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A New Species of Brontotheriidae (*Perissodactyla*, Mammalia) from the Santiago Formation (Duchesnean, Middle Eocene) of Southern California

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ABSTRACT.—Recent construction excavations in the Duchesnean portion of the Santiago Formation at the Ocean Ranch Corporate Centre in Oceanside, San Diego County, California, USA, have produced well-preserved fossil remains of a previously undocumented genus and species of Brontotheriidae that we name *Parvicornus occidentalis*. The abundant remains of this new taxon, including numerous skulls, mandibles, dentitions, and postcranial elements, indicate a species roughly similar in size to the modern African black rhinoceros, *Diceros bicornis*. A saddle-shaped skull, short frontonasal horns, and incisors that are reduced both in size and in number suggest that this species belongs within the Brontotheriita, a subtribe of advanced brontotheriids of the middle and late Eocene of North America and Asia. *Parvicornus occidentalis* is unique among the Brontotheriita in retaining an incisor arcade that is strongly anteriorly arched and characterized by semiglobular upper incisor crowns. These more plesiomorphic conditions contrast with the more derived fully globular incisors and straight incisor rows of the other Brontotheriita. Phylogenetic analysis of the Brontotheriidae confirms that *P. occidentalis* is a member of the Brontotheriita but places it as a more basal member with close phylogenetic ties to *Protitanops curryi* and *Eubrontotherium clarnoensis*, two other species of Brontotheriita of western North America. *Parvicornus occidentalis* also compares favorably to fossil material from the Duchesnean Slim Buttes Formation of North Dakota that had previously been referred to *Duchesneodus thyboi*. The holotype of *D. thyboi* is not a diagnosable specimen, and this species remains a *nomen dubium*. However, a single rostral fragment (SDSM 63690) of a brontothere skull from the Slim Buttes Formation exhibits a suite of characters, including two pairs of semiglobular upper incisors that form a strongly arched incisor row, characteristic of *P. occidentalis*. This specimen suggests that the geographic range of *P. occidentalis*, or species closely related to it, may have extended well beyond its type locality in southern California.

INTRODUCTION

The family Brontotheriidae originated in the early Eocene during the initial holarctic radiation of the Perissodactyla (Rose 2006). More than any other perissodactyl clade, the Brontotheriidae seem to have adhered to a “live fast, die young” pattern of evolutionary radiation: brontotheres diversified rapidly in the middle Eocene, became one of the most diverse groups of large mammals in North America and Asia, then went extinct at the close of the Eocene. Estimates of the diversity of the Brontotheriidae have remained dubious for nearly 80 years because the group was oversplit by Osborn (1929) and others (e.g., Granger and Gregory 1943). However, as larger sample sizes, including large bone-bed assemblages of brontotheres, have become available through the years (Scott 1941, Turnbull and Martill 1988, Mhlbachler et al. 2004a), it has become clear that early paleontologists did not recognize sexual dimorphism and other forms of intraspecific variation sufficiently. Therefore, earlier estimates of brontothere diversity were inflated, most dramatically so for those species bearing frontonasal horns from the late-middle and late Eocene of North America.

Further considerations of brontothere taxonomy consistently suggest that localized (basin-, formation-, or locality-specific) taxonomic diversity of brontotheres is lower than previous estimates (Clark et

al. 1967, Mader and Alexander 1995, Mader 1998, Mhlbachler et al. 2004a, Mhlbachler 2008). For instance, Osborn (1929) accepted 37 species of horned brontotheres from the late Eocene Chadron Formation of central North America; however, when sexual dimorphism and other patterns of intraspecific variability are considered (Mhlbachler et al. 2004a), there appear to be only two species of Chadron brontotheres, both belonging to the genus *Megacerops*: *M. coloradensis* Leidy, 1870, and *M. kuwagatarhinus* Mader and Alexander, 1995. Nonetheless, continued discoveries across North America and Asia consistently yield new species of Brontotheriidae, particularly of late middle and late Eocene Brontotheriita, the infratribe that includes *Megacerops* and other relatively advanced horned brontotheres with reduced anterior dentitions (Mhlbachler 2007). In addition to the classic Chadronian genus *Megacerops*, known members of the Brontotheriita include *Duchesneodus uintensis* (Peterson, 1931), *Protitanops curryi* Stock, 1936, *Notiotitanops mississippiensis* Gazin and Sullivan, 1942, *Parabrantops gobiensis* (Osborn, 1925), *Dianotitan lunanensis* (Chow and Hu, 1959), and *Eubrontotherium clarnoensis* Mhlbachler, 2007. Data on the ages and biogeographic distribution of diagnosable species of the Brontotheriita as summarized by Mhlbachler (2007, 2008) are listed in Table 1.

A large collection of brontothere material from the Ocean Ranch

TABLE 1. Valid species of Brontotheriita and their geographic distributions and ages.

Species	Distribution	Type locality	Other localities	Land mammal age	Age
<i>Parvicornus occidentalis</i>	Southwestern USA	Ocean Ranch, Santiago Fm., California	—	Duchesnean	Middle Eocene
<i>Parabronops gobiensis</i>	Inner Mongolia	Urtyn Obo Fm.	—	Ulangochuian	Middle Eocene
<i>Eubrontotherium clarnoensis</i>	Northwestern USA and Central Asia	Clarno Fm., Oregon	Ergilin Dzo, Outer Mongolia	Ergilian (Asia), Duchesnean (North America)	(North America), Late Eocene (Asia)
<i>Protitanops curryi</i>	Southwestern USA	Titus Canyon Fm., California	—	Early Chadronian ?	Late Eocene Middle Eocene
<i>Dianotitan lunanensis</i>	Yunnan, China	Lumeiyi Fm.	—		
<i>Duchesneodus uintensis</i>	Western and southwestern USA	Duchesne River Fm., Utah	Galisteo Fm., New Mexico; Vieja Fm., Texas	Duchesnean	Middle Eocene
<i>Notiotitanops mississippiensis</i>	Southeastern USA	Cook Mountain Fm., Mississippi	—	Late Uintan	Middle Eocene
<i>Megacerops coloradensis</i>	Central North America	White River Fm., Colorado	Many localities within region	Chadronian	Late Eocene
<i>Megacerops kuwagatarhinus</i>	Central North America	White River Fm., Montana	Colorado, Saskatchewan	Chadronian	Late Eocene

