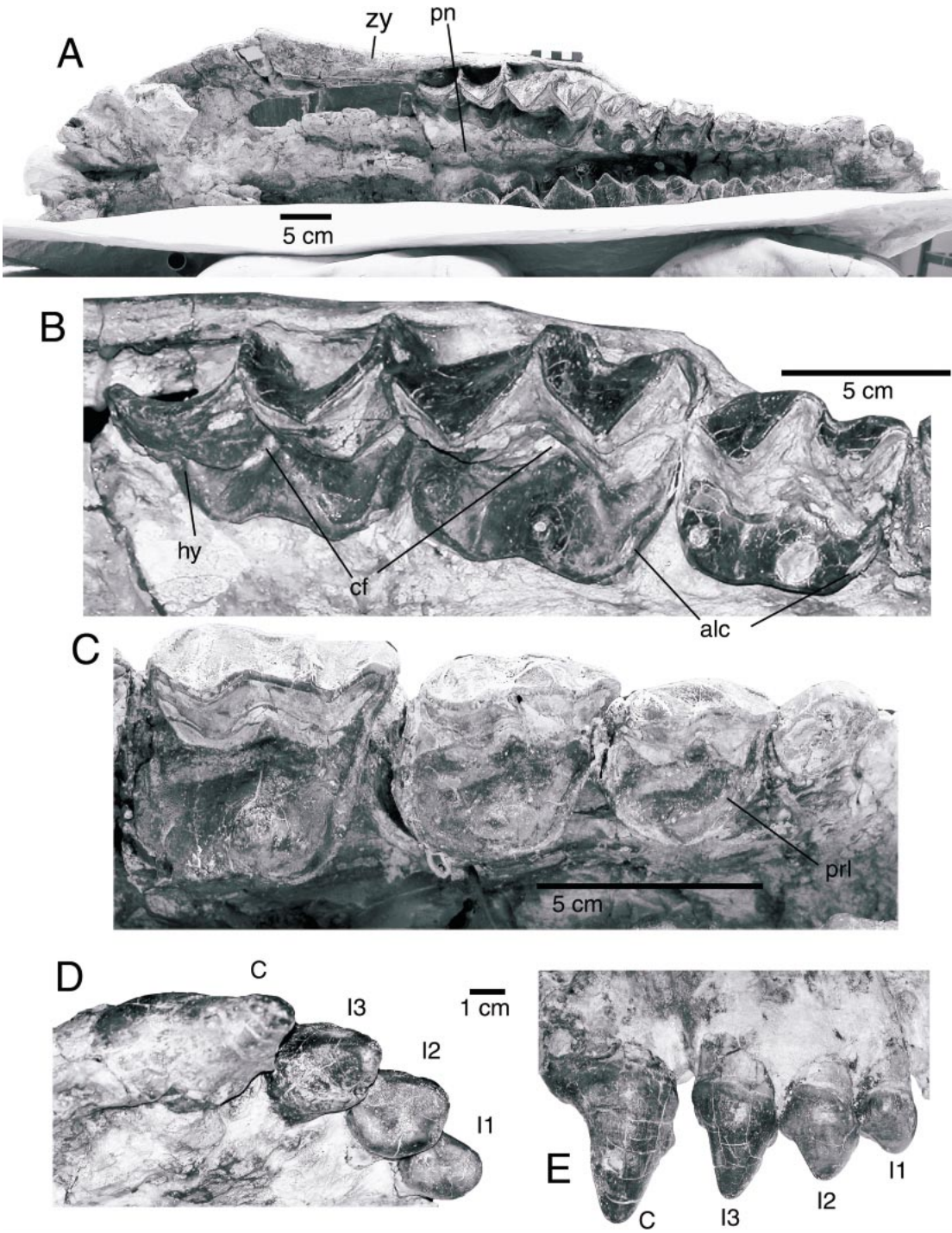


Fig. 6. Ventral view of *Aktautitan hippopotamopus* holotype skull (KAN N2/875). (A) Ventral view of skull, (B) molars, (C) premolars, (D) right incisors and canine, lingual view, and (E) right incisors and canine, labial view.

upper molar ectoloph is extremely thin, much thinner than the outer (labial) band. A thinner inner band of enamel is a character common to all but the most primitive of brontotheres (e.g., *Lambdaotherium* and *Palaeosyops*), where the inner band of enamel is much thicker, particularly around the apices of the paracone and metacone. Hypocones are present on all three molars of *Aktautitan* and are always smaller than the protocone. All vestiges of paraconules, metaconules, proto-lophs, and metalophs are absent on the molars. Each molar has a small, shallow central fossa that is positioned at the lingual base of the ectoloph, directly between the paracone and metacone, and labial to the protocone. This fossa is absent among some hornless brontotheres, and is present among all large, horned brontotheres (Mihlbachler, unpubl. data). The depth of the central molar fossa in *Aktautitan* is similar to that of *Protitan* and *Rhinotitan*. It is much deeper in *Metatitan* and *Embolotherium*. The cingulum on the anterior (mesial) side of the molars rises to a short peak near the anterolingual corner of the crown. This shallow peak is identifiable on M1 and M2 in KAN N2/875 (fig. 6B) by the development of small wear facets on the anterior cingulum. This anterolingual cingular cusp is a distinctive feature common to *Aktautitan*, *Metatitan*, and *Embolotherium*, although it is significantly taller and more distinct in *Embolotherium* in comparison to the other two genera.

MANDIBLE AND LOWER DENTITION

The mandible is rather tall with a tall, slender coronoid process (fig. 7A). The proportions of the ramus are similar to those of *Rhinotitan* and *Metatitan*. The posterior extent of the symphysis is obscured by matrix in KAN N2/875 (fig. 7B). In KAN N2/873 the symphysis extends to below the trigonid of the p4 (fig. 5B). The incisors are short, conical, and recurved with blunt points and thin lingual cingulids (fig. 7D, E). They are packed tightly together. The lower incisors of *Rhinotitan* are similar in size but are more spatulate; those of *Metatitan* are globular and much smaller in size. In *Aktautitan hippopotamopus*, the lingual cingulid is strongest on the central incisors and progressively

weakens in more distal incisors. The incisors are positioned anterior to the canines and the entire anterior toothrow forms a semicircular arch. The i2 is the largest lower incisor. This is most notable in labio-lingual width and crown height.

The only diastema in the lower dentition is the postcanine diastema, which is similar in length to the mesiodistal length of p2. The p1 is mesiodistally elongate with a single cusp (fig. 7C). From p2 to p4 the premolars grade distally into a progressively molari-form morphology. In p2, the talonid and trigonid are nearly the same width. In p3 and p4 the width of the talonid is notably wider than the trigonid. The paralophid of the p2 is short and angles only slightly lingually. In p4 the paralophid is longer and curves lingually a full 90°, as do the paralophids of the molars. The p3 is intermediate in its length and degree of curvature of the paralophid. The p2 lacks a metaconid. The protocristid extends posteriorly and lingually from the apex of the protoconid and joins the cristid obliqua posteriorly and slightly lingually from the protoconid. A small metaconid is present on p3 and is positioned about equally lingually and posteriorly from the protoconid. The cristid obliqua joins the metaconid of the p3. The p4 possesses a fully molari-form metaconid that is positioned mostly lingually from the paraconid. Finally, the hypolophid of the p2 is relatively short and projects posterolingually from the hypoconid at about 45° from an anteroposterior orientation. In p3 and p4 the hypolophids are longer and arch a full 90° from an anteroposterior orientation from the hypoconid.

As a general observation, the lower molars of brontotheres are almost morphologically static and possess few features of taxonomic interest. However, a few noteworthy observations can be made about those of *Aktautitan hippopotamopus* (fig. 7B). Despite the rather tall ectolophs of the upper molars, the lophids of the lower molars are remarkably low, with shallow talonid and trigonid valleys. A thin, beaded cingulid traces entirely around the hypoconulid heel of the m3. The molars of *A. hippopotamopus* are notably elongate. Elongation of the molars is generally thought to correlate to the relative degree of cranial elongation among brontotheres

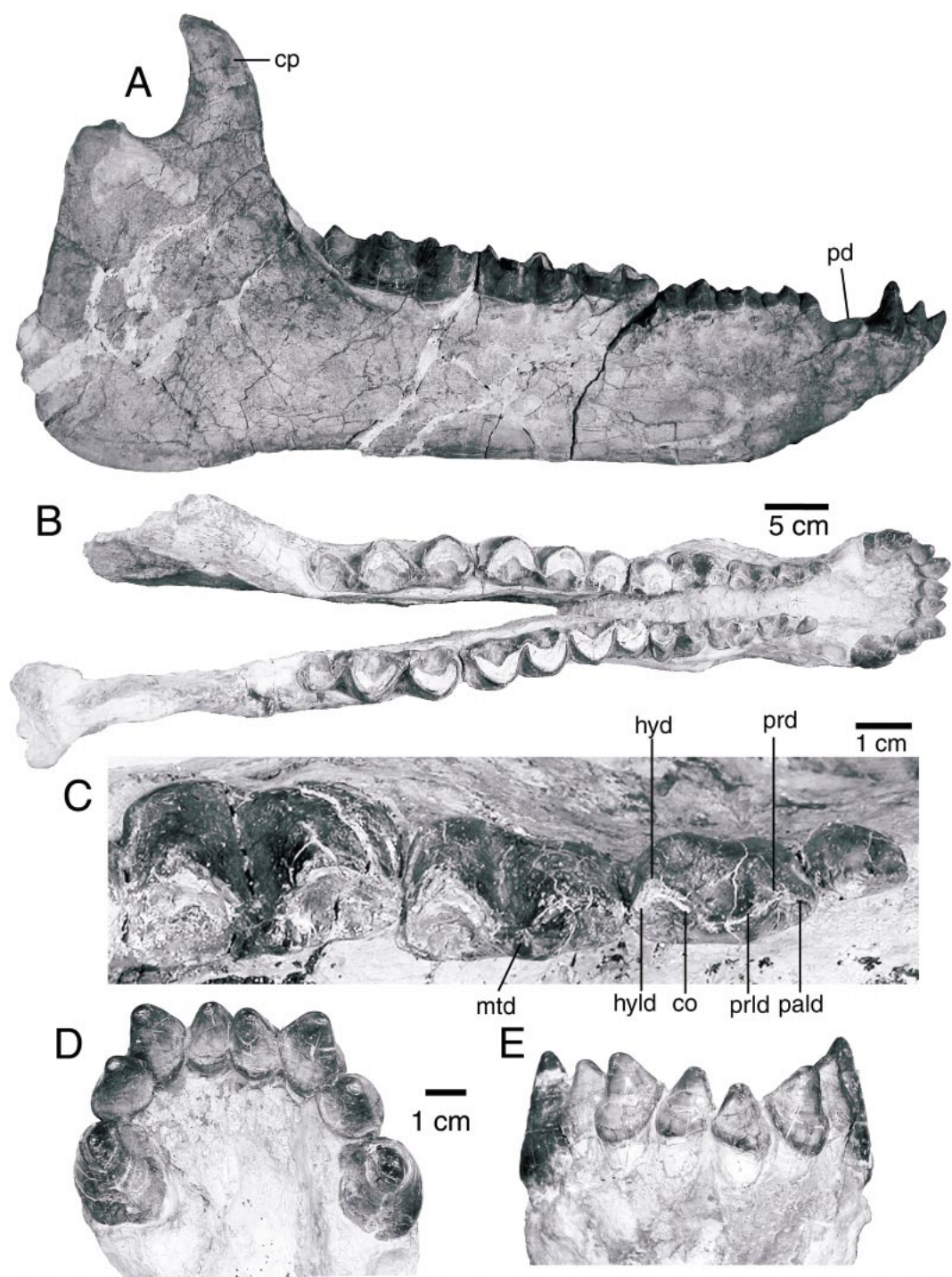


Fig. 7. Mandible and lower dentition of *Aktautitan hippopotamopus* holotype (KAN N2/875). (A) Lateral view of right ramus, (B) anterior view of mandible, (C) premolars, (D) incisors and canines, lingual view, and (E) incisors and canines, labial view.

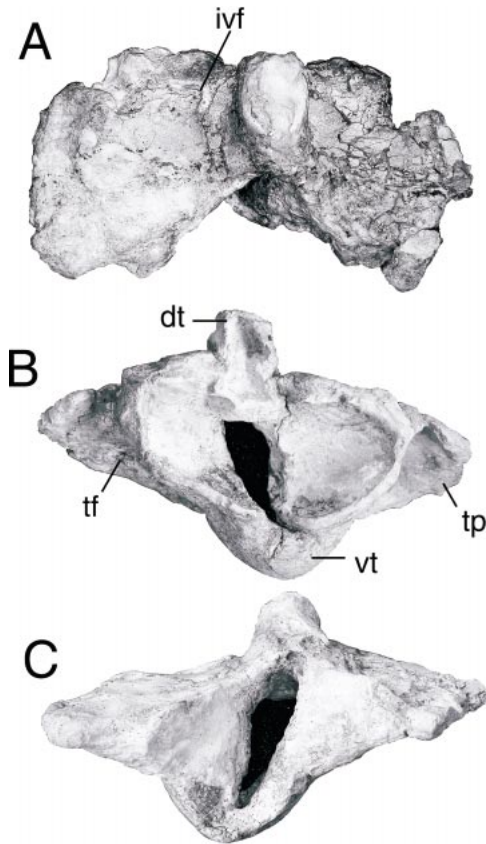


Fig. 8. Atlas of *Aktautitan hippopotamopus* holotype (KAN N2/875). (A) Anterior view, (B) anterior view, and (C) posterior view.

(Osborn, 1929a). Molar elongation in brontotheres is most evident in the m3, where the length/width ratio varies from a minimum of 1.59 (*Eotitanops borealis*) to a maximum of 2.94 (*Gnathotitan berkeyi*) (Mihlbachler, unpubl. data). The m3 of *A. hippopotamopus* is among the most elongate among brontotheres with a length/width ratio of 2.93. This ratio is similar in magnitude to a number of middle and late Eocene Asian brontotheres, including *Protitan*, *Microtitan*, *Gnathotitan*, *Rhinotitan*, *Metatitan*, and *Embolotherium*.

VERTEBRAE

The atlas (fig. 8) has been laterally compressed and the transverse processes are partial, preventing measurement of transverse width. The dorsal and ventral arches support tall, massive medial tubercles, although the

height of these tubercles seems exaggerated by the lateral distortion. The intervertebral foramen is visible on the dorsal surface of the left lateral mass and is similar in size to that of other brontotheres. The transverse foramen is large in early brontotheres such as *Telmatherium* and *Palaeosyops*, but is lost in many late Eocene North American brontotheres (e.g., *Brontops*) (Osborn, 1929a). The transverse foramen is visible in the atlantes of *Rhinotitan mongoliensis* and cf. *Parabrontops gobiensis*. In *Aktautitan hippopotamopus*, damage to the specimen complicates description of the transverse foramen, but it is evident that it was either very small or absent. A small dimple can be seen on the ventral surface of the right lateral body in the position where the vertebral artery would be expected to pierce the atlas, but there is no sign of the transverse foramen on the posterior side of the lateral body where the vertebral artery would be expected to exit the atlas. There is an additional cervical vertebra with a relatively short neural spine, a transversely wide but anteroposteriorly short centrum, and steeply angled prezygophyses (fig. 9A, B). Two thoracic vertebrae have been completely removed from the matrix block, one with a very tall, posteriorly angled neural spine (fig. 9C, D) and one with a much shorter neural spine (fig. 9E, F). Preservation of these elements is poor, but the sizes and proportions are similar to those of other large brontotheres, including *Rhinotitan mongoliensis* and cf. *Parabrontops gobiensis*.