Corporate Centre (ORCC) in Oceanside, San Diego County, California, USA (Figure 1), belongs to yet another species, *Parvicornus occidentalis*, of the infratribe Brontotheriita from the Duchesnean North American Land Mammal Age (NALMA) of southern California. The Oceanside brontothere most closely resembles brontothere material from the Slim Buttes Formation (Duchesnean NALMA) of northwest South Dakota that had been previously assigned to a *nomen dubium*, *Duchesneodus thyboi* (Bjork, 1967). From our analysis we conclude that (1) *Parvicornus occidentalis* is a new species belonging to the infratribe Brontotheriita; (2) *Duchesneodus thyboi* remains a *nomen dubium* because its holotype is an undiagnostic juvenile specimen; however, (3) some of the fossil material previously assigned to this dubious species is consistent with *P. occidentalis*.

The identification of *P. occidentalis* as a species follows operational guidelines detailed by Mhlbachler (2008), in which patterns of intraspecific variation common within the Brontotheriidae, including ontogeny and sexual dimorphism, are considered. Only those characters found to be intraspecifically monomorphic or, at least, more variable between species than within species, are considered to be taxonomically and phylogenetically informative. The taxonomic methods we employ are consistent with the paradigm of the phylogenetic species, in which the smallest diagnosable clusters of specimens are partitioned into species (Cracraft 1989, Nixon and Wheeler 1990, Wheeler and Platnick 2000).

INSTITUTIONAL ABBREVIATIONS

AMNH	Division of Vertebrate Paleontology, American Museum of Natural History, New York, New York, USA
CMNH	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA
IVPP	Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China
KAN	Institute of Zoology, Kazakh Academy of Sciences, Almaty, Kazakhstan
LACM/CIT	California Institute of Technology collection now housed in the Natural History Museum of Los Angeles County, Los Angeles, California, USA

PIN

Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia

NMC
SDSM

National Museum of Canada, Ottawa, Canada
Specimens from Custer National Forest housed in the Museum of Geology, South Dakota School of Mines and Technology, Rapid City, South Dakota, USA
Department of Paleontology, San Diego Natural History Museum, San Diego, California, USA

SDSNH

USNM

United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA

YPM

Yale Peabody Museum of Natural History, Yale University, New Haven Connecticut, USA

STRATIGRAPHY AND BIOCHRONOLOGY

The holotype and referred specimens of the new brontothere were collected from strata of the Santiago Formation as exposed by heavy earthmoving equipment during construction of ORCC in the city of Oceanside, San Diego County, California, USA. Woodring and Popenoe (1945) originally named the Santiago Formation for a sequence of Eocene marine siltstones and sandstones that crop out in the western foothills of the Santa Ana Mountains in Orange County, California. Later, Wilson (1972) recognized lithostratigraphic and biostratigraphic similarities between the Santiago Formation in Orange County and a sequence of Eocene marine and nonmarine strata in northwestern San Diego County. On the basis of these similarities, Wilson (1972) assigned these strata in the Oceanside and Carlsbad areas to the Santiago Formation and subdivided the formation into three informal members: a basal marine member (A), a middle marine member (B), and an upper nonmarine member (C). In his summary of the mammalian biochronology of Eocene rocks in San Diego County, Walsh (1996) indicated that member B of the Santiago Formation is correlative with the early Uintan NALMA, member C at its base with the late Uintan NALMA and at its top with the Duchesnean NALMA.

This lithostratigraphic and biochronologic framework for the Santiago Formation places Eocene sedimentary deposits exposed at ORCC with both members B and C of the Santiago Formation and correlates them with the early Uintan, late Uintan, and Duchesnean

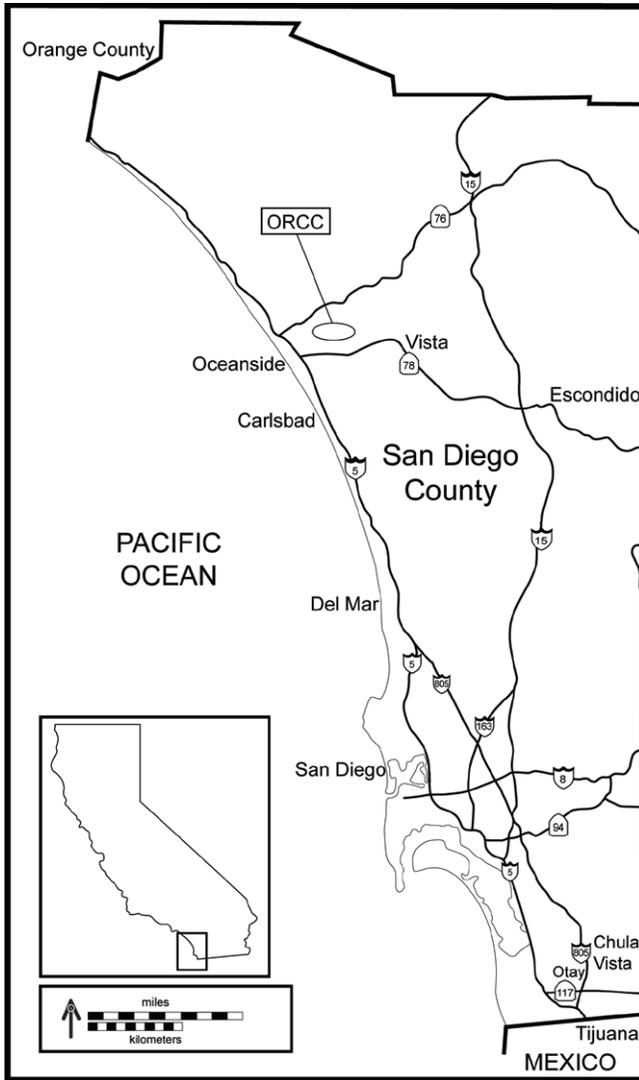


FIGURE 1. Location of the Ocean Ranch Corporate Centre in northwestern San Diego County, California.