FORELIMB

Both scapulae (fig. 10) of the holotype are nearly complete. Both are figured because, together, they allow a complete description of its shape. The scapular neck is short and broad. The supraspinous fossa is narrower than the infraspinous fossa. The anterior border is slightly curved. The posterior border is triangular in outline. The infraspinous fossa widens proximally from the glenoid cavity and reaches its widest point about two-thirds of the length of the scapula from the glenoid cavity. Proximal to this point, the infraspinous process narrows. The anterior margin of the scapula is rounded. These characteristics

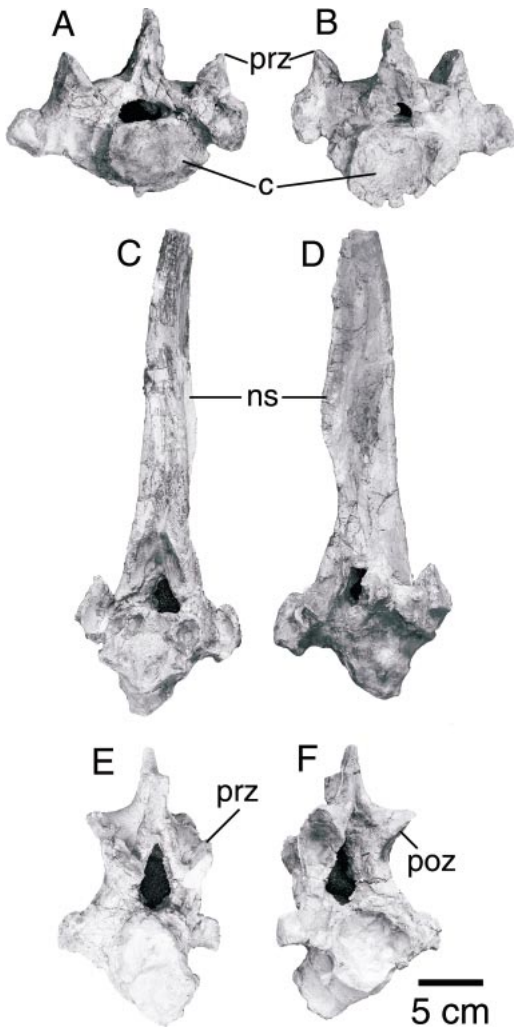


Fig. 9. Vertebrae of *Aktatitan hippopotamopus* holotype (KAN N2/875). (A) Cervical, anterior view, (B) cervical, posterior view, (C) thoracic, anterior view, (D) thoracic, posterior view, (E) thoracic, anterior view, and (F) thoracic, posterior view.

are typical of brontothere scapulae (Osborn, 1929a). The shape and proportions, particularly the very wide, triangular infraspinous fossa, are similar to the scapulae of *Brontops robustus* and *Metatitan relictus*. The scapula of *Rhinotitan* is somewhat narrower and resembles more closely those of hornless brontotheres, particularly that of *Dolichorhinus*.

The humerus (fig. 11) is similar in appearance to that of *Rhinotitan* and *Metatitan*

relictus. It is relatively short and highly constricted at the midshaft. The lateral tuberosity is anteroposteriorly wide, but transversely it is slender and rises well above the humeral head. The deltoid tuberosity does not rise higher in relief than the deltoid crest that connects it with the lateral tuberosity. This differs markedly from that of *Brontops*, where the deltoid tuberosity stands much higher than the deltoid crest, forming a distinct tubercle. On the distal end of the humerus, the lateral epicondyle is large, rugose, and expanded laterally. The olecranon fossa is very wide. The trochlea itself is very shallow and is markedly asymmetrical, with the medial condyle being larger than the lateral condyle.

The articulated lower elements of the forelimb, distal to the humerus, of the holotype (KAN N2/875) remain in the large block of matrix and are not readily described. However, the articulated lower forelimbs of KAN N2/873 (fig. 12) are readily described. The radius and ulna appear to have been relatively straight and are not notably different from those of other brontotheres. The olecranon process of the ulna is missing. The fully articulated forefoot indicates a digitigrade foot of graviportal proportions, with four digits. The articulated and heavily cemented state of the carpals prevents a detailed description of individual articular facets, but from what can be discerned, the articular relationships of the individual carpals are essentially the same as those of other brontotheres. The carpus is relatively broad, but not as flattened as those of *Embolotherium andrewsi* or *Brontops robustus*. The metacarpals are remarkably short and stout, more so than any other brontothere for which a relatively complete manus is known, although this effect has been exaggerated by vertical crushing of the left manus. The proportions of the metacarpals of the right manus are more nearly intact.

HINDLIMB

The innominate (fig. 13) is relatively slender and somewhat intermediate in its length. The superior border of the iliac crest is rugose, but the iliac blade is relatively narrow and slender. The iliac crests of *Brontops robustus*, *Metatitan relictus*, and *Rhinotitan*

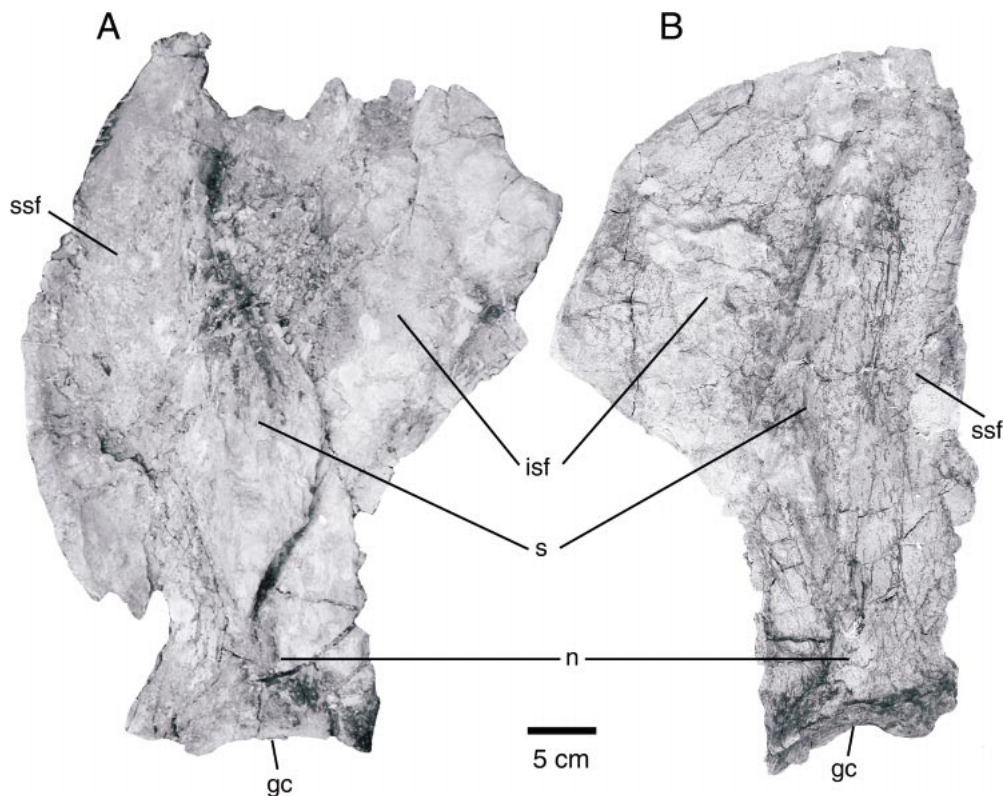


Fig. 10. Scapulae of *Aktautitan hippopotamopus* holotype (KAN N2/875). (A) Left, (B) right.

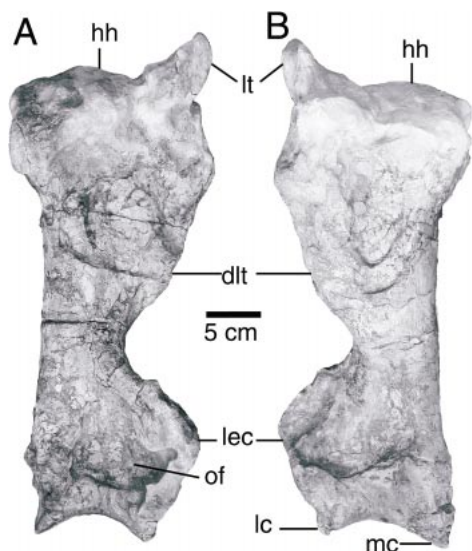


Fig. 11. Right humerus of *Aktautitan hippopotamopus* holotype (KAN 2/875). (A) posterior view, (B) anterior view.

mongoliensis are broader, although it is not known how much of this difference is a result of distortion. The proportions of the iliac shaft and the remainder of the innominate are more intact. They are similar in proportion to those of *Metatitan relictus* and *Rhinotitan mongoliensis*, which in turn are similar to those of hornless brontotheres such as *Telmatherium validus* and *Dolichorhinus hyognathus*. The iliac shaft of *Brontops robustus* is shorter and broader, whereas those of very primitive brontotheres, such as *Palaeosyops*, are longer and more slender.

Both femora (fig. 14) are preserved in the holotype but are distorted in different ways; the left femur is crushed vertically, and the right side is crushed anteroposteriorly. Due to the distortion, the two bones are of different lengths. The left specimen is artificially shortened due to the vertical collapse of the head of the femur, but both femora are nearly

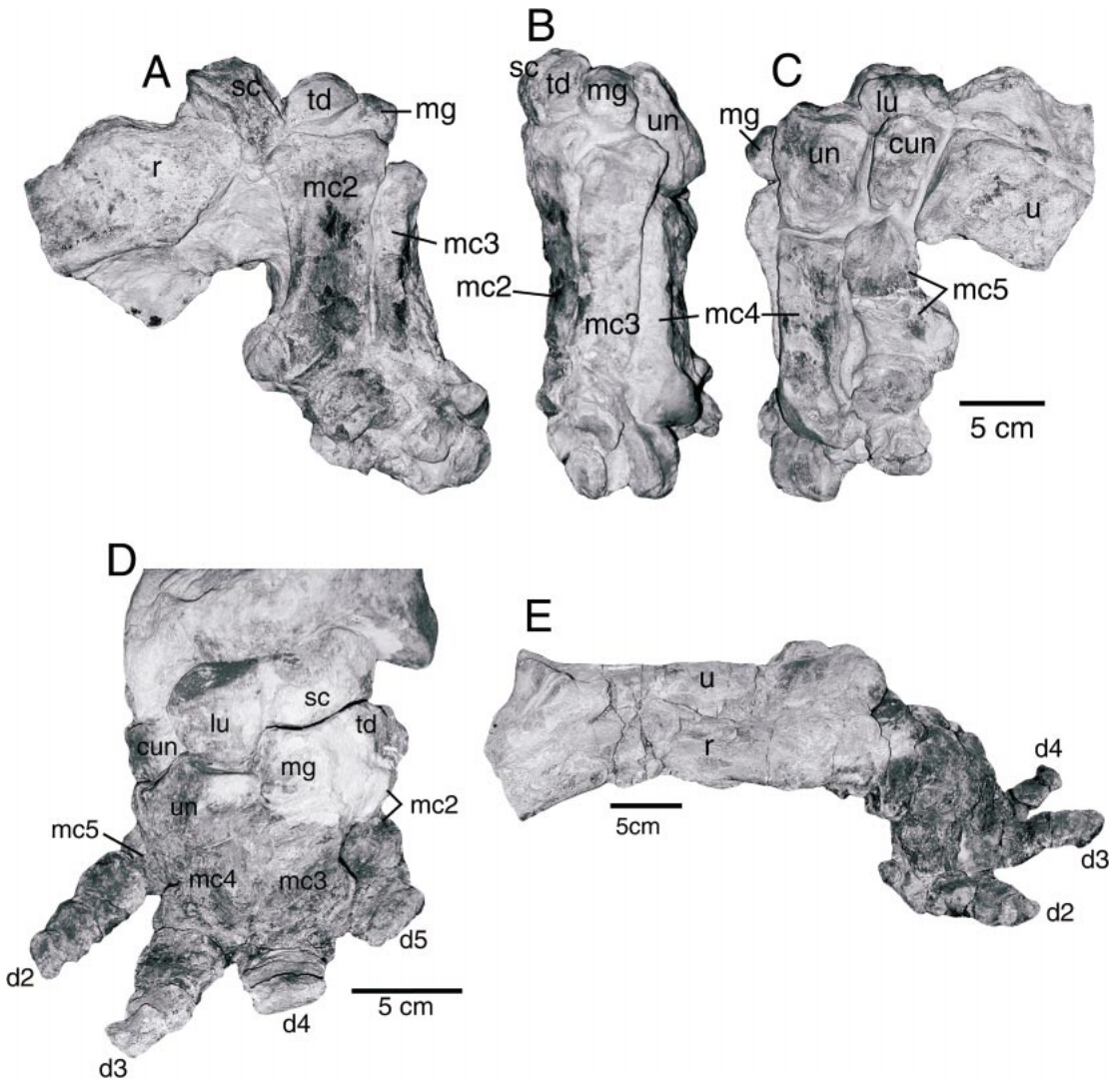


Fig. 12. Lower forelimb and manus referred to *Aktautitan hippopotamopus* (KAN N2/873). (A) Left manus, medial view, (B) left manus, anterior view, (C) left manus, lateral view, (D) right manus, anterior view, (E) and right lower forelimb, medial view.

proportionate in length from the distal end to the third trochanter. The right femur seems to more closely approximate the true length. Notable aspects of femoral morphology of *Aktautitan hippopotamopus* are the nearly flat femoral head, the curved shaft, and the very small, indistinct second and third trochanters. The third trochanter is much lower on the shaft than the second trochanter.

More primitive, hornless brontotheres differ from *A. hippopotamopus* in having a

more spherical head and more prominent second and third trochanters. *Rhinotitan mongoliensis* and *Metatitan relictus* differ from *A. hippopotamopus* in similar respects, although the trochanters of these species are intermediate in size. (Note that the femoral head of *Metatitan relictus* is unknown). The femur of *Brontops robustus* is straighter than that of *A. hippopotamopus*, and the third and second trochanters are more nearly opposite each other, although the sphericity of the

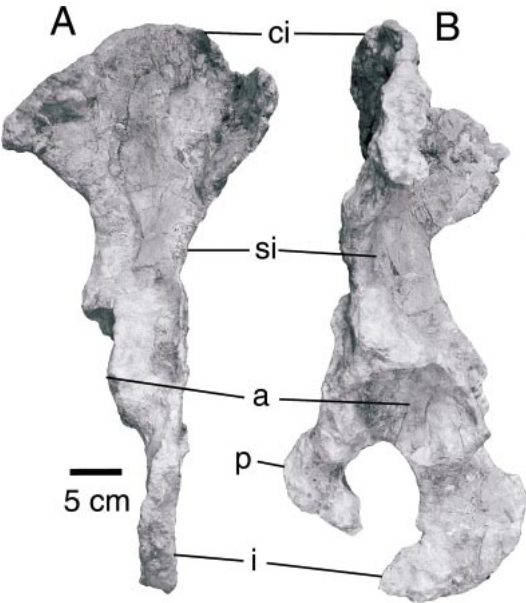


Fig. 13. Left innominate of *Aktautitan hippopotamopus* holotype (KAN N2/875). (A) posterior view, (B) lateral view.

femoral head of *Brontops robustus* is similar to that of *A. hippopotamopus*. The distal end of the left femur of *A. hippopotamopus* is intact. The medial side of the distal extremity of the femur is significantly wider antero-posteriorly than the lateral side. This is partly due to a medial trochlear ridge and a medial condyle that are larger than the lateral counterparts. Although there is some variability in the degree of asymmetry of the trochlea of the distal femur among brontotheres, the degree of asymmetry never approaches the extreme asymmetry found in the distal femoral trochlea among horses and rhinos (Hermanson and MacFadden, 1996).

The patella (fig. 15) is rather narrow, much more so than that of extant horses and rhinos, as are those of other brontotheres. The patella of KAN N2/875 has a flat superior margin and a prominent apex. The lateral margin is relatively flat, and the mesial margin is strongly rounded. These characteristics fall within the range of brontothere patellar morphologies. The superior surfaces of brontotheres patellae are sometimes slightly concave (e.g., *Brontops robustus*). The mesial and lateral margins can be slightly concave as well (e.g., *Rhinotitan mongoliensis*), giving the

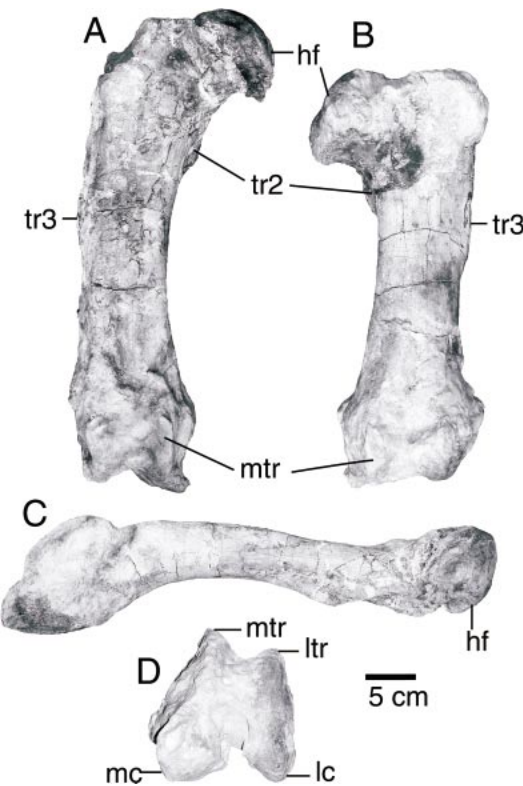


Fig. 14. Femora of *Aktautitan hippopotamopus* holotype (KAN N2/875). (A) Left, anterior view, (B) right, anterior view, (C) right, medial view, and (D) left, distal view.

patella a somewhat “waisted” appearance, although this is not the case in *A. hippopotamopus*.

The lower elements of the left hind limb (fig. 16) consist of an articulated tibia, fibula, and pes. The tibia is much shorter and stouter

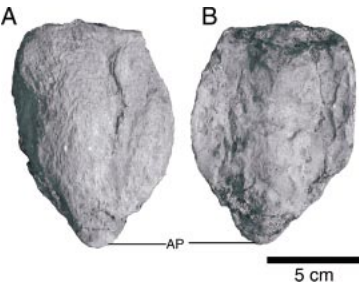


Fig. 15. Right patella of *Aktautitan hippopotamopus* holotype (KAN N2/875). (A) Anterior side, (B) ventral side.

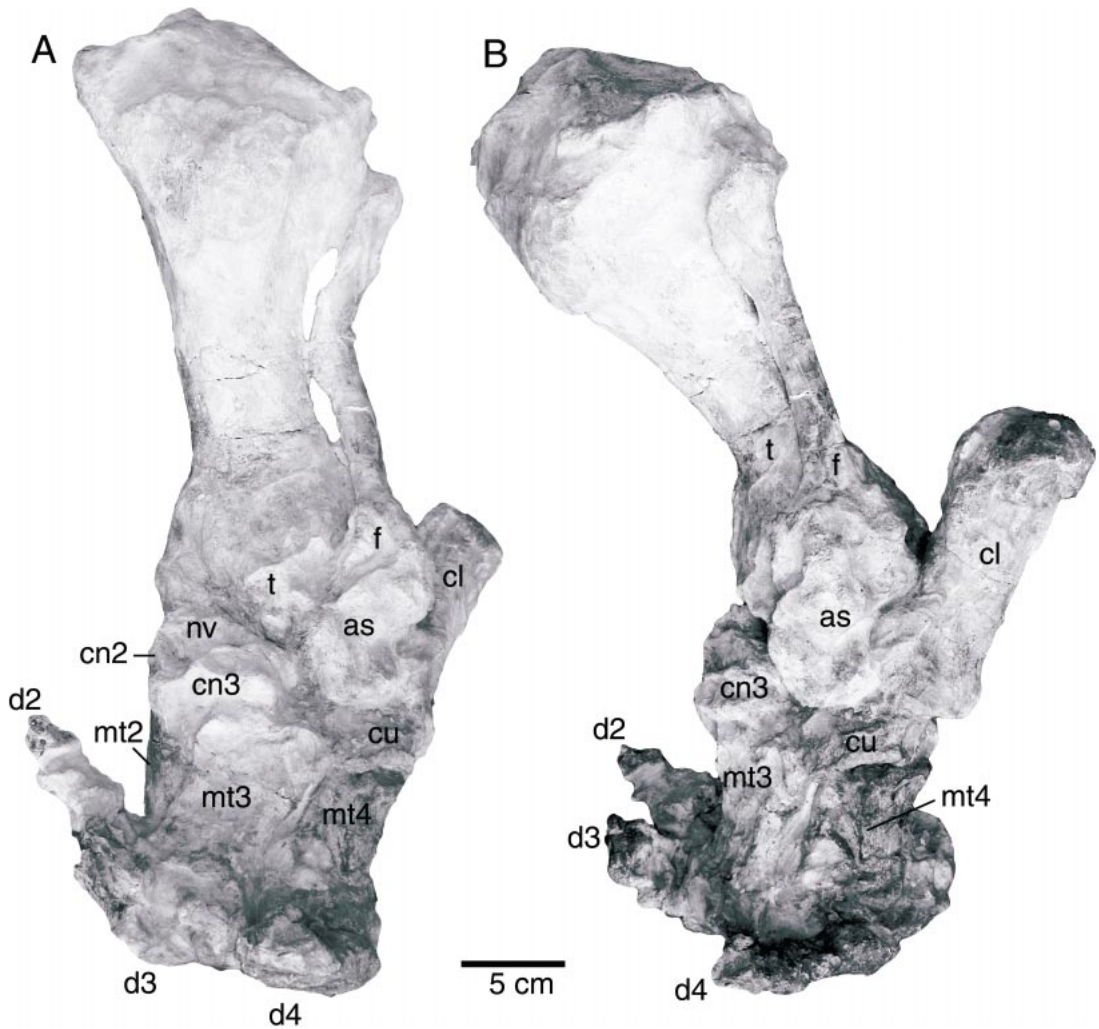


Fig. 16. Lower left hindlimb and pes of *Aktautitan hippopotamopus* holotype (KAN N2/875). (A) Anterior view, (B) posterior view.

than the femur; its relative length is similar to that of other large, horned brontotheres. The metatarsals are very short and flat in proportion to the length of the more proximal limb elements and the calcaneal tuber. The calcaneal tuber is comparatively very long and is actually longer than the third metatarsal. The calcaneum itself is not necessarily derived in this respect; the calcaneal tubers of other brontothere tend to be elongate; however, the very short metatarsals of *Aktautitan* is an extreme condition among brontotheres whose limbs are known. The articulated feet of *Rhinotitan mongoliensis*, cf.

Parabrontops gobiensis, *Brontops robustus* and more primitive hornless brontotheres are taller and more slender.

POSSIBLE AKTAUTITAN TRACKWAYS

Aktautitan? tracks are exposed at Kyzyl Murun near Aktau Mountain (fig. 1) at UTM zone 44, 362307E, 4873406N (datum: WGS 84). They are in the Kyzylbulak Formation in the upper part of unit 26 of the measured section of Lucas et al. (1997: fig. 3) (see fig. 2 of this paper). The track-bearing stratum is a 0.1-m-thick bed of light greenish-gray (5

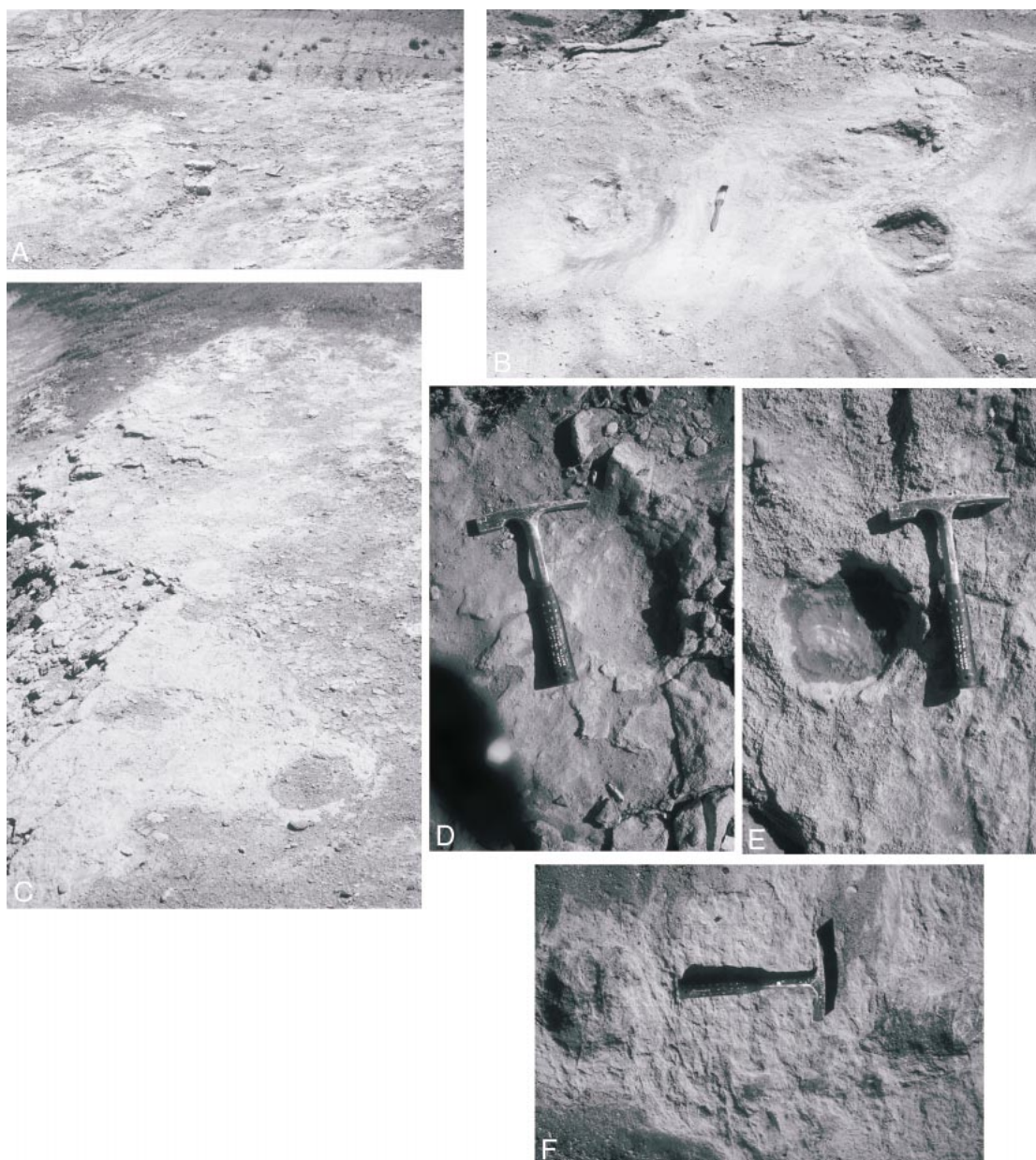


Fig. 17. *Aktautitan?* footprints from Kyzyl Murun in the Ily basin, Kazakhstan. **A–C**, Overviews of multiple tracks on the trampled surface, **D–F**, close-up views of individual tracks. Rock hammer is 28 cm long.

GY 8/1), very fine-grained calcareous silty sandstone that is ~ 0.5 m above the bonebed dominated by the complete, articulated skeletons of *Aktautitan hippopotamopus*.

At Kyzyl Murun, about 100 tracks are preserved as “potholes” in sandstone (fig. 17).

The footprints are preserved in concave epirelief, generally lack clear orientation, and are crowded and superimposed to indicate a trampled surface. All are round, ovoid, or oblong in shape and have diameters of ~ 0.2 m and depths of up to ~ 0.1 m. They lack clear

indications of digits, pads, or hooves and obviously are underprints. A single partial trackway indicates the trackmaker was a quadruped with a gleno-acetabular length of ~ 1.2 m and a trackway width of ~ 0.4 m.

The mammal tracks reported here closely resemble those previously reported Paleogene mammal tracks attributed to brontotheres or rhinoceroses. Thus, the tracks attributed to large perissodactyls and described by Hamblin et al. (1998, 1999) from the Uintan (middle Eocene) of Utah are approximately the same size and shape as those from Kyzyl Murun. Sarjeant and Langston (1994: p. 40–41, pls. 4, 24) described and illustrated large perissodactyl tracks from the Chadronian (late Eocene) of Texas that are larger than, but otherwise very similar to, the Kyzyl Murun tracks. Other tracks attributed to Chadronian brontotheres (e.g., Chaffee, 1943) are also larger than, but similar to, the Kyzyl Murun tracks.

The Kyzyl Murun tracks are undertracks that poorly record the foot shape and other anatomical details of the trackmaker. Thus, a precise identification is impossible, though a large perissodactyl trackmaker seems most likely. Body fossils from the underlying strata of the Kyzylbulak Formation belong to the brontothere *Aktautitan hippopotamopus* and the amynodont rhinocerotoid *Sharamynodon*, both possible trackmakers. Although it is difficult to reconstruct the general body proportions of *A. hippopotamopus* from the material at hand, *Rhinotitan mongoliensis* is of similar size and is known from a mounted skeleton and can therefore be used for size estimates (Wang, 1982). Thus, femur lengths suggest *A. hippopotamopus* is about 70% the size of *Rhinotitan*, which would give *A. hippopotamopus* an estimated gleno-acetabular length of about 1.1 m and manus and pes diameters (minus any fleshy pads) of 14–19 cm. Based on Osborn (1936), *Sharamynodon* has a gleno-acetabular length of 1.4 m and manus and pes diameters (minus fleshy pads) of 16–19 cm. Thus, based on size and foot shape, either *Aktautitan* or *Sharamynodon* are plausible trackmakers of the Kyzyl Murun footprints. The abundance of the brontothere and the relative rarity of the amynodont lead us to suggest that the brontothere was the more probable trackmaker.

The Kyzyl Murun tracks are the first report of fossil mammal tracks from Kazakhstan. They fit well into what is known of Paleogene mammal tracks, namely that they are mostly the footprints of primitive large ungulates and carnivores. Paleogene tracks are known mostly from North America and are dominantly the footprints of primitive perissodactyls, artiodactyls, and carnivores (e.g., Chaffee, 1943; Curry, 1957; Sarjeant and Wilson, 1988; Lucas and Williamson, 1993; Sarjeant and Langston, 1994; Hamblin et al., 1998, 1999). Records from outside of North America—from China, Peru, western Europe, and Iran—also fit this pattern (e.g., Lockley et al., 1999; Ataabadi and Sarjeant, 2000).

PHYLOGENETIC ANALYSIS

Granger and Gregory (1943) presented the first explicit hypothesis of Asiatic brontothere phylogeny (fig. 18A) and regarded the horned members of the family as a single radiation. These were included in the Epimanteocerotinae (paraphyletic) and Embolotheriinae (a monophyletic clade nesting within the Epimanteocerotinae). Granger and Gregory (1943) viewed this radiation as separate from that of the North American horned brontotheres (diplacodonts sensu lato, Mader, 1989). Asian horned brontothere evolution was depicted as a bushlike middle Eocene (Irdinmanhan) radiation stemming from a *Telmatherium*-like North American ancestor. Two temporally persistent lineages extending to the terminal Eocene (considered early Oligocene at the time) were interpreted as rising from the primitive Irdinmanhan horned genus *Protitan*: a *Rhinotitan-Parabrontops-Metatitan* lineage and a separate *Embolotherium* lineage. Yanovskaya (1980) and Wang (1982), using methods no more sophisticated than those of Granger and Gregory (1943), suggested a different hypothesis with a *Protitan-Rhinotitan-Embolotherium* lineage and a separate *Metatitan* lineage originating independently from *Telmatherium* (fig. 18B).