NALMAs. The overall Eocene stratigraphic sequence at ORCC consists of approximately 85 m of west-dipping marine, estuarine, and fluvial mudstones, siltstones, sandstones, and conglomerates (Figure 2). As measured and mapped by B. O. Riney, sedimentary rocks of member B consist of siltstones and fine- to medium-grained sandstones. The basal strata of member B contain middle Eocene marine invertebrate fossils (Schweitzer and Feldman 2002), while the upper strata contain early Uintan land mammal fossils (S. L. Walsh, personal communication). An irregular erosion surface (disconformity) at the top of member B is overlain by almost 55 m of member C strata. The lower 12 m of member C consists of a maroon sandstone unit containing late Uintan land mammal fossils. Disconformably overlying the late Uintan maroon sandstone unit is approximately 40 m of interbedded white arkosic sandstone, brown siltstone, and medium- to coarse-grained cross-bedded sandstone. A distinct 1-m-thick brown, massive, silty, fine-grained sandstone and siltstone stratum near the middle of this interbedded sequence yielded the stratigraphically lowest Duchesnean land mammal fossils (SDSNH locality 5721) in the section (Figure 3). The upper portion of the member C section is characterized by a channel-fill sequence, 10–15 m thick, with a basal unit of white to light gray, extremely

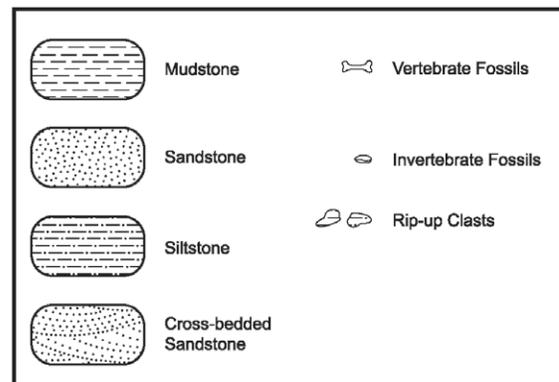
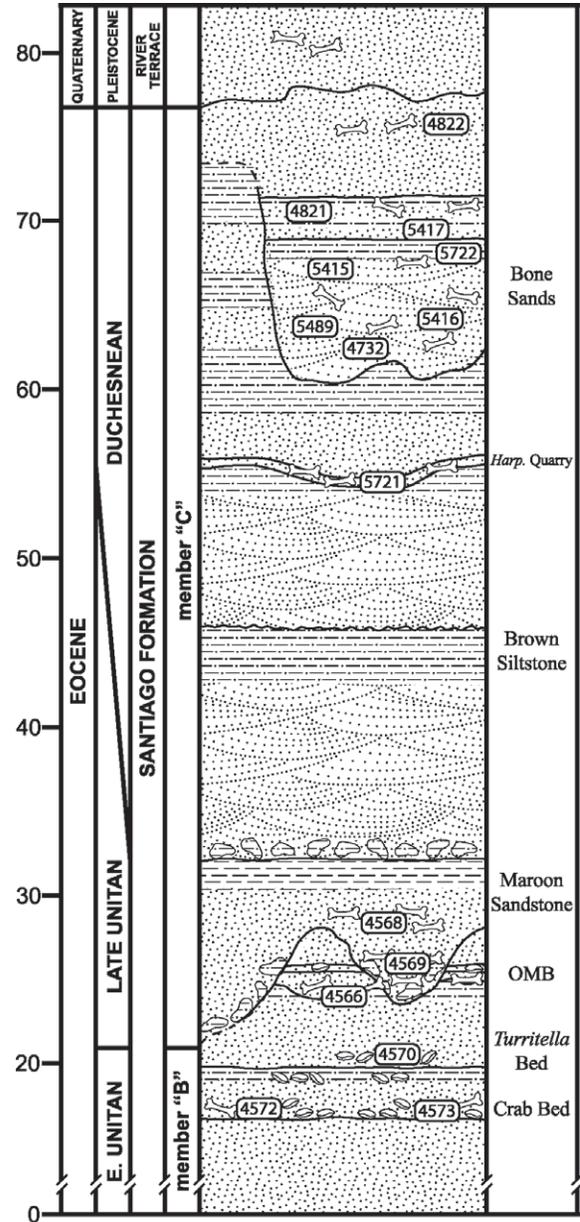


FIGURE 2. Generalized stratigraphic column for the Ocean Ranch Corporate Centre area. Stratigraphic thickness in meters. Four-digit numbers represent SDSNH collecting localities discussed in text.



FIGURE 3. Interbedded sandstone and mudstone strata of member C of the Santiago Formation as exposed at the Ocean Ranch Corporate Centre. Note excavation site (SDSNH locality 5721) on left side of graded slope.

friable, cross-bedded, coarse-grained, arkosic, gravelly sandstone containing large rip-up clasts of fine-grained silty sandstone. This unit, informally called the “Bone Sands,” produced the majority of the brontothere fossils described in this report.

Biochronologically significant fossils from the Bone Sands included specimens of the Duchesnean index creodonts *Hyaenodon* sp. and *Hyaenodon venturae*, specimens of a pantolestid close to *Simidectes merriami* known only from Duchesnean strata in southern California, specimens of *Epihippus* sp., and important specimens of Duchesnean rodents, including the myomorphs *Griphomys* sp. and *Simimys* sp., the eomyid *Metanoimys* sp. cf. *M. marinus*, the cylindrodontid *Pareumys* sp., the ailuravine *Eohaplomys* sp. cf. *E. serus*, and the ischyromyids *Microparamys* sp. cf. *M. tricrus* and *Rapamys fricki* (S. L. Walsh, personal communication). A searchable database of all catalogued specimens from the ORCC Duchesnean localities is available at www.paleoportal.org or www.sdnhm.org/research/paleontology/searchdata.html. The small-mammal fossils from member C of the Santiago Formation at ORCC are especially significant. They suggest a correlation with the early Duchesnean Pearson Ranch Local Fauna recovered from the middle member of the Sespe Formation in Ventura County, California, USA (Kelly 1990, Robinson et al. 2004). The absolute age of the Duchesnean NALMA is poorly constrained but ranges from approximately 40 to 37 Ma (Robinson et al. 2004).