It is widely recognized that Asiatic brontothere phylogeny is minimally understood (Schoch, 1983; Prothero, 1994). The only published cladistic hypotheses of brontothere

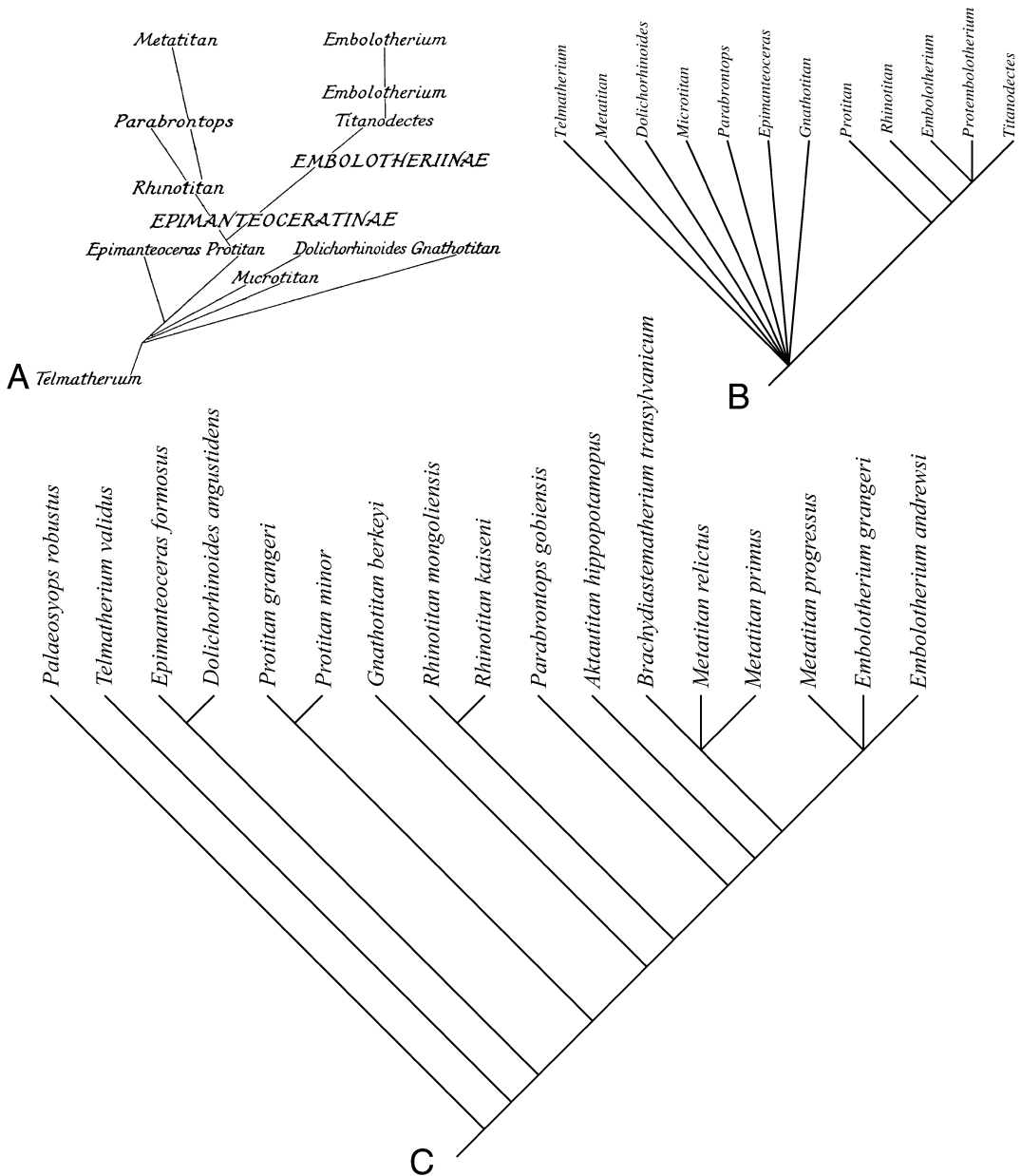


Fig. 18. Phylogenies of Asian and European horned Brontotheriidae (Epimanteocerotinae and Embolotheriinae of Granger and Gregory, 1943). (A) Hypothesis of Granger and Gregory (1943), (B) hypothesis of Yanovskaya (1980), converted to a cladistic representation, and (C) strict consensus of nine trees (97 steps, CI = 0.63, RI = 0.74).

phylogeny exclude Asian taxa (Mader, 1989, 1998). Nevertheless, emerging evidence indicates that North American and Asiatic brontotheres form phylogenetically mixed assemblages, due to several intercontinental

dispersal events in the middle Eocene (Mihlbachler, 2003a). A more comprehensive analysis of brontothere phylogeny will be presented elsewhere, but a preliminary analysis is reported here to gain an initial understand-

ing of Asiatic brontothere interrelationships and the phylogenetic status of *Aktautitan hipopotamopus*.

A cladogram of 17 taxa was generated from 40 characters (23 skull, 8 upper dentition, 2 dentary, 7 lower dentition) with 58 character-state transformations via PAUP version 4.0b10 (Swofford, 2001) utilizing the branch-and-bound search option. The North American Bridgerian brontotheres *Palaeosyops robustus* and *Telmatherium validus* were used as outgroups. *Palaeosyops* is generally regarded as the most primitive brontothere known from abundant fossil material. *Telmatherium* is widely regarded as the ancestor or sister taxon of horned brontotheres of North America and Asia (Osborn, 1929a; Granger and Gregory, 1943; Mader 1989, 1998). *Brachydiastematherium transylvanicum*, the only brontothere known from Europe, was included in the analysis due to its obvious paleogeographic significance in relation to *Aktautitan*.

An analysis with ordered multistate characters (except character 35, which lacked a clear morphoclineal order) yielded nine trees, 97 steps long (CI = 0.62, RI = 0.73), with a relatively resolved strict consensus cladogram (fig. 18C). Inclusion of *Microtitan mongoliensis* generates a substantially less well-resolved tree with a polytomy including *Epimateoceras-Dolichorhinoides*, *Protitan*, and *Microtitan*. This polytomy can be attributed to missing data in *Microtitan*, a taxon known only from cheekteeth. Our results are neither congruent with Granger and Gregory's (1943) phylogenetic hypothesis nor with those of Yanovskaya (1980) and Wang (1982). These earlier hypotheses suggested that *Embolotherium* and *Metatitan* are widely separate lineages. In our tree, *Metatitan* and *Embolotherium* form a robust clade. The genus *Metatitan* is paraphyletic; *Metatitan progressus* groups with *Embolotherium*; and *Brachydiastematherium* resides in an unresolved trichotomy with *Metatitan relictus* (the type species of *Metatitan*) and *Metatitan primus*. *Aktautitan* is the sister taxon to the *Metatitan-Embolotherium-Brachydiastematherium* clade. Remaining taxa form a relatively comb-shaped succession down to the base of the cladogram. The multispecific

genera *Protitan* and *Rhinotitan* were recovered as monophyletic.

TAXONOMIC REVISIONS

Emry et al. (1997), Lucas and Emry (2001), and Emry and Lucas (2002, 2003), based largely on comparison to Yanovskaya (1980), provisionally attributed the Ily Basin brontothere to *Protitan*. This assignment is contradicted by the phylogenetic evidence presented above, but this misdiagnosis has led us to realize a misleading problem with the taxonomic histories of both *Protitan* and *Metatitan*. Yanovskaya (1980) named two new species, *Protitan khaitshinus* and *Protitan reshetovi*, with material from the Khaychin Formation, Mongolia. The referral of these species to *Protitan* seems to have been based on the presence of two characteristics: (1) large paired pits on the ventral surface of the body of the sphenoid and (2) a wide emargination surrounding the anterior and lateral margins of the posterior nares. However, neither character is diagnostic of *Protitan* (sensu Granger and Gregory, 1943). Specimens originally referred to *Metatitan relictus* Granger and Gregory, 1943, including the holotype (AMNH 26391), seem to possess the paired sphenoidal pits as well, although a conclusive interpretation based on the material originally described by Granger and Gregory (1943) is hindered by the state of preservation of the specimens. It is nonetheless possible that *Metatitan relictus* possessed the paired sphenoidal pits seen in *Protitan*. Paired pits on the ventral surface of the body of the sphenoid can also be found in a variety of North American taxa such as *Sphenocoelus uintensis*, *Pseudodiplacodon progressus*, and *Sthenodectes australis* (= ? *Protitanotherium emarginatum*) (Osborn, 1895; Mhlbachler, unpubl. data). Additionally, *Metatitan* and *Embolotherium* share the wide emargination of the posterior nares seen in *Protitan*. Therefore, the criteria used by Yanovskaya (1980) to assign the species *P. khaitshinus* and *P. reshetovi* to the genus *Protitan* are also consistent with *Metatitan*. Further comparison indicates that these species are actually more similar to *Metatitan*.

Protitan Granger and Gregory, 1943 is characterized by a relatively wide flat fore-

head, with small elliptical horns positioned far apart and very low on the skull (fig. 19A, B). The dorsal surface of the skull behind the orbits is convex, and the parasagittal ridges are greatly constricted medially over the sagittal region of the skull. Dentally, *Protitan* is recognizable by its conical upper and lower incisors, often with small diastemas between them, that form a broad arch anterior to the canines, a postcanine diastemata, and a metaconid present only on p4.

Metatitan Granger and Gregory, 1943 can be distinguished from *Protitan* by the more deeply concave forehead, closely positioned, elevated frontonasal horns, and raised nasal process (fig. 19C, D). In *Metatitan*, the region of the skull posterior to the orbits is greatly widened with expanded parietal and squamosal sinuses and a greatly widened occiput. The parasagittal ridges are widely separated over the parietal region. The incisors are reduced in size, and all but the I3 are globular in shape and form a straight line between the canines. A postcanine diastema is absent and a metaconid is present on p3 and p4 (but lacking on p2).

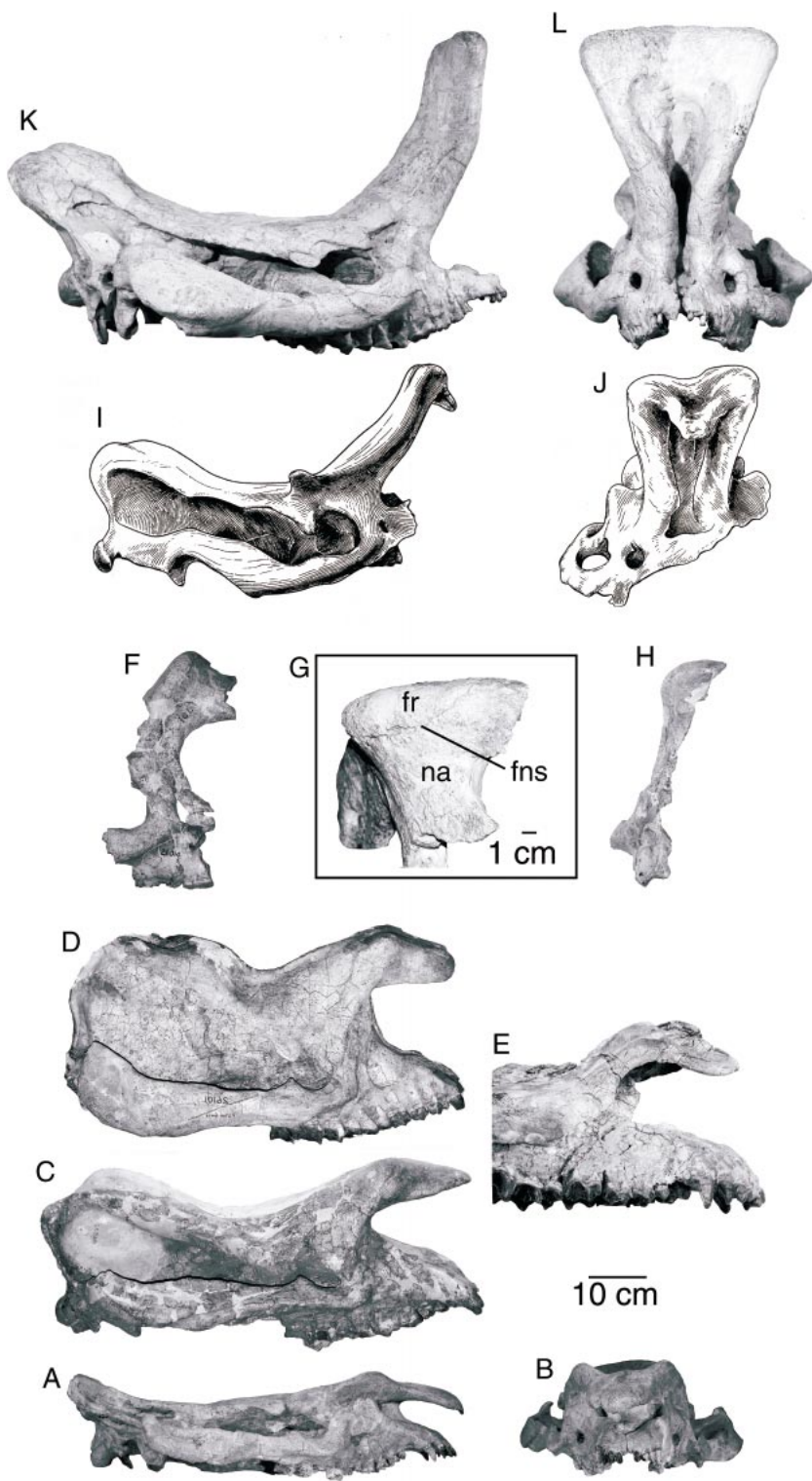
The skulls of *Protitan khaitshinus* (PIN 3745-1, PIN 3745-2) match *Metatitan* in every respect (except the incisors, which are missing) and should be referred to *Metatitan*. Specifically, they most closely resemble *Metatitan relictus*. Therefore, we consider *Protitan khaitshinus* to be a junior objective synonym of *Metatitan relictus*. The skull of *Protitan reshetovi* (PIN 3745-11) possesses a partial set of diagnostic *Metatitan* features, including elevated and closely positioned frontonasal protuberances with elevated nasal processes, no postcanine diastema, and

widely separated parasagittal ridges with a widened occiput. However, the premolars are significantly more molarized than those of *Metatitan relictus*, with two distinct lingual cusps, and the posterior region of the skull lacks the swollen appearance seen in *Metatitan relictus* and *Metatitan primus*. Additionally, the incisors (known only from a partial I3 crown) appear not to have been reduced in size in contrast to *M. relictus* and *M. primus*. In most of these respects, *P. reshetovi* resembles *Aktautitan hippopotamopus*. However, the premolars of *A. hippopotamopus* are significantly less molarized than those of *P. reshetovi*. *Protitan reshetovi* is probably a valid species that is somewhat intermediate in morphology between *Aktautitan* and *Metatitan*. We hesitate to assign it to either of these genera without directly examining the material, but we state with confidence that *Protitan reshetovi* should be removed from the genus *Protitan*.

In addition to these errors, Yanovskaya (1980) referred skeletal material (PIN 3109) from the Ergilin Dzo Formation, Mongolia, to *Metatitan relictus*. The skull (PIN 3109-90), however, does not compare favorably with *Metatitan relictus* Granger and Gregory, 1943. The frontonasal horns and nasal processes are more massive and not highly elevated above the orbits. The anterior margin of the posterior nares is positioned anterior to the M3, the posterior portion of the cranium is not expanded or widened, the zygomatic arch is more massive, there is a postcanine diastema, and the number of incisors is reduced. The description of this material conforms very closely to that of *Parabrontops gobiensis* (Osborn, 1925).

→

Fig. 19. Series of brontothere skulls demonstrating morphological gradation from small, paired frontonasal horns such as those of *Protitan*, to the elevated frontonasal battering ram of *Embolotherium andrewsi*. (A) *Protitan grangeri* (AMNH 20103), right lateral view, (B) *Protitan grangeri* (AMNH 20103), anterior view, (C) "*Metatitan*" *relictus* (AMNH 26399), reflection of left lateral view, (D) "*Metatitan*" *relictus* (AMNH 26101), reflection of left lateral view, (E) *Aktautitan hippopotamopus* holotype (N2/875), right view of face, (F) "*Metatitan*" *progressus* (AMNH 26014), right lateral view, (G) "*Metatitan*" *progressus* (AMNH 26014), dorsal view, (H) "*Metatitan*" *progressus* (AMNH 26014), anterior view, (I) *Protembolotherium efremovi* (PIN 3109-40, from Yanovskaya, 1980), right lateral view, (J) *Protembolotherium efremovi* (PIN 3109-40, from Yanovskaya, 1980), anterior view, (K) *Embolotherium andrewsi* (AMNH 26009), right lateral view, (L) and *Embolotherium andrewsi* (AMNH 26009), anterior view.



The discovery of *Aktautitan hippopotamopus* in the Ily Basin of Kazakhstan does not contribute substantially to the total geographic range of the Brontotheriidae, but it is the first relatively complete brontothere found west of the Gobi and therefore offers significantly improved knowledge of Old World brontotheres toward the western periphery of their distribution. A single specimen of *Brachydiastematherium transylvanicum* Böckh and Maty, 1876, from Andrashaza, Romania, is the only known record of a European brontothere. Although it is known only from its holotype, an incomplete mandible, it is of extraordinary importance because it is the extreme westward occurrence of Old World middle Eocene Brontotheriidae. Lucas (1983) and Lucas and Schoch (1989) considered *B. transylvanicum* a synonym of the North American *Diplacodon*. Although *Diplacodon* is currently recognized as a nomen dubium (Mader, 2000), it was considered at the time to be a senior synonym of another North American genus, *Protitanotherium* (Lucas, 1983). *Protitanotherium* is currently recognized as a valid genus (Mader, 1989); however, *Brachydiastematherium* differs from *Protitanotherium* in two significant ways; there is no postcanine diastema, and the p3 possesses a large molariform metaconid.

The *Metatitan*-like brontothere, *Aktautitan*, from Kazakhstan establishes the occurrence of middle Eocene brontotheres in the region between Europe and the Gobi. It now seems more parsimonious to presume that *B. transylvanicum* shares closer phylogenetic affinities with an Asiatic taxon than with North American *Protitanotherium*. Among these, only *Metatitan* shares with *Brachydiastematherium* the previously mentioned derived conditions, a molariform p3 metaconid, and the lack of a postcanine diastema. The phylogenetic position of *B. transylvanicum* among Asian brontotheres suggests that it is most closely related to, if not synonymous with, *Metatitan relictus* or *Metatitan primus*, rather than *Protitanotherium*. If this hypothesis is further corroborated by more extensive phylogenetic analysis, *Metatitan* Granger and Gregory, 1943 is a junior synonym of *Brachydiastematherium* Böckh and Maty, 1976. At present, we hesitate to judge the taxonomic validity of *Metatitan* pending

a more comprehensive phylogenetic analysis that includes North American brontotheres.

EVOLUTION OF FRONTAL NASAL "RAM" IN EMBOLOTHERIINAE

A limited number of the derived frontonasal characteristics seen in *Metatitan* and *Aktautitan* (frontonasal protuberances and nasal processes elevated on tall superorbital pillars) can be found in other brontothere taxa. For instance, the horns in the North American species *Pseudodiplacodon progressum* and the Asian species *Rhinotitan mongoliensis* are also raised above the orbits on tall superorbital pillars. However, the frontonasal horns remain separate and widely spaced. The nasal processes of *Pseudodiplacodon* are not elevated as in *Aktautitan* and *Metatitan*. The nasal processes of *Rhinotitan* are thicker and are not elevated to the level of the horn peaks as in *Metatitan* and *Aktautitan*. Also, they are angled slightly upward in contrast to the downwardly angled nasal processes of *Aktautitan*. The frontonasal horns of the North American Chadronian brontotheres *Megacerops* and *Brontops* are often connected by a tall crest of bone that stretches transversely between the frontonasal horns and connects them at their bases (Osborn, 1929a). The nasal processes are raised on this crest, and in lateral view the appearance of the entire region bears superficial resemblance to the frontonasal process of *Metatitan* and *Aktautitan*. However, the frontonasal horns of these taxa are massive and widely divergent rather than convergent toward the midline.

Although the exact relationships of Asian brontotheres with North American species is not yet understood, the cladogram topology indicates close phylogenetic affinities between *Aktautitan*, *Metatitan*, and *Embolotherium* and resolves conflicting interpretations made by earlier researchers on the homology of one of the most bizarre cranial specializations in mammalian history, the "battering ram" of *Embolotherium*. Osborn (1929b) believed that the distinctive *Embolotherium* battering ram was a novel structure, formed by an enlarged and uplifted nasal process, and was not homologous to the paired frontonasal horns of other bronto-



Fig. 20. Right lateral view of cranial fragment of a juvenile specimen of *Embolotherium grangeri* (AMNH 26040) (from Osborn, 1929b).

theres, as represented by *Protitan grangeri* (fig. 19A, B). He therefore assigned *Embolotherium* to its own subfamily, Embolotheriinae. Osborn's primary evidence regarding the structural components of the ram came from a juvenile specimen of *Embolotherium grangeri* (AMNH 26040) in which the frontonasal suture was visible on the right side of the skull just above the orbit (fig. 20). Although the frontal appears not to ascend the dorsal surface of the ram, the cranial fragment of the *Embolotherium grangeri* juvenile is too incomplete to determine whether a frontal process rides up over the nasal bone. Realistically, one cannot readily discern from the available specimens whether the ram of *Embolotherium grangeri* incorporates the frontal element. This raises difficulties for phylogenetic reconstruction because one must postulate homologies a priori to analysis. In considering Osborn's (1929b) theory, the ram of *E. grangeri* could be interpreted as a nasal process that has been enlarged and angled upward to nearly 45°, having nothing to do structurally with a frontonasal horn.

The nasal process of *Rhinotitan mongo-liensis* is similarly oriented upward, albeit at a shallower angle. Additionally, the nasal process of *Epimanteoceras formosus*, although thinner and horizontally oriented, is

remarkably similar in other respects to the ram of *Embolotherium grangeri*. Both widen distally, are very rectangular in cross section, and both have a wide flat distal edge. For lack of better evidence, *Embolotherium grangeri* was coded in the phylogenetic analysis as having an enlarged and upwardly angled nasal-process and as lacking frontonasal horns. *Embolotherium andrewsi* was interpreted differently, as explained below.

Following his theory that the *Embolotherium* ram was not homologous to the frontonasal horns, Osborn (1929b: fig. 3C; reprinted in Granger and Gregory, 1943: fig. 7C) illustrated a frontonasal suture in *Embolotherium andrewsi* showing that the ram was formed entirely by the nasal bone. In reexamining the available specimens that preserve the ram (AMNH 26001, 26003, 26009), we conclude that this was an inference rather than a concrete observation. A suture between the nasal and maxilla is clearly identifiable in these specimens as they appear in Osborn's figure, but we cannot locate a discernible frontonasal suture where Osborn (1929b) had inferred it to be.

In contrast to Osborn's idea that the ram was an enlarged nasal bone, Granger and Gregory (1943) interpreted the battering ram as homologous to the paired frontonasal horns of other brontotheres and described a transformational sequence from a *Metatitan*-like configuration to an elevated, fused frontonasal process, with the frontal stretching to the peak of the ram. The nasal process itself was regarded as being absorbed by the transverse crest at the peak of the structure. (Note that despite the similarities between *Metatitan* and *Embolotherium* described by Granger and Gregory, they regarded these taxa as only distantly related, as depicted in their phylogeny shown here in fig. 18A.)

The frontonasal battering ram hypothesis of Granger and Gregory (1943) is supported by a series of taxa that are essentially transitional forms between an *Aktautitan*-*Metatitan*-like morphology and that of *Embolotherium andrewsi*. "*Metatitan*" *progressus* is one of these transitional forms, represented only by a cranial fragment (AMNH 26014) that includes a portion of the orbit, frontonasal process, and a nasal process. The frontonasal process is nearly vertical and in-

intermediate in height between the *Aktautitan-Metatitan* condition and that of *Embolotherium andrewsi* (fig. 19F, H). The frontonasal suture is clearly discernible on the dorsal surface of AMNH 26014, indicating that the frontal bone ascended to the peak of the ram (fig. 19G). At the peak, the frontal bone is joined by the nasal bone in forming a continuous transverse ridge of bone. “*Metatitan*” *progressus* retains a large nasal process, with deeply downfolded lateral sides, that projects anteriorly from the peak of the frontonasal process. A similar groove that could actually be visible remnants of the frontonasal suture is usually visible at the peak of the ram in most specimens of *Embolotherium andrewsi*. This would confirm that the full length of the battering ram of *Embolotherium andrewsi* is indeed formed by both the frontal and nasal bones.

Protembolotherium efremovi Yanovskaya, 1954 is another transitional form further derived toward the direction of *Embolotherium andrewsi* (fig. 19I, J). The frontonasal process forms a large *Embolotherium*-like ram, but this species often retains a small horizontal nasal process elevated at the peak (Yanovskaya, 1980). These morphologically transitional taxa and the apparent remnants of the frontonasal suture in *E. andrewsi* specimens suggest that the ram in this species is best interpreted as homologous to the frontonasal horns of other brontotheres. The actual nasal process appears to have been lost (or “absorbed” in the words of Granger and Gregory, 1943).

Therefore, the battering rams of two *Embolotherium* species are structurally contradictory; one species seems to possess an enlarged and raised nasal process (*E. grangeri*), whereas a series of transitional forms clearly indicates that the ram of *Embolotherium andrewsi* is actually homologous to the frontonasal horns of other brontotheres. Despite

these dissimilarities, which are reflected in multiple characters used in the phylogenetic analysis presented above, these two species, together with “*Metatitan*” *progressus*, form a monophyletic trichotomy and are positioned in a larger clade with *Aktautitan* and other species of *Metatitan*. The recovered phylogeny clearly suggests that the *Embolotherium* ram is likely to have been derived from an *Aktautitan-Metatitan*-like morphology, as Granger and Gregory (1943) conjectured. That the ram of *Embolotherium grangeri* superficially resembles the nasal processes rather than the frontonasal horns of other brontotheres appears to have been a secondarily derived autapomorphic modification.

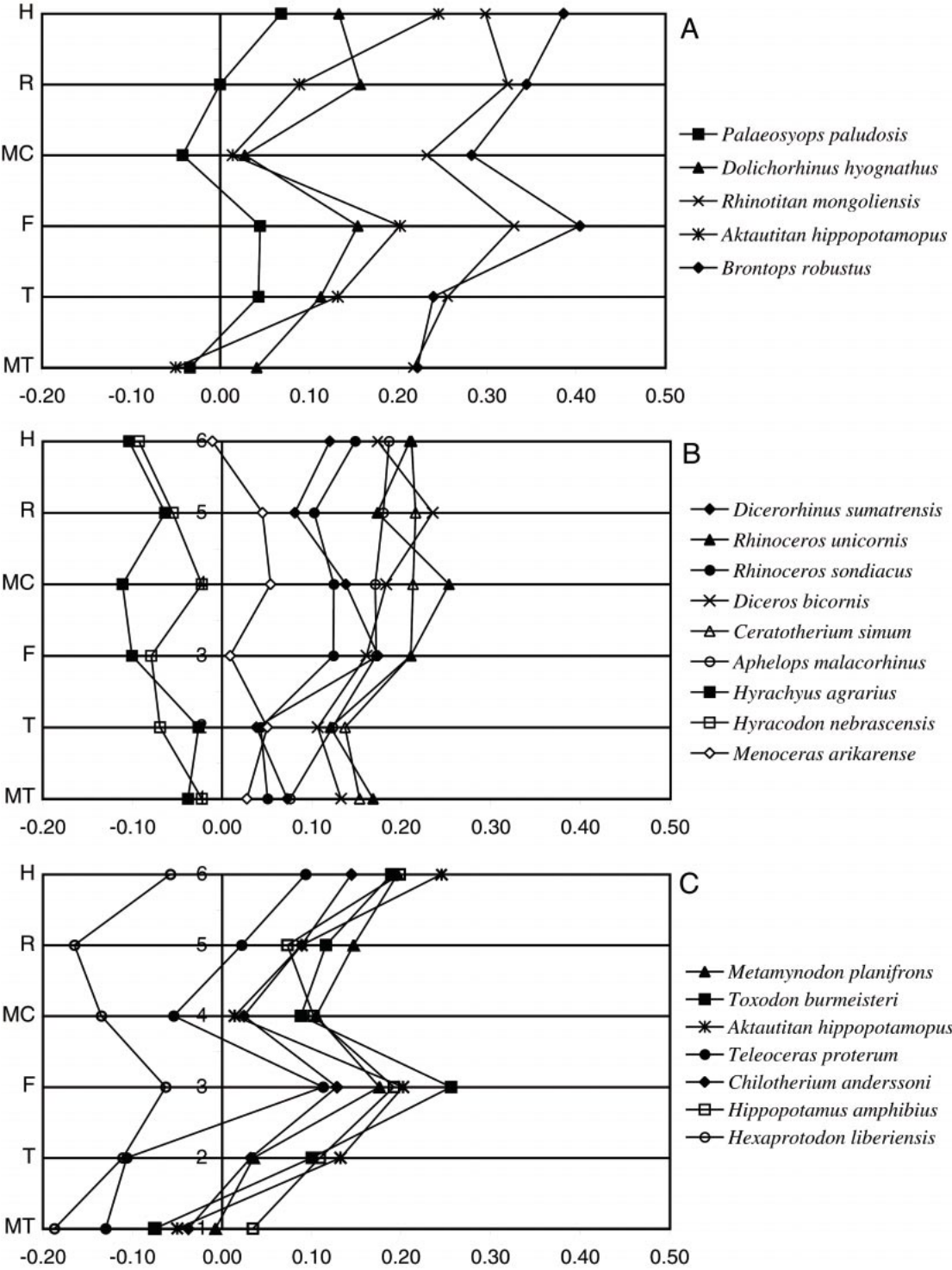
In light of the structural similarities of the frontonasal structures and their apparent common phylogenetic origin, we suggest that the subfamily Embolotheriinae be extended to include *Aktautitan*, *Metatitan*, “*Metatitan*” *progressus*, *Protembolotherium*, and *Embolotherium*, with *Brachydiastematherium* as a provisional member. *Titanodectes*, a somewhat dubious taxon, represented by partial mandibles, may also belong to Embolotheriinae (Granger and Gregory, 1943).

ECOLOGICAL SIGNIFICANCE OF LIMB PROPORTIONS

The limb proportions of *Aktautitan hippopotamopus* are conspicuously short in comparison to other brontotheres, and are convergent upon those of hippos and a variety of other large ungulates (hence, the significance of the trivial name applied to this new species). Log-ratio diagrams (Simpson, 1941) of the main limb segments (humerus, radius, third metacarpal, femur, tibia, and third metatarsal) were constructed to compare the limb proportions of various brontotheres and those of other large ungulates

→

Fig. 21. Log-ratio diagrams of the main limb segments of (A) brontotheres, (B) *Hyrachyus* and various rhinocerotoids, and (C) and a phylogenetically disparate assemblage of species, including extant hippos (*Hippopotamus* and *Hexaprotodon*) and extinct species with hippolike limb proportions including rhinocerotids (*Teleoceras* and *Chilotherium*), an amynodontid (*Metamynodon*), and a notoungulate (*Toxodon*). Abbreviations: (H), humerus; (R), radius; (MC), third metacarpal; (F), femur; (T), tibia; (MT), third metatarsal.