Taphonomy

The majority of the brontothere specimens recovered from ORCC occurred in the Bone Sands channel-fill sequence in the upper portion of member C of the Santiago Formation. Most specimens were found as single skulls, jaws, or postcranial elements in bone and gravel lags at the base of individual channels. Although rare, associated or partially articulated specimens were also found, primarily in silty fine-grained sandstones near the top of normally graded channel-fill sedimentation units. Other specimens were discovered in silty fine-grained sandstone rip-up clasts that had presumably been eroded from channel-margin settings and incorporated into the Eocene stream bedload. There were no dense concentrations of skeletal elements suggestive of a mass mortality event.

For the most part, the brontothere fossils are preserved as permineralized bones and teeth. Tooth enamel has typically taken on a very dark brown color, which stands out in stark contrast with the generally white color of tooth roots and associated bones. Bone surfaces show limited predepositional weathering, from stage 0 to stage 1 (Behrensmeier 1978). Some bones also preserve evidence of predepositional breakage and current abrasion, while most bones preserve little to no such evidence. Postdepositional modification of bone surfaces is more extensive, with minor to moderate degrees of crushing due to stratigraphic load. Because of the obvious

destructiveness of excavation with heavy equipment, many of the brontothere specimens show some degree of equipment damage. In some cases, the dorsal portions of skulls have been planed off, leaving only the basicranium and palate. In other cases, only the dorsal portions of skulls remain. Long bones show similar patterns of missing portions, with distal or proximal ends predominating over anterior or posterior remnants. The most unfortunate cases involve recovery of only portions of what were most likely complete skeletons. This, however, is the nature of salvage paleontology, in which the adage “half a skull is better than no skull” is a familiar mantra.

SYSTEMATIC PALEONTOLOGY

CLASS: MAMMALIA Linnaeus, 1758
 ORDER: PERISSODACTYLA Owen, 1848
 FAMILY: BRONTOTHERIIDAE Marsh, 1873
 SUBFAMILY: BRONTOTHERIINAE Marsh, 1873
 TRIBE: BRONTOTHERIINI Marsh, 1873
 SUBTRIBE: BRONTOTHERIINA Marsh, 1873
 INFRATRIBE: BRONTOTHERIITA Marsh, 1873

Parvicornus, new genus

Diagnosis of Genus.—The diagnosis of the genus shall remain identical to that of the species *Parvicornus occidentalis* until further species are named in the genus *Parvicornus*.

Type and Only Included Species.—*Parvicornus occidentalis*, new species.

Etymology.—The genus name is a neologism composed of the elements *parvi* (from *parvus*, Lat., little) and *cornus* (from *cornu*, Lat., horn), reflecting the small nasal horns of this genus of brontothere.

Parvicornus occidentalis, new species

Holotype.—SDSNH 107667, a nearly complete and partially crushed skull with right I3–M3 and left I2, C–M3 (Figure 4).

Type Locality.—SDSNH locality 5416, Ocean Ranch 2C, Bone Sands, Santiago Formation, member C, Oceanside, San Diego County, California, USA.

Age.—Middle Eocene (Late Duchesnean NALMA).

Etymology.—The species name, *occidentalis*, refers to the occurrence of this species of brontothere on the west coast of North America (from *occidens*, Lat., west).

Referred Specimens.—SDSNH locality 4732, Rancho Del Oro Extension, Bone Sands, Santiago Formation, member C, Oceanside, San Diego County, California, USA: SDSNH 92041, juvenile maxilla with left dp2 (partial), dp3, dp4 (partial); SDSNH 92042, canine; SDSNH 92043, left P2; SDSNH 92044, P4 fragment; SDSNH 92045, lower molar fragment; SDSNH 92046, left M2–M3; SDSNH 92047, mandible with fragmented teeth including complete right p2, p4, left p1, p4; SDSNH 92048, mandibular symphysis with canine roots and right p2–p3; SDSNH 92049, juvenile jaw with left dp4, m1, m2, and isolated p2; SDSNH 92050, partial skull with right and left C–M3; SDSNH 92051, partial skull with right P3, M1–M3, left I2–I3, C (partial), P3 (partial), and M3; SDSNH 92052, mandible with right and left p2–m3; SDSNH 92053, mandible fragment with right p3–m2; SDSNH 92054, partial skull with dentition except for right I1 SDSNH 92055, upper incisor; SDSNH 92056, partial skull with right P3–P4, M2, left C, P2–P4, M1–M2, two isolated upper incisors, mandible with right i1–m2, unerupted m3, left i1–i2, c–m2, unerupted m3, and other postcranial fragments including a phalanx and distal femur; SDSNH 92057, left dp4; SDSNH 92058, right p3; SDSNH 92059, left p4; SDSNH 92060, right m1; SDSNH 92061, left m1; SDSNH 92062, left m2; SDSNH 92063, left m2 fragment; SDSNH 92064, right m3 fragment; SDSNH 92080, partial right humerus; SDSNH 107844, right M3; SDSNH 107845, C.