(fig. 21). *Tapirus indicus* was used as the species of reference, so that the y-axis (a straight line) represents the limb proportions of the tapir.

In comparison to the tapir, the central (tibia and radius) and distal (metacarpal and metatarsal) limb segments of brontotheres are proportionately shorter relative to the proximal segments (humerus and femur) (fig. 21A). In two exceptions, *Rhinotitan* and *Dolichorhinus*, the tibia is proportionately longer. *Aktautitan* is an extreme case with greatly shortened distal limb segments. The log-ratios of *Aktautitan* form a broad S-shaped curve. The curves of *Palaeosyops* and *Dolichorhinus* are generally S-shaped as well, but are much narrower than those of *Aktautitan*. The log-ratio curves of *Rhinotitan* and *Brontops* are not S-shaped. Figure 21B displays the log-ratios of various rhinocerotoids and the primitive ceratomorph *Hyrachyus*. The curves of these species are relatively narrow, with proportions similar to that of the tapir.

Brontotheres are often confused as early rhinos by nonspecialists, not only because of the similarity in the position of their horns, but because their body plans are superficially similar. However, it is apparent from the log-ratios that brontotheres have shorter distal limb segments than do modern rhinoceroses. The final log-ratio diagram (fig. 21C) includes the two modern hippo species, *Hippopotamus* and *Hexaprotodon*, and other extinct species that have convergently evolved hippolike limb proportions. Note that the S-shaped curved of *Hexaprotodon* most resembles that of *Palaeosyops*. The curves of *Hippopotamus*, the amynodont rhinocerotoid (*Metamynodon*), two rhinos (*Chilotherium* and *Teleoceras*), and the notoungulate (*Toxodon*) are more broadly S-shaped and closely resemble the curve of *Aktautitan*.

The remarkable similarity in size and proportions of this phylogenetically disparate group of taxa begs the question of the adaptive significance of the unusually shortened limb proportions. Cope (1879) first noted the superficial similarities in limb proportions between *Teleoceras* (a Miocene rhinoceros) and *Hippopotamus*. Osborn (1929a) observed that hippolike proportions had convergently evolved in several extinct large un-

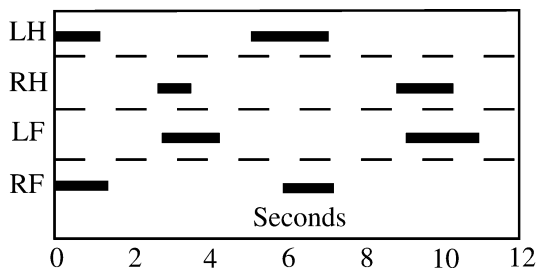


Fig. 22. A 12-second sequence of the submerged gait of an adult hippo reconstructed from video camera footage. The solid lines represent the length of time a particular foot was in contact with the ground. The sequence of steps is analogous to a trotting gait. Abbreviations: (LH), left hindfoot; (RH), right hindfoot; (LF), left forefoot; (RF), right forefoot.

gulates (many of those seen in fig. 21C) and grouped them into a separate locomotor category, graviportal short-limbed digitigrades. Because the only living member of this morphological group was a hippo, Osborn considered these animals semiaquatic. (Semiaquatic animals are those that spend significant proportions of their lives on land and in water but are not fully adapted to either environment). Although Osborn's (1929a) locomotor category has fallen into obscurity, the unusually short-limbed ungulates lumped into this category have been consistently interpreted as semiaquatic hippo-analogs by many paleontologists (Scott, 1913; Troxell, 1921; Simpson, 1980; Webb, 1983; Prothero et al, 1989; Prothero, 1998; Wall, 1998).

Skeletal adaptations of other semiaquatic mammals (e.g., beavers) include increased bone density, shortened hind limbs, and increased hind limb musculature (Stein, 1989). However, the skeletal modifications of most semiaquatic mammals are arguably adaptations for swimming. This argument is invalid for hippos because they do not swim, but rather, perform a peculiar form of "submarine" locomotion best described as running on the bottom substrate (fig. 22). It has been said that hippos cannot float or swim (Eltringham, 1999). To resolve this issue, one of us (M.C.M.) spent several days observing and filming hippos in a large pool (~3 m deep) from behind a glass wall that allows onlookers to view the hippos from a "submerged" point of view at Busch Gardens,

Tampa Bay, Florida. Hippos were never seen swimming at the surface. All locomotor activity involving forward locomotion for more than a few seconds was achieved, literally, by adopting a gait kinematically analogous to the trot of a horse slowed down by at least an order of magnitude. This gait is described in more detail by Mhlbachler (2001). At no time were hippos observed swimming or floating, but quite frequently juvenile hippos were witnessed leaping from the bottom of the pool to the water's surface to reach floating fruit. During these leaps the hippos usually would "dogpaddle" vigorously at the surface, but within a few seconds would begin to sink, rump first. Hippos are known to have denser limb bones than those of similarly sized modern rhinos, due primarily to increased cortical bone thickness (Wall, 1983). This increased density, at least partially, accounts for the apparent inability of hippos to float or swim at the surface. (Note that this conclusion applies to freshwater only. We do not reject the possibility that hippos could achieve buoyancy in denser salt water.)

The shortened limbs of the large hippolike ungulates, therefore, cannot readily be explained as a swimming adaptation. Wall (1999) argued, using lever mechanics, that the shortened limbs provide mechanical advantage for slogging through the muddy substrate of a river, lake, or marsh. Wall's argument that the shortened distal limb elements and elongated input arms, such as the olecranon process and calcaneal tuber, provide greater mechanical advantage is mechanically sound. However, the conclusion that increased mechanical advantage is specifically an adaptation for aquatic locomotion is arguable. All observed hippo locomotion was very slow, about 0.5 meters per second (msec^{-1}), and hippos moving underwater do not appear to be under great strain. Viscous forces would be negligible for objects as large as a hippo, and drag is relatively unimportant at low velocities (Vogel, 1988). Adult hippos trot underwater with a stride frequency of 1 stride every 6–7 sec with suspension phases (total time that no feet touch the ground during a complete stride) lasting about 20% of that time (1.2–1.5 sec). This stride frequency is about 12–14 times slower

than that of trotting and galloping cursorial ungulates (Heglund and Taylor, 1988). Despite a very slow stride frequency and long suspension phases, hippos visibly move through liquid at a constant velocity, confirming that water resistance is nearly an insignificant force at a velocity of 0.5 msec^{-1} . If water had presented a significant resistance force, the hippo's motion would have been noticeably jerky.

Although water was not a significant resistance force to horizontal motion, buoyancy (upward force exerted on a submerged object by the water) severely limits the amount of horizontal (frictional) force that can be exerted during the submerged gait. The weight of a submerged hippo is the difference of its mass and the mass of the equivalent volume of water. Most animals are similar in density to water, and although hippos may be somewhat denser than most vertebrates, their weight underwater would be only a small fraction of their land weight. Because friction is a function of force (weight), the amount of horizontal force a hippo could exert during submerged locomotion is minimized by the reduced amount of friction generated between the feet and the substrate. More horizontal force could be exerted if the feet were planted deeply in mud, but the limited weight would also limit a hippo's ability to do this. For these reasons, the argument that increased mechanical advantage is an adaptation to underwater locomotion is questionable.

Wall (1999) identified other potential semiaquatic adaptations in hippos. The most promising of these includes elevated orbits and reduced thoracic dorsal spines. However, neither of these characters is totally correlated with the occurrence of shortened limbs. While orbital position may indeed be an aquatic adaptation among hippos, none of the extinct large hippolike ungulates in question possesses elevated orbits. (Wall [1999] interpreted *Metamynodon* as having elevated orbits, but the orbital position of *Metamynodon* is, realistically, only subtly different from that of other amynodont rhinos and is less extreme than the raised orbits of a hippo.) Reduced thoracic spines could relate to an aquatic lifestyle because the nuchal ligaments do not support the head and neck

when submerged. *Metamynodon* and hippos share relatively short thoracic spines, but those of *Teleoceras*, *Toxodon*, and *Aktautitan* are remarkably long and do not visibly differ in proportion from those of many brontotheres and rhinoceroses.

Depositional environments are also cited as evidence for the hippo analogy. For instance, the rhinocerotoid *Metamynodon* primarily occurs in sandstone channels (Wall, 1998). *Teleoceras* remains are found in large numbers in fluvial or pond settings (Prothero, 1998). Likewise, the *Aktautitan hippopotamopus* bonebed was found in what appears to be a lacustrine environment. Nevertheless, many mammals (e.g. equids) from the same types of deposits are clearly terrestrial. Nor does the relative abundance of the fossil material occurring in such an environment indicate a hippolike lifestyle. All of the largest living land mammals (hippos, elephants, rhinos) are metabolically dependent on standing water and frequently wallow in shallow water (Owen-Smith, 1988). Extant rhinos, which are all predominantly terrestrial species, tend to die in or near water (Hitchins and Anderson, 1983; Dinerstein and Price, 1991). Thus, the occurrence of large bone beds does not indicate aquatic behaviors different from those of large terrestrial mammals such as rhinos. It has also been argued that the demographic structures of large *Teleoceras* fossil assemblages resemble those of hippos rather than rhinos, supporting the hippo analogy (Mead, 2000). However, it has been subsequently demonstrated that the mortality patterns of *Teleoceras* fossil assemblages are more like those of modern rhinos than those of hippos (Mihlbachler, 2003b). Its remains possible that shortened limbs prevent hippos from becoming fatally mired in mud on banks or in marshes. Elephants are known to become fatally mired (Haynes, 1991), but (to our knowledge) there are no adequate data to compare the frequency of fatal mirings in rhinos and hippos to indicate that the difference between hippo and rhino limb proportions gives hippos a selective advantage against the possibility of fatal mirings. The apparently mired condition of *Aktautitan hippopotamopus* skeletons indicates that this particular species could have been susceptible to mirings, despite the shortened

distal limb segments. (Regarding apparently mired fossil animals such as large extinct ungulates or dinosaurs, the fossil record does not usually reveal whether the miring itself was fatal or if an already sick or weakened animal simply died while in a mired position, but the miring itself was not necessarily the cause of death.)

Hippos emerge from the water at night and are known to travel long distances to feeding areas (Eltringham, 1999). Therefore, hippos expend more energy on terrestrial locomotion than on aquatic locomotion and depend on the terrestrial environment for food. An alternative explanation for the short limbs is as an adaptation for feeding close to the ground. Many grazing ungulates possess a downwardly flexed cranium (Osborn, 1929a; Zeuner, 1945; Loose, 1975). This has been interpreted as an adaptation for grazing on short grasses. The grazing African rhino, *Ceratotherium*, for instance, possesses such a downwardly flexed head orientation. All of the short-limbed ungulates in question, including hippos, retain the horizontal head orientation, but Heissig (1989) suggested, for *Chilotherium*, that shortened limbs are an alternative solution for grazing close to the ground. Most other short-limbed taxa seem to conform to this interpretation. Hippos are short-grass grazers and are short enough to feed close to the ground without kneeling. *Teleoceras* and *Toxodon* retain the horizontal head orientation. Both possess relatively hypsodont molars and have been interpreted as grazers or mixed feeders from isotopic evidence (MacFadden and Shockey, 1997; MacFadden, 1998). However, *Aktautitan* contradicts the grazing hypothesis for the origin of hippolike limb proportions. Dental microwear patterns of brontotheres indicate that all brontotheres were leaf-dominated browsers (Mihlbachler, 2002). Microwear analysis has not been done on *Aktautitan*, although the dental morphology and macroscopic wear of the teeth offer no indication that the diet of *Aktautitan* was unusual. Additionally, all brontotheres lived before the spread of grass-dominated ecosystems (Jacobs et al., 1999). *Aktautitan*, nonetheless, might have specialized in feeding on very low browse. The minimal amount of wear on its incisors suggests that cropping low ter-

restrial plants was not a significant aspect of its feeding behavior. It remains possible that *Aktautitan* fed on low, soft aquatic vegetation and thus benefited energetically from shortened limbs. However, this interpretation is little more than speculation.

Unfortunately, we cannot reach a strong conclusion on the ecological significance of the hippolike limb proportions in *Aktautitan* and other extinct “hippo-ecomorphs”. Neither the semiaquatic or grazing hypotheses are entirely satisfactory, although the grazing hypothesis is congruent with the probable grazing adaptations of most of the hippolike taxa and is entirely testable (e.g., with dental microwear techniques). It is entirely possible that there is no single adaptive explanation for these convergent limb configurations. Due to the dubious paleoecological significance of this character, we do not recommend that it be used to infer a semiaquatic lifestyle for *Aktautitan* or any other extinct hippolike ungulate, as has been frequently done in the past.

ACKNOWLEDGMENTS

The National Geographic Society and Charles Walcott Fund of the Smithsonian Institution supported fieldwork in Kazakhstan. In 1996, Alexander Slovar of the Institute of Geology, Academy of Sciences of Kazakhstan, provided much assistance in collecting specimens in the field and later facilitated shipping of the 1996 specimen to Washington, DC. For assistance in fieldwork in 1997 in Kazakhstan, we thank Pyruza Tleuberdina and Dmitry Malakhov of the Laboratory of Paleozoology of the Institute of Zoology of Kazakhstan, and Dr. Irina Koretsky and Steven Jabo of the National Museum of Natural History, Smithsonian Institution. Preparation and casting of the specimens in Washington, DC was by Frederick Grady, Peter Kroehler, and Steve Jabo of the USNM Vertebrate Paleontology Preparation Laboratory, and by Seth Honig, a volunteer in the same laboratory. Jin Meng (AMNH), Dave Webb (FLMNH), and Linda Gordon (NMNH) provided access to specimens that in their care. Denny Dively, Rick Edwards, Robert Evander, and Carl Mehling assisted in repairing, photographing, and re-curating many of the

large AMNH brontothere specimens, making them much more accessible to researchers. Chad Schennum provided some assistance on postcranial measurements of the *Aktautitan hippopotamopus* specimens. Mariko Mhlbachler assisted with the collection of data on hippo locomotion. Brian Beatty participated in valuable discussion with the senior author regarding aspects of hippo locomotion. Finally, we thank Bryn Mader and Don Prothero for kindly reviewing the manuscript.