SDSNH locality 5415 Ocean Ranch 2C, Bone Sands, Santiago Formation, member C, Oceanside, San Diego County, California, USA: SDSNH 93246, juvenile skull with complete dentition, mandible with complete dentition, articulated partial skeleton including rib fragments, right forelimb, and partial left forelimb; SDSNH 93465, left dentary with c–m3; SDSNH 105789, partial skull with right M1–M3 and left P4–M3, complete mandible with complete dentition; SDSNH 105790, partial right M2; SDSNH 105791, right mandible fragment with partial m2 and m3; SDSNH 105792, left m2; SDSNH 105793, left partial jaw with m1–m3; SDSNH 105794, partial jaw with right p3–m3 and left p2–p4; SDSNH 105795, jaw fragments with right m1, m2 (partial), and other dental fragments; SDSNH 105796, partial mandible with left p3–m3; SDSNH 105813, right scapula; SDSNH 105819, partial right humerus; SDSNH 105824, right partial femur; SDSNH 105833, partial right humerus.

SDSNH locality 5416 [holotype locality], Ocean Ranch 2C, Bone Sands, Santiago Formation, member C, Oceanside, San Diego County, California, USA: SDSNH 93245, skull with right C, P1, M2, M3, left C, P1–P3, M2–M3; SDSNH 93322, skull with complete dentition; SDSNH 93464, partial skull with right P1–M1 (crushed), M2–M3, left incisor, P1–M2 (crushed), M3; SDSNH 107664, skull fragment with horn and nasal bone; SDSNH 107665, right maxilla with C–M3 and left maxilla with C–M1, M2–M3 (partial), and fragment of frontonasal horn; SDSNH 107666, partial skull with dentition complete except for canines; SDSNH 107668, horn fragment; SDSNH 107669, right M2–M3; SDSNH 107670, maxilla fragment with left P1–P3, P4 (incomplete); SDSNH 107671, right M2; SDSNH 107672, left P4 and partial left p3; SDSNH 107673, right M2; SDSNH 107674, partial left M2; SDSNH 107675, dentary fragment with partial left m1; SDSNH 107676, mandible fragment with unerupted molar; SDSNH 107677, partial mandible with right p4–m3; SDSNH 107694, atlas, axis, and vertebral fragments; SDSNH 107698, left humerus, femur, patella, scapula.

SDSNH locality 5489 Ocean Ranch 2A, middle Bone Sands, Santiago Formation, member C, Oceanside, San Diego County, California, USA: SDSNH 105899, crushed juvenile skull with right P1–M3, and left P3, M2, M3 (unerupted), with isolated P4 and M1 (partial).

SDSNH locality 5722, Ocean Ranch 2C, middle Bone Sands, Santiago Formation, member C, Oceanside, San Diego County, California, USA: SDSNH 107728, right P2–M1, M2–M3 (partial), left P1–M3; SDSNH 107729, skull and fragments of teeth including a canine, right M1–M2, partial left M1, frontonasal fragments; SDSNH 107730, jaw fragment with left m2–m3, isolated canine; SDSNH 107731, partial mandible of a juvenile with right i1–i2, c–p2, and left i1–m2; SDSNH 107732, partial mandible with right c, p4–m3; SDSNH 107733, partial mandible with right i1–i2, i3 root, c, p2–m2, m3 (partial), left i1–i2, c, p3, p4 (partial), m2, m3 (partial).

SDSNH locality 4821, Rancho Del Oro Extension, upper Bone Sands, Santiago Formation, member C, Oceanside, San Diego County, California, USA: SDSNH 92095, right P3; SDSNH 92098, right and left M2–M3.

Diagnosis.—*Parvicornus occidentalis* is a large-bodied brontothere with small frontonasal horns that are positioned anterodorsally relative to the orbits. The posterior margin of the nasal incision is positioned above P4. The anterior rim of the orbit is directly dorsal to the anterolateral root of M1. The nasal process is broad, horizontal, slightly downturned, of nearly constant width throughout its length, strongly rounded anteriorly, and with shallow and thickened lateral walls. The premaxillomaxillary rostrum thickens posteriorly and is not enclosed by bone dorsally. Other cranial characteristics include a saddle-shaped cranium, a dorsal cranial surface that is only moderately constricted posteriorly by parasagittal ridges, a bony emargination surrounding the posterior nares, moderately curved zygomatic arches, and a ventrally constricted and mediolaterally angled external