REFERENCES

- Ataabadi, M.M., and W.A.S. Sarjeant. 2000. Eocene mammal footprints from eastern Iran: a preliminary study. *Comptes Rendus de l'Academie des Sciences Series II A. Sciences de la Terre et des Planetes Paris* 331: 543–547.
- Böckh, J. 1876. *Brachydiastematherium transylvanicum* Böckh et Maty, ein neues Pachydermen-Genus aus den eocänen Schichten Siebenburgens. *Mitteilungen aus dem Jahrbuch der Ungarischen Geologischen Anstalt* 4: 125–150.
- Chaffee, R.G. 1943. Mammal footprints from the White River Oligocene. *Notulae Naturae (Philadelphia)* 116: 1–13.
- Colbert, E.H. 1938. Fossil mammals from Burma in the American Museum of Natural History. *Bulletin of the American Museum of Natural History* 74: 255–436.
- Cope, E.D. 1879. On the extinct rhinoceroses and their allies. *American Naturalist* 13: 771a–771j.
- Curry, H.D. 1957. Fossil tracks of Eocene vertebrates, southwestern Uinta basin, Utah. In O.G. Seal (editor), *Guidebook to the geology of the Uinta Basin*: 42–47. Intermountain Association of Petroleum Geologists.
- Dehm, R., and T.Z. Oettingen-Spielberg. 1958. Die mitteleocänen Saugertiers von ganda Kas bei Basal in Nordwest Pakistan. *Bayerische Akademie Der Wissenschaften, New Series* 91: 1–54.
- Dinerstein, E., and L. Price. 1991. Demography and habitat use of the greater one-horned rhinoceros in Nepal. *Journal of Wildlife Management* 55: 401–411.
- Eberle, J.J., and J. E. Storer. 1999. Northernmost record of brontotheres, Axel Heiberg Island, Canada—implications for age of the Buchanan Lake Formation and brontothere paleobiology. *Journal of Paleontology* 73: 979–983.
- Eltringham, S.K. 1999. *The hippos: natural history and conservation*. London: Academic Press.
- Emry, R.J., and S.G. Lucas. 2002. Brontothere

- (Mammalia, Perissodactyla) footprints from the Eocene of the Ily Basin, Kazakstan. *Journal of Vertebrate Paleontology* 22(suppl.): 51A.
- Emry, R.J., and S.G. Lucas. 2003. New ceratomorphs (Mammalia, Perissodactyla) from the Eocene of the Ily Basin, Kazakstan. *Journal of Vertebrate Paleontology* 23(suppl.): 48A.
- Emry, R.J., S.G. Lucas, and B.U. Bayshashov. 1997. Brontothere bone bed in the Eocene of eastern Kazakstan. *Journal of Vertebrate Paleontology* 17(suppl.): 44A.
- Gazin, C.L. 1942. A new titanotheres from the Eocene of Mississippi with notes on the correlation between the marine Eocene of the Gulf Coastal Plain and continental Eocene of the Rocky Mountain region. *Smithsonian Miscellaneous Collections* 101: 1–13.
- Granger, W., and W.K. Gregory. 1943. A revision of the Mongolian titanotheres. *Bulletin of the American Museum of Natural History* 80: 349–389.
- Gregory, W.K. 1912. Notes on the principles of quadrupedal locomotion and the mechanism of the limbs in hoofed mammals. *Annals of the New York Academy of Sciences* 22: 267–294.
- Hamblin, A.H., W.A.S. Sarjeant, and D.A.E. Spalding. 1998. A remarkable mammal trackway in the Uinta Formation (late Eocene) of Utah. *Brigham Young University Geology Studies* 43: 9–18.
- Hamblin, A.H., W.A.S. Sarjeant, and D.A.E. Spalding. 1999. Vertebrate footprints in the Duchesne River and Uinta formations (middle to late Eocene), Uinta basin, Utah. *Utah Geological Survey Miscellaneous Publication* 99-1: 443–454.
- Haynes, G. 1991. *Mammoths, mastodons, and elephants: biology, behavior and the fossil record*. Cambridge: Cambridge University Press.
- Heglund, N.C., and C.R. Taylor. 1988. Speed, stride frequency and energy cost per stride: How do they change with size and gait? *Journal of Experimental Biology* 138: 301–318.
- Heissig, K. 1989. The Rhinocerotidae. In D.R. Prothero and R.M. Schoch (editors), *The evolution of perissodactyls*: 399–417. New York: Oxford University Press.
- Hermanson, J.W., and B.J. MacFadden. 1996. Evolutionary and functional morphology of the knee in fossil and extant horses (Equidae). *Journal of Vertebrate Paleontology* 16: 349–357.
- Hitchins, P.M., and J.L. Anderson. 1983. Reproduction, population characteristics and management of the black rhinoceros *Diceros bicornis minor* in the Hluhluwe/Corridor/Umfolozzi game reserved complex. *South African Journal of Wildlife Research* 13: 78–85.
- Holroyd, P.A., and R.L. Ciochon. 2000. *Bunobrontops savagei*: a new genus and species of brontotheriid perissodactyl from the Eocene Pondaung fauna of Myanmar. *Journal of Vertebrate Paleontology* 20: 408–410.
- Jacobs, B.F., J.D. Kingston, and L.L. Jacobs. 1999. The origin of grass-dominated ecosystems. *Annals of the Missouri Botanical Garden* 86: 590–643.
- Kumar, K., and A. Sahni. 1985. Eocene mammals from the upper Subathu Group, Kashmir Himalaya, India. *Journal of Vertebrate Paleontology* 5: 153–168.
- Lavrov, V.V., and G.S. Rayushkina. 1983. Oligotsyen-Miotsyenoviye floronosnii gorizont v raryezye (Ilinskaya vpadina, yuzhnii Kazakhstan) [Oligocene-Miocene floral horizon at the Aktau section (Ily basin, southern Kazakhstan)]. *Doklady Akademii Nauk SSSR* 1983: 397–399.
- Lockley, M.G., and A.P. Hunt. 1995. *Dinosaur tracks and other fossil footprints of the western United States*. New York: Columbia University Press.
- Lockley, M.G., B.D. Ritts, and G. Leonardi. 1999. Mammal track assemblages from the early Tertiary of China, Peru, Europe and North America. *Palaaios* 14: 398–404.
- Loose, H. 1975. Pleistocene Rhinocerotidae of Western Europe with reference to the recent two-horned species of Africa and Southeast Asia. *Palaevothera* 16: 191–212.
- Lucas, S.G. 1983. *Protitanotherium* (Mammalia, Perissodactyla) from the Eocene Baca Formation, west-central New Mexico. *New Mexico Journal of Sciences* 23: 39–47.
- Lucas, S.G., B.U. Bayshashov, L.A. Tyutkova, A.K. Zhamangara, and B.Z. Aubekerov. 1997. Mammalian biochronology of the Paleogene-Neogene boundary at Aktau Mountain, eastern Kazakhstan. *Paläontologische Zeitschrift* 71: 305–314.
- Lucas, S.G., and R.J. Emry. 2001. *Sharamynodon* (Mammalia: Perissodactyla) from the Eocene of the Ily Basin, Kazakstan and the antiquity of Asian amynodonts. *Proceedings of the Biological Society of Washington* 114: 517–525.
- Lucas, S.G., and R.M. Schoch. 1989. European brontotheres. In D.R. Prothero and R.M. Schoch (editors), *The evolution of perissodactyls*: 485–489. New York: Oxford University Press.
- Lucas, S.G., and T.E. Williamson. 1993. Eocene vertebrates and late Laramide stratigraphy of New Mexico. *New Mexico Museum of Natural History and Science, Bulletin* 2: 145–158.
- MacFadden, B.J. 1998. Tale of two rhinos isotopic ecology, paleodiet, and niche differentiation of

- Aphelops* and *Teleoceras* from the Florida Neogene. *Paleobiology* 24: 274–286.
- MacFadden B.J., and B.J. Shockey. 1997. Ancient feeding ecology and niche differentiation of Pleistocene mammalian herbivores from Tarija Bolivia: morphological and isotopic evidence. *Paleobiology* 23: 77–100.
- Mader, B.J. 1989. The Brontotheriidae: a systematic revision and preliminary phylogeny of North American genera. In D.R. Prothero and R.M. Schoch (editors), *The evolution of perissodactyls*: 458–484. New York: Oxford University Press.
- Mader, B.J. 1998. Brontotheriidae. In C.M. Janis, K.M. Scott, and L.L. Jacobs (editors), *Evolution of Tertiary mammals of North America*. Vol. I. Terrestrial carnivores, ungulates, and ungulate-like mammals: 525–536. Cambridge: Cambridge University Press.
- Mader, B.J. 2000. *Pseudodiplacodon*, a new generic name for *Diplacodon progressum* Peterson (Mammalia, Perissodactyla, Brontotheriidae). *Journal of Vertebrate Paleontology* 20: 164–166.
- Mead, A.J. 2000. Sexual dimorphism and paleoecology in *Teleoceras*, a North American Miocene rhinoceros. *Paleobiology* 26: 689–706.
- Mihlbachler, M.C. 2001. Aspects of the Paleobiology of the Neogene Rhinoceroses of Florida. Master's thesis, University of Florida, Gainesville.
- Mihlbachler, M.C. 2002. Body size, dental microwear, and brontothere diets through the Eocene. *Journal of Vertebrate Paleontology* 22(suppl.): 88A.
- Mihlbachler, M.C. 2003a. Preliminary cladistic phylogeny of the Brontotheriidae (Mammalia, Perissodactyla). *Journal of Vertebrate Paleontology* 23(suppl): 78A.
- Mihlbachler, M.C. 2003b. Demography of Late Miocene Rhinoceroses (*Teleoceras proterum* and *Aphelops malacorhinus*) from Florida: linking mortality patterns and sociality in fossil assemblages. *Paleobiology* 29: 413–429.
- Miyata, K., and Y. Tomida. 2003 First discovery of brontotheres from the Eocene of Japan. *Journal of Vertebrate Paleontology* 23(suppl.): 79A.
- Osborn, H.F. 1895. Fossil mammals of the Uinta Basin. Expedition of 1894. *Bulletin of the American Museum of Natural History* 7: 71–105.
- Osborn, H.F. 1925. Upper Eocene and Lower Oligocene titanotheres of Mongolia. *American Museum Novitates* 202: 1–12.
- Osborn, H.F. 1929a. Titanotheres of ancient Wyoming, Dakota, and Nebraska. *United States Geological Survey Monographs* 55: 1–894.
- Osborn, H.F. 1929b. *Embolotherium*, gen. nov., of the Ulan Gochu, Mongolia. *American Museum Novitates* 353: 1–20.
- Osborn, H.F. 1936. *Amynodon mongoliensis* from the upper Eocene of Mongolia: *American Museum Novitates* 859: 1–9.
- Owen-Smith, R.N. 1988. Megaherbivores: the influence of very large body size on ecology. Cambridge: Cambridge University Press.
- Peterson, O.A. 1924. Osteology of *Dolichorhinus longiceps* Douglass, with a review of the species of *Dolichorhinus* in the order of their publication. *Memoirs of the Carnegie Museum* 9: 405–472.
- Pilgrim, G.E. 1925. The Perissodactyla of the Eocene of Burma. *Paleontologia Indica* 8: 1–28.
- Prothero, D.R. 1994. The Eocene-Oligocene transition: paradise lost. New York: Columbia University Press.
- Prothero, D.R. 1998. Rhinocerotidae. In C.M. Janis, K.M. Scott, and L.L. Jacobs (editors), *Evolution of Tertiary mammals of North America*. Vol. I. Terrestrial carnivores, ungulates, and ungulate-like mammals: 595–605. Cambridge: Cambridge University Press.
- Prothero, D.R., C. Guerin, and E. Manning. 1989. The history of the Rhinocerotidae. In D.R. Prothero and R.M. Schoch (editors), *The evolution of perissodactyls*: 321–340. New York: Oxford University Press.
- Qi, T., and K.C. Beard. 1996. *Nanotitan shanghuangensis*, gen. et sp., nov.: the smallest brontothere (Mammalia: Perissodactyla). *Journal of Vertebrate Paleontology* 16: 578–581.
- Ringström, T. 1924. Nashörner der Hipparion-fauna Nord-Chinas. *Palaeontologia Sinica Series C* 1: 1–159.
- Sarjeant, W.A.S., and W. Langston, Jr. 1994. Vertebrate footprints and invertebrate traces from the Chadronian (late Eocene) of Trans-Pecos Texas. *Texas Memorial Museum Bulletin* 36: 1–86.
- Sarjeant, W.A.S., and J.A. Wilson. 1988. Late Eocene (Duchesnean) mammal footprints from the Skyline Channels of Trans-Pecos Texas. *Texas Journal of Science* 40: 439–446.
- Schoch, R.M. 1983. Review of N.M. Yanovskaya, *The Brontotheres of Mongolia*. *Journal of Vertebrate Paleontology* 3: 65–66.
- Scott, W.B. 1913. A history of land mammals in the Western Hemisphere. New York: MacMillan.
- Simpson, G.G. 1941. Large Pleistocene felines of North America. *American Museum Novitates* 1136: 1–27.
- Simpson, G.G. 1980. *Splendid isolation: the curious history of South American mammals*. New Haven, CT: Yale University Press.
- Stine, B.R. 1989. Bone density and adaptation in

- semiaquatic mammals. *Journal of Mammalogy* 70: 467–476.
- Swofford, D.L. 2001. PAUP* (phylogenetic analysis using parsimony [*and other methods] version 4.0b10 [PPC]). Sunderland, MA: Sinauer.
- Takai, F. 1939. Eocene mammals found from the Hosan Coal-field, Tyosen. *Journal of the Faculty of Science Imperial University of Tokyo* 5: 199–217.
- Troxell, E.L. 1921. New amynodonts in the Marsh collection. *American Journal of Science* 5: 21–34.
- Vogel, S. 1988. *Life's devices: the physical world of plants and animals*. Princeton, NJ: Princeton University Press.
- Wall, W.P. 1983. The correlation between high limb-bone density and aquatic habitats in recent mammals. *Journal of Paleontology* 57: 197–207.
- Wall, W.P. 1998. Amynodontidae. In C.M. Janis, K.M. Scott, and L.L. Jacobs (editors), *Evolution of Tertiary mammals of North America*. Vol. I. Terrestrial carnivores, ungulates, and ungulate-like mammals: 583–588. Cambridge: Cambridge University Press.
- Wall, W.P. 1999. Locomotor adaptations in *Metamynodon planifrons* compared to other Amynodontids (Perissodactyla, Rhinocerotidae). *National Parks Paleontological Research* 4: 8–17.
- Wang, B. 1982. Osteology and phylogenetic relationships of *Rhinotitan mongoliensis*. Academia Sinica Institute of Vertebrate Paleontology and Paleoanthropology Memoirs 16: 1–75.
- Webb, S.D. 1983. The rise and fall of the late Miocene ungulate fauna in North America. In M.H. Nitecki (editor), *Coevolution*: 267–306. Chicago: University of Chicago Press.
- West, R.M. 1980. Middle Eocene large mammal assemblage with Tethyan affinities, Ganda Kas region, Pakistan. *Journal of Paleontology* 54: 508–533.
- Yanovskaya, N.M. 1954. A new genus of Embolotheriinae from the Paleogene in Mongolia. *Trudy Paleontologicheskogo Instituta, Akademii Nauk SSSR* 55: 4–43.
- Yanovskaya, N.M. 1980. The Brontotheres of Mongolia. *Trudy Sovmestnaia Sovetsko-Mongolskaia Paleontologicheskaiia Ekspeditsiia* 12: 1–220.
- Zeuner, F.E. 1945. New reconstructions of the woolly rhinoceros and Merck's rhinoceros. *Proceedings of the Linnean Society of London* 156: 183–195.

APPENDIX 1
MEASUREMENTS OF *AKTAUTITAN HIPPOPOTAMOPUS* (mm)

	KAN N2/873	KAN N2/875
SKULL		
Ventral length	750.0	840.0
Incision-postorbital process of jugal, at midline	350.0	360.0
M3-occipital condyles, at midline		380.0
UPPER TEETH		
I1 mesiodistal width	16.2	16.0
I1 labiolingual width	17.7	18.0
I2 mesiodistal width	21.1	20.4
I2 labiolingual width	24.6	22.8
I3 mesiodistal width	25.3	23.9
I3 labiolingual width	25.8	21.4
C mesiodistal width	26.2	34.6
C labiolingual width	19.5	27.3
C crown height	32.6	42.2
P1 anteroposterior length	16.3	19.1
P1 labiolingual width	16.6	14.4
P2 anteroposterior length	29.4	28.0
P2 labiolingual width	28.2	29.2
P3 anteroposterior length	34.9	37.3
P3 labiolingual width	33.8	37.5
P4 anteroposterior length	40.7	45.0
P4 labiolingual width		45.4
M1 anteroposterior length	52.6	61.5
M1 labiolingual width (protocone-mesostyle)		57.0
M2 anteroposterior length	78.2	87.7
M2 labiolingual width (protocone-mesostyle)		68.5
M3 anteroposterior length	99.5	95.9
I1–I3 incisor row length		57.1
P1–P4 length	116.0	128.0
P2–P4 length	99.7	110.0
M1–M3 length	222.0	232.0
P1–M3 length	330.0	360.0
P2–M3 length	315.0	342.0
C–P1 diastema	18.0	
MANDIBLE		
total length	630.0	660.0
height of ascending ramus (from mandibular condyle)		248.0
depth of ramus below M3	109.0	
width of mandible between c and p1		88.3
LOWER TEETH		
i1 mesiodistal width	17.3	20.9
i1 labiolingual width	18.17	18.7
i2 mesiodistal width	23.5	23.1
i2 labiolingual width	22.8	22.3
i3 mesiodistal width	22.3	22.4
i3 labiolingual width	19.6	19.5
c mesiodistal diameter	24.3	32.8
c labiolingual diameter	25.2	31.7
c crown height		46.9
p1 anteroposterior length	18.1	18.9
p1 labiolingual width	12.0	10.9

APPENDIX 1
(Continued)

	KAN N2/873	KAN N2/875	
p2 anteroposterior length	31.0	30.0	
p2 trigonid width	14.6	15.3	
p2 talonid width		17.4	
p3 anteroposterior length	33.6	36.6	
p3 trigonid width		17.5	
p3 talonid width	21.1	22.2	
p4 anteroposterior length	38.4	44.2	
p4 trigonid width	24.7	24.7	
p4 talonid width		27.9	
m1 anteroposterior length	49.8	63.6	
m1 trigonid width	30.9	26.9	
m1 talonid width	38.5	32.2	
m2 anteroposterior length	69.0	79.7	
m2 trigonid width		35.6	
m2 talonid width		40.1	
m3 anteroposterior length		118.5	
m3 talonid + trigonid length (excluding hypoconulid)		82.4	
m3 trigonid width		40.5	
m3 talonid width		39.7	
m3 hypoconulid width		29.5	
i1–i3 length		54.2	
p1–p4 length		124.3	
p2–p4 length		110.5	
m1–m3 length		260.0	
p1–m3 length	352.0	385.0	
p2–m3 length		371.0	
c–p1 diastema	24.2	33.6	

	KAN N2/873	KAN N2/875	
	left	left	right
SCAPULA			
maximum length		520	500
maximum width		370	
glenoid fossa length		130	
HUMERUS			
length (head to medial condyle)		380 ^a	440
length (lateral tuberosity to lateral condyle)		430	470
midshaft (min. circumference)			233
distal width (condyles)			132
distal width (epicondyles)			160
humeral head (anteroposterior)			111
humeral head (transverse) 11.1			114
total proximal width			175
RADIUS			
length	280		
proximal transverse width			135
proximal anteroposterior depth			61 ^a

APPENDIX 1
(Continued)

	KAN N2/873	KAN N2/875	
	left	left	right
MCII			
length	137		
MCIII			
length	124		
MCIV			
length	122		
MCV			
length	98		
INNOMINATE			
total length			640
width of iliac blade			460
FEMUR			
length (head to condyles)		400 ^a	510
midshaft circumference		241	
distal width		160	
head (anteroposterior width)		104	105
head (transverse width)		95	960
PATELLA			
length			120
width			90
TIBIA			
length		300	350
proximal width		142	124
proximal depth		130	NA
midshaft circumference		190	NA
MT2			
MT2 length		111 ^b	830
MT3			
MT3 length		114	107
MT3 proximal width		520	650
MT3 distal width		460	
MT4 length		720	105
MT4 distal width		370	
calcaneum length			148
calcaneal tuber length			102

^aDimension shortened by distortion.

^bDimension expanded by distortion.

APPENDIX 2
LIMB SEGMENT DATA (mm)

Taxon	Specimen	Humerus	Radius	MC3	Femur	Tibia	MT3	Source
<i>Tapirus indicus</i>	?	250	228	120	320	258	120	Gregory, 1912
<i>Palaeosyops paludosis</i>	AMNH 11689	293	228	109	355	285	111	Gregory, 1912
<i>Dolichorhinus hyognathus</i>	CM 11071	340	328	128	457	335	132	Peterson, 1924
<i>Rhinotitan mongoliensis</i>	IVPP V3254	497	480	205	685	465	198	Wang, 1982
<i>Aktaitian hippopotamopus</i>	KAN N2/875 + N2/873	440	280	124	510	350	107	new data
<i>Brontops robustus</i>	YPM 12048	608	504	230	812	448	200	Osborn 1929a
<i>Hyrachyus aeriarius</i>	AMNH 5065	197	197	93	254	243	110	Gregory, 1912
<i>Hyracodon nebrascensis</i>	?	202	210	114	267	220	114	Gregory, 1912
<i>Metanynodon planifrons</i>	AMNH 546	393	320	153	480	280	118	Gregory, 1912
<i>Menoceras arikarene</i>	AMNH (Agate Springs) ^a	244	253	136	327	290	128	new data
<i>Chilotherium anderssoni</i>	composite skeleton	349	280	127	430	278	110	Ringström, 1924
<i>Aphelops malacorhinus</i>	FLMNH (Love Bone Bed) ^a	384	345	178	476	343	143	new data
<i>Teleoceras proterum</i>	AMNH (Mixson's Bone Bed) ^a	310	240	106	415	202	89	new data
<i>Dicerorhinus sumatrensis</i>	NMNH 49561	330	275	165	478	282	142	new data
<i>Rhinoceros sondiacus</i>	NMNH 269392	352	289	160	426	285	135	new data
<i>Rhinoceros unicornis</i>	NMNH 336953	405	340	215	520	341	177	new data
<i>Diceros bicornis</i>	NMNH 162935	373	392	183	464	330	163	new data
<i>Ceratotherium simum</i>	NMNH 164635	407	375	196	520	354	171	new data
<i>Hexaprotodon liberiensis</i>	NMNH 581892	219	156	88	277	200	78	new data
<i>Hippopotamus amphibius</i>	?	395	270	152	498	332	130	Gregory, 1912
<i>Toxodon burmeisteri</i>	AMNH 14943	387	298	147	577	325	101	Gregory, 1912

^aData are composites based on means of a large number of specimens from a single locality.

APPENDIX 3

PHYLOGENETIC CHARACTERS

1. Position of anterior margin of posterior nares: (0) anterior to M3, (1) approximately between the M3 protocone, (2) posterior to the M3.
2. Large paired pits on the ventral surface of the body of the sphenoid: (0) absent, (1) present.
3. External auditory meatus: (0) wide U-shaped opening, (1) constricted ventrally, (2) posttympanic process touching (or nearly touching) postglenoid process, external auditory meatus forming a tube.
4. Posterior nares: (0) not emarginate, (1) narrow emargination, (2) wide emargination.
5. External auditory meati: (0) straight, (1) strongly angled.
6. Dorsal surface of skull (excluding region anterior to orbits): (0) flat or somewhat convex, (1) concave in center of skull, convex in posterior region of skull, (2) completely concave.
7. Parasagittal ridges: (0) nearly make contact over the parietal region but remain separate, (1) remain separated but form a constriction over the parietal region of the skull, (2) are widely separated.
8. Pit or depression between parasagittal ridges: (0) absent, (1) present.
9. Elevation of frontonasal horns: (0) low, horns rest directly above orbits, (1) horns elevated on short superorbital pillars, (2) horns elevated on tall superorbital pillars, (3) frontonasal process extremely elevated.
10. Depth of nasal incision: (0) P2 to P3, (1) P4 to M1, (2) M2.
11. Position of orbit: (0) above the anterior lateral root of M3 and the posterior lateral root of M2, (1) above M2.
12. Frontonasal horn: (0) absent, (1) small bony thickening on nasal bone and overlapping frontal bone, (2) enlarged frontonasal protuberance (or horn).
13. Nasal process: (0) not elevated, (1) elevated.
14. Nasal process: (0) tapers distally, (1) moderately constricted proximally but otherwise more or less constant width throughout, (2) significantly widens distally.
15. Nasal process: (0) does not arch downward distally (1) small downturned distal process at midline.
16. Distal margin of nasal process: (0) not strongly rounded, (1) strongly rounded.
17. Nasal process: (0) lateral margins deeply downfolded, forming an upside-down U-shaped cross section, (1) thick with thickened lateral edges, lateral margins not deeply downfolded.
18. Large flat rugosity at distal end of nasal: (0) absent, (1) present.
19. Posterior zygomatic process: (0) absent, (1) present.
20. Swelling of zygomatic arch at junction between jugal and squamosal: (0) absent, (1) present.
21. Orientation of nasal processes: (0) more or less straight or slightly angled downward, (1) angled upward less than 45°, (2) angled upward at about 45°.
22. Occiput: (0) not widened, (1) widened occiput associated with swelled parietal and squamosal sinuses.
23. Upper incisors: (0) conical with pointed tips, (1) globular-subglobular I1–I2, conical I3, (2) all globular.
24. P1: (0) single cusp with distal heel, (1) paracone, metacone, and lingual heel possibly with a protocone or a small lingual crest.
25. P2 hypocone: (0) absent, (1) present.
26. P3 hypocone: (0) absent, (1) present.
27. P4 hypocone: (0) absent, (1) present.
28. Central molar cavity between the lingual bases of the paracone and metacone: (0) absent, (1) present.
29. Small lingual cusp on mesial cingulum of molars: (0) absent, (1) present.
30. M3 hypocone: (0) smaller than protocone, (1) absent or rarely present, vestigial when present.
31. Lower postcanine diastema: (0) short, always less than twice the length of P2, (1) absent.
32. Incisors: (0) large, unreduced in size, (1) I1 and I2 greatly reduced, I3 not greatly reduced, (2) all incisors greatly reduced.
33. Shape of incisor row: (0) arched, incisor row extends anteriorly from canines, (1) forms nearly a straight row between the canines.
34. Symphysis of mandible: (0) extends to a point between the P2 talonid and P3 trigonid, (1) extends to a point between the P3 talonid and P4 trigonid, (2) extends to a point between the P4 talonid or M1 trigonid.
35. Lower incisor morphology: (0) i1–i2 spatulate with rounded occlusal edge, i3 conical with pointed apex, (1) all conical, increasingly recurved and pointed distally, (2) crown forms a very blunt, globular, or flat surface, (3) all spatulate.

36. Relative incisor size: (0) i2 is slightly smaller or about the same size as i3, (1) i2 is significantly large than i3 in crown height and buccolingual width.

37. Lower molar relief: (0) low lophids and shallow talonid and trigonid valleys, (1) tall lophids and deep talonid and trigonid valleys.
38. P2 metaconid: (0) absent, (1) present.

39. P3 metaconid: (0) absent, (1) small, (2) large.

40. Frontonasal horns: (0) widely separated and divergent, (1) positioned closely together near midline of the skull, (2) completely fused together forming a single transverse crest.

APPENDIX 4
PHYLOGENETIC CHARACTER MATRIX

	1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 3 3 3 3 3 3 3 3 3 4																																								
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0											
<i>Palaeosyops robustus</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-										
	1																																								
<i>Telmatherium validus</i>	0	0	0	1	0	1	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0					
<i>Epimanteoceras formosus</i>	1	0	0	1	0	1	1	1	0	0	0	1	0	2	1	0	0	0	0	0	0	0	0	0	0	1	0	?	0	0	0	0	?	?	?	?	?	-			
<i>Dolichorhinoides angustidens</i>	1	?	?	1	0	1	?	1	0	0	0	1	0	1	0	0	0	0	0	0	0	?	0	1	1	0	1	0	0	?	?	?	?	?	?	?	0				
<i>Protitan minor</i>	?	1	0	?	0	2	1	0	1	1	0	2	0	1	?	?	?	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	?	?	?	?	?	0		
<i>Protitan grangeri</i>	1	1	0	2	0	2	1	0	1	0	0	2	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0		
<i>Rhinotitan kaiseni</i>	1	0	2	1	0	1	2	0	1	0	1	2	0	1	0	0	0	0	0	0	1	0	1	?	?	1	1	1	0	0	0	0	1	0	1	0	0	1	0		
<i>Rhinotitan mongoliensis</i>	1	0	2	1	0	1	2	0	2	0	1	2	0	1	0	0	1	0	0	0	1	0	1	1	1	0	0	0	1	0	0	0	0	1	0	1	0	0	1	0	
	1 1 1 1																																								
<i>Aktautitan hippopotamopus</i>	1	?	2	2	?	2	1	?	2	1	1	2	1	1	0	0	0	0	0	0	?	1	1	0	0	1	1	1	1	0	0	0	1	1	1	0	0	1	1		
	2																																								
<i>Metatitan relictus</i>	2	1	2	2	0	1	2	0	2	1	0	2	1	1	0	0	0	0	1	0	0	1	1	1	1	1	1	1	0	1	1	1	2	2	1	0	0	2	1		
<i>Metatitan primus</i>	2	?	2	2	0	1	2	1	2	1	0	2	1	1	0	0	0	0	1	0	0	1	?	1	1	1	1	1	0	1	?	1	2	2	1	0	1	2	1		
<i>Metatitan progressus</i>	?	?	?	?	?	?	?	?	?	2	1	1	2	1	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Embolotherium grangeri</i>	2	0	2	2	1	2	2	0	0	2	1	0	0	2	0	0	0	1	0	1	2	0	2	1	1	1	1	1	1	0	0	0	2	3	1	1	1	2	-		
<i>Embolotherium andrewsi</i>	2	0	2	2	1	2	2	0	3	1	1	2	-	-	-	-	-	1	0	1	-	0	2	1	1	1	1	1	1	1	0	2	0	2	2	?	1	1	2	2	
<i>Parabrontops gobiensis</i>	1	0	2	1	0	2	2	0	0	1	1	2	0	1	1	1	1	0	0	1	0	0	2	1	1	1	1	1	1	0	0	2	1	?	?	?	?	?	?	0	
	1																																								
<i>Gnathotitan berkeyi</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Microtitan mongoliensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Brachydiastematherium transylvanicum</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

APPENDIX 5

ANATOMICAL ABBREVIATIONS USED IN FIGURES

a	acetabulum	mg	magnum
alc	anterior-lingual cusp	mt2	second metatarsal
ap	apex	mt3	third metatarsal
as	astragalus	mt4	fourth metatarsal
c	centrum	mtd	metaconid
cf	central fossa of upper molars	mtr	medial trochlear ridge
ci	crest of ilium	mx	maxilla
cl	calcaneum	n	neck of scapula
cn2	mesocuneiform	na	nasal
cn3	ectocuneiform	nc	nuchal crest
co	cristid obliqua	np	nasal process
cp	coronoid process	ns	neural spine
cu	cuboid	nv	navicular
cun	cuneiform	o	orbit
d2	second digit	of	olecranon fossa
d3	third digit	p	pubis
d4	fourth digit	pald	paralophid
d5	fifth digit	pd	postcanine diastema
dlt	deltoid tuberosity	pgp	postglenoid process
dt	dorsal tubercle	pn	posterior nares
eam	external auditory meatus	poz	postzygopophysis
f	fibula	pr	parasagittal ridges
fnp	frontonasal process	prld	protolophid
fns	frontonasal suture	prd	protoconid
fr	frontal	prl	paraconule
gc	glenoid cavity	pmx	premaxilla
hf	head of femur	prz	prezygopophysis
hh	head of humerus	ptp	posttympanic process
hy	hypocone	r	radius
hyd	hypoconid	s	spine of scapula
hyld	hypolophid	sc	scaphoid
i	ischium	si	shaft of ilium
ifv	intervertebral foramen	ssf	supraspinous fossa
isf	infraspinous fossa	t	tibia
lc	lateral condyle	td	trapezoid
lec	lateral epicondyle	tf	transverse foramen
lt	lateral tuberosity	tp	transverse process
ltr	lateral trochlear ridge	tr2	second trochanter
lu	lunate	tr3	third trochanter
mc	medial condyle	u	ulna
mc2	second metacarpal	un	unciform
mc3	third metacarpal	vt	ventral tubercle
mc4	fourth metacarpal	zy	zygomatic arch
mc5	fifth metacarpal		