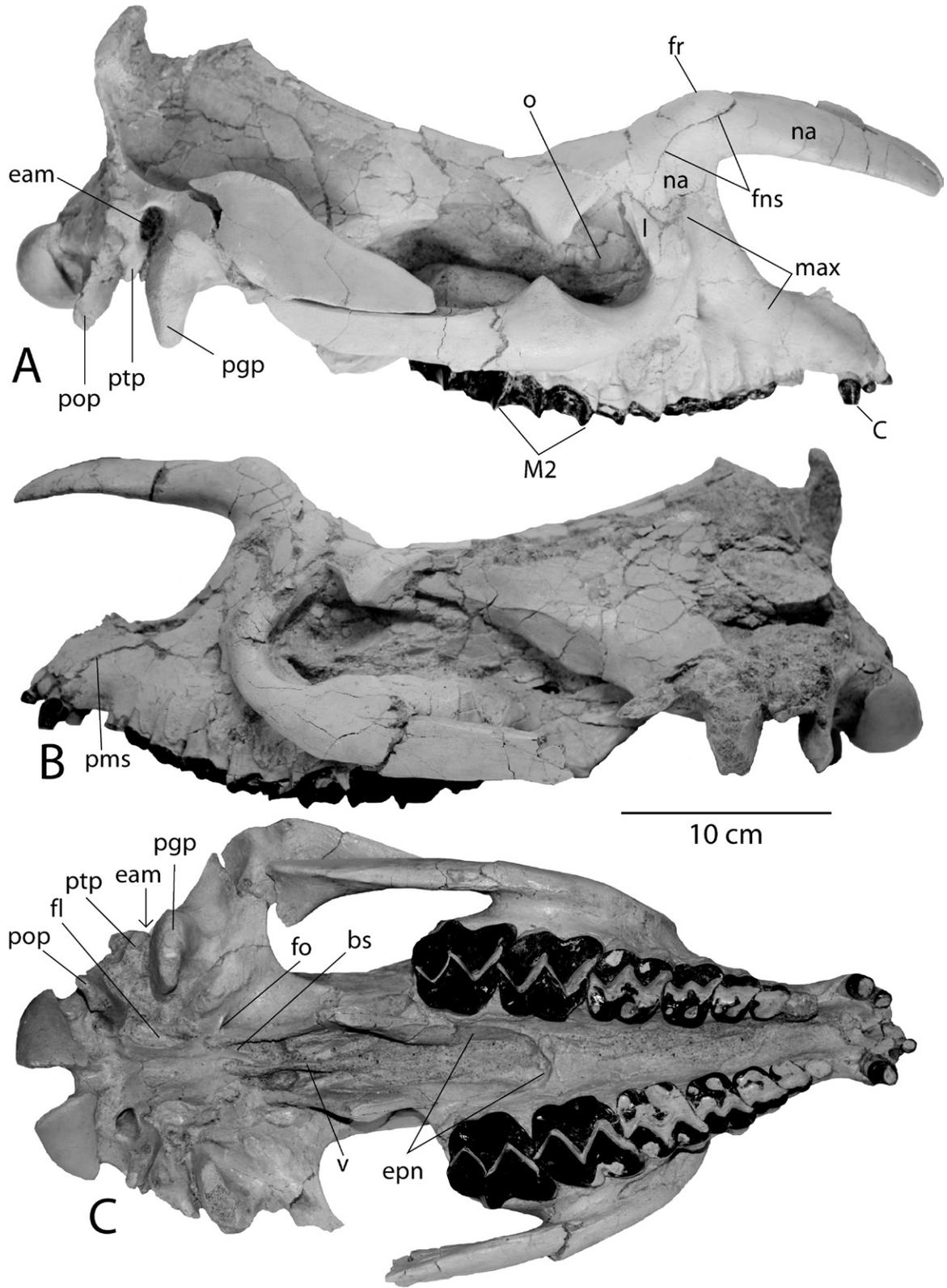


FIGURE 4. Holotype skull of *Parvicornus occidentalis* (SDSNH 107667). (A) Right view, (B) left view, (C) ventral view.

auditory pseudomeatus. Ventral sphenoidal fossae, postzygomatic processes, and lateral zygomatic swellings are absent.

Dentally, *P. occidentalis* is characterized by two small semiglobular upper incisors (I1, 2) that form a strongly anteriorly arched row, a long postcanine diastema, a morphologically complex (semimolariform) P1, a distinct metacone on P2, and premolar hypocones on P2–P4. The molars have tall, lingually angled ectoloph with weak labial ribs and thinned lingual ectoloph enamel with wedge-shaped paracones and metacones. A cingular parastyle shelf is absent. Central molar fossae and anterolingual cingular cusps are present. Paraconules and metalophs are absent. The lower dentition of *P. occidentalis* includes three very small wedge-shaped lower incisors; i2 is larger than i3. There is a distinct postcanine diastema. A metaconid is present on p4, variably present or absent on p3, and absent on p2. The trigonid of p2 is less than twice the length of the talonid. The lower molars are typical of most other brontotheres, with shallow talonid and trigonid basins and an elongate slender m3.

Parvicornus occidentalis is one of two brontothere species, along with *Eubrontotherium clarnoensis*, that both lack large zygomatic swellings and have only two pairs of semiglobular or globular upper incisors. *Parvicornus occidentalis* retains an incisor row that is strongly arched anterior to the canines, while the incisor row of *Eubrontotherium clarnoensis* is straighter and positioned between the canines.

DESCRIPTION

Parvicornus occidentalis is roughly similar in body size to a modern black rhino (*Diceros bicornis*), although it is smaller than most horned brontotheres of North America from the middle and late Eocene. In size, it closely resembles *Duchesneodus uintensis* and *Diplacodon elatus* Marsh, 1875. Measurements are provided in Appendix 1, with explanations of measurements in Appendix 2. Summary statistics are given in Tables 2 and 3. Terminology used in the descriptions of skulls, mandibles, and dentitions follows Muhlbachler (2008). Terminology for postcrania follows Muhlbachler

et al. (2004b) and Sisson and Grossman (1953). Abbreviations for anatomical terminology, corresponding to labeled figures, are given in Appendix 3. We compare the skull and upper dentition of *P. occidentalis* to those of other members of the Brontotheriita and more basal horned brontotheres, including *Protitanotherium emarginatum* Hatcher, 1895, and *Diplacodon elatus*. Because the genera to which most of these species belong are monotypic, we refer to these species by genus only, except for *Megacerops*, which contains at least two species, *M. coloradensis* and *M. kuwagatarhinus*. Use of the genus *Megacerops* without a species refers to *M. coloradensis* (*sensu* Muhlbachler et al. 2004a), the more abundant and well known of the two. We compare the mandible and lower dentition of *Parvicornus* with those of *Protitanotherium*, *Diplacodon*, and those species of Brontotheriita whose lower dentitions are known, including *Eubrontotherium*, *Duchesneodus*, *Megacerops*, and, to a lesser extent, *Notiotitanops*.

We compare postcranial elements of *Parvicornus occidentalis* from Ocean Ranch to a more disparate array of brontothere taxa because only a limited number of species are known from postcranial material associated with diagnostic skulls, jaws, or dentitions. Because there is very little information about intraspecific variation among brontothere postcrania, we compare postcrania of *Parvicornus* with those of other brontotheres by specimen. Illustrations of many of the postcranial specimens mentioned below are found in Peterson (1924), Osborn (1929), Yanovskaya (1980), Wang (1982), and Muhlbachler et al. (2004b). At this point, we do not presume that all observed variations in postcranial characters are species-level differences.

Skull.—To portray the complete and undistorted cranial morphology of *Parvicornus* accurately, we must illustrate and describe several specimens. The holotype skull (SDSNH 107667) is a nearly complete skull of a young adult with fully erupted but only moderately worn dentition (Figure 4). This skull is minimally distorted, and the right side is basically intact. The left side is considerably more crushed and is missing portions of the left parietal, occipital, and squamosal, including part of the zygomatic arch. Another skull, SDSNH 93245 (Figures 5 and 6), is a more complete and nearly un-

TABLE 2. Summary statistics for skull and upper dental measurements of *Parvicornus occidentalis*.

Variable	Mean	SD	CV	Min	Max	n
I1L	8.9	0.3	2.8	8.7	9.3	6
I1W	10.0	0.7	7.2	9.1	10.9	6
I2L	9.5	0.3	3.0	9.1	9.8	5
I2W	10.9	0.9	7.9	10.1	12.4	5
CL	17.9	2.4	13.2	15.7	21.3	7
P1L	17.1	0.8	4.8	16.0	18.9	11
P1W	13.1	1.1	8.3	11.9	15.2	10
P2L	21.3	1.5	7.0	19.1	24.4	12
P2W	23.0	1.2	5.4	21.2	24.8	12
P3L	25.0	2.4	9.5	21.7	29.4	12
P3W	29.3	1.1	3.7	27.3	31.7	12
P4L	30.7	2.4	7.9	27.4	35.2	10
P4W	36.8	1.9	5.3	34.7	40.3	10
M1L	45.6	4.5	9.9	38.9	53.1	11
M1W	43.6	2.5	5.8	40.0	48.1	9
M2L	56.1	4.9	8.7	47.4	62.4	17
M2W	53.6	3.6	6.7	49.5	61.1	16
M3L	61.4	4.6	7.6	53.2	70.9	14
M3W	56.8	3.7	6.5	50.2	63.7	14
P2–P4	72.9	1.7	2.3	70.1	75.4	8
M1–M3	15.3	7.4	4.9	140.4	161.5	8
P2–M3	218.5	6.5	3.0	211.4	227.5	7
VL	533.8	29.2	5.5	507.0	560.0	4
MVL	486.3	30.8	6.3	440.0	530.0	6
SW	354.8	7.4	2.1	344.0	360.0	5

TABLE 3. Summary statistics for lower dental measurements of *Parvicornus occidentalis*.

Variable	Mean	SD	CV	Min	Max	n
i1L	8.5	0.6	6.4	8.0	9.3	4
i1W	8.9	1.4	16.0	6.9	10.0	4
i2L	9.9	1.3	13.5	8.0	10.9	4
i2W	12.8	0.8	6.6	12.2	13.7	3
i3L	9.9	0.6	6.0	9.3	10.5	3
i3W	9.9	1.3	13.2	8.5	11.0	3
cL	23.4	3.3	14.0	19.0	27.3	6
p1L	13.3	0.6	4.5	12.2	14.0	6
p1W	9.8	0.6	5.9	9.3	10.5	5
p2L	23.0	0.8	3.3	21.9	24.2	9
p2W	14.4	1.0	6.6	12.5	15.9	9
p3L	25.6	1.6	6.3	23.4	28.5	11
p3W	17.1	1.5	8.7	14.4	19.5	10
p4L	30.2	1.5	5.0	27.7	33.5	13
p4W	21.0	1.8	8.7	18.4	25.3	12
m1L	41.8	2.4	5.8	37.0	45.1	16
m1W	25.3	1.6	6.5	22.6	28.3	15
m2L	52.3	3.1	5.9	46.6	56.8	16
m2W	30.4	2.0	6.6	27.0	35.1	15
m3L	73.7	4.7	6.4	66.7	81.4	11
m3W	30.0	1.8	5.9	27.7	33.9	10
p2–p4	78.4	3.4	4.3	75.1	85.5	8
m1–m3	168.0	9.5	5.7	155.0	180.2	9
p2–m3	250.6	6.7	3.9	240.4	263.6	4

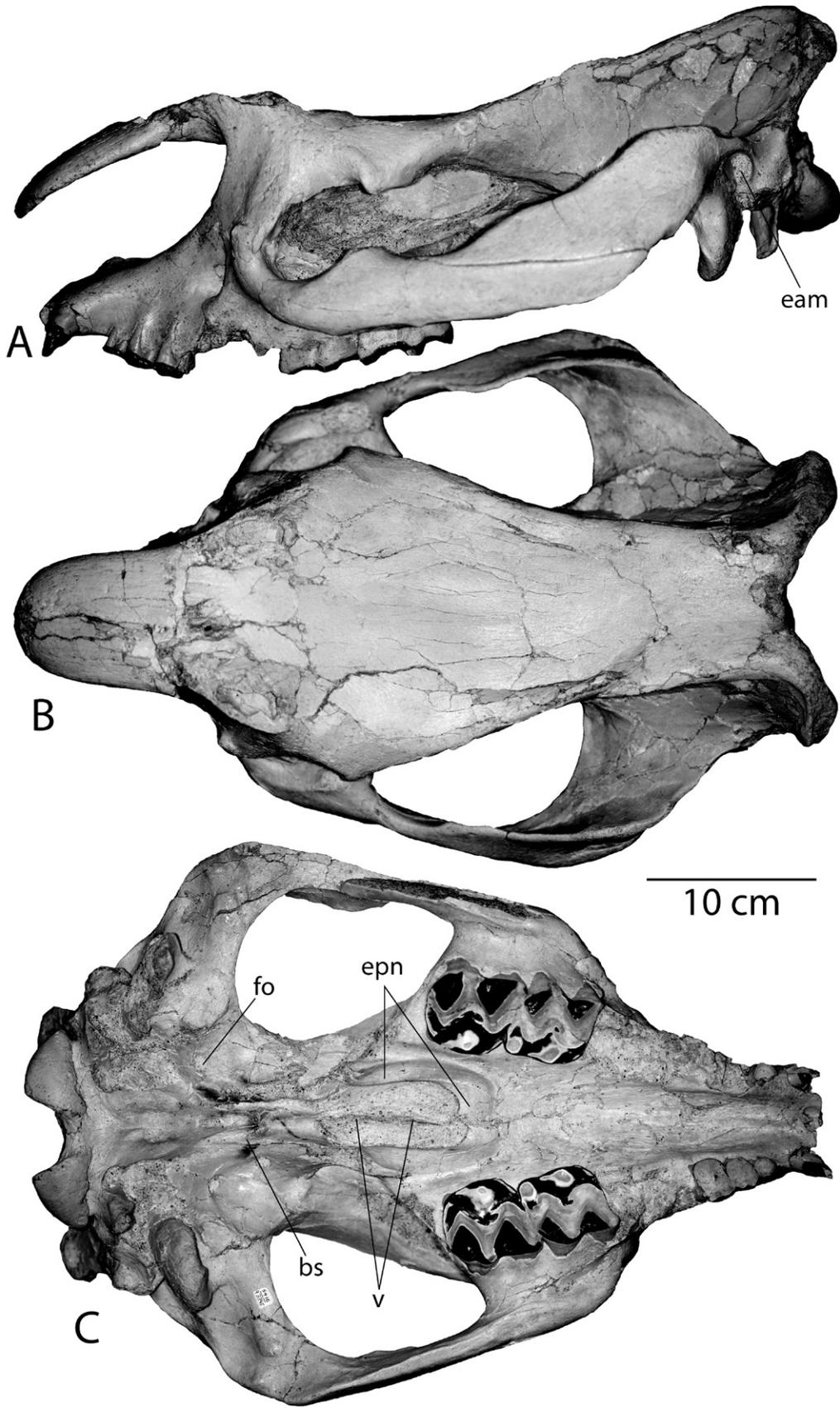


FIGURE 5. Skull (SDSNH 93245) referred to *Parvicornus occidentalis*. (A) Left view, (B) dorsal view, (C) ventral view.

distorted specimen representing an ontogenetically older individual with heavily worn dentition and missing only the peaks of the horns. SDSNH 92050 (Figure 7) is a partial skull that has been flattened dorsoventrally, as indicated by the oval orbits, but demonstrates variation in the frontonasal horns, nasal bone, and zygomatic arches that is probably related to intraspecific sexual dimorphism. Other adult skulls not figured but providing details pertinent to the cranial morphology of *Parvicornus* are SDSNH 92054, SDSNH 93322, SDSNH 93464, SDSNH 105789, and SDSNH 107667. Finally, two juvenile skulls, SDSNH 93246 and SDSNH 105899, provide additional details about skull ontogeny. With a complete set of deciduous dentition but without any erupted permanent teeth SDSNH 93246 (Figure 8) is the younger and better preserved of the two.

Every adult specimen with a completely preserved frontonasal region exhibits a pair of small frontonasal protuberances (“horns”). The horns are positioned entirely anterior to the orbits and are supported by a pillarlike extension formed by the frontal and nasal bones that extends anterodorsally from above the orbit at an angle of $\sim 45^\circ$. As in other horned brontotheres, the apex of the horn is structurally a projection of the frontal bone that overrides the dorsolateral margin of the nasal bone. On the holotype skull the contact of the frontal and nasal bone is clearly discernable in lateral view, running from above the orbit to the anterior edge of the horn itself (Figure 4a). The frontonasal horns of the holotype skull are small, smooth, and elliptical with the longest axis in the anteroposterior direction. Other specimens vary in horn size. For instance, the skull of SDSNH 92050 (Figure 7) is larger and more robust overall with taller horns with more rugose tips. On the juvenile skull (SDSNH 93246) the frontonasal contact is plainly visible in the same configuration as on the adult skulls, but it had not yet developed into a large protuberance (Figure 8). Despite some variation in size and robusticity, the horns of other specimens share the same elliptical shape and dorsolateral angle seen in the holotype. The horns of *Parvicornus* are smaller and less

massive than horns of the known skulls of *Protitanops*, *Dianotitan*, and *Parabrantops*, but they are within the range of sizes seen among specimens of *Protitanotherium*, *Diplacodon*, *Eubrntotherium*, and *Duchesneodus*.

All three of the figured adult skulls as well as the juvenile skull have complete nasal processes. The nasal bones of ontogenetically younger specimens (Figures 4 and 7) are incompletely co-ossified and have become separated at the midline. In ontogenetically older specimens, such as SDSNH 93245 (Figure 5b), the nasal bones are strongly co-ossified without a visible midline suture. In lateral view, the nasal process extends as far anteriorly as the premaxilla (SDSNH 92050) or slightly past the anterior margin of the premaxilla (SDSNH 107667 and SDSNH 93245). The dorsal surface of the nasal process is convex, while the inferior surface is slightly concave. The nasal processes of most skulls of *Parvicornus* curve downward (anteroventrally) slightly. The nasal process of SDSNH 93245 (Figure 5a) is more severely angled anteroventrally as a result of the damage to the frontonasal region of that skull.

The lateral margins of the nasal processes are thickened and curved ventrally. In dorsal view, the nasal process of SDSNH 93245 appears broad and tapers slightly distally (Figure 5b). The distal margin of the nasal process is strongly rounded. The distal edge of the nasal process is thin in comparison to the lateral margins. The nasal process of SDSNH 92050 is notably broader (Figure 7b), but its overall thickness and general shape are otherwise very similar to those of other specimens.

The nasal bone of *Parvicornus* is distinctly different from that of *Protitanotherium* and *Diplacodon*. The nasal process of *Protitanotherium* tends to have a flatter anterior margin that is more consistently notched mesially. The nasal processes of skulls of *Parvicornus* all lack a mesial notch at the anterior edge of the nasal process. *Diplacodon* lacks this mesial notch as well; however, the lateral margins of the nasal process are autapomorphically curved dorsally. In general, the nasal bone of *Parvicornus* closely resembles nasal bones of other members of the Brontotheriita, although within a species there is considerable variation in the overall thickness of the nasal bones.

Note that the apparent dorsoventral depth of the lateral nasal incision is strongly influenced by the degree of diagenetic dorsoventral flattening. The least distorted specimens (Figures 4 and 5) convey the size and shape of the nasal incision the best. The posterior margin of the nasal incision is nearly flat and angled posterodorsally, with a sharp notch in the posterodorsal corner. The dorsal margin of the nasal incision is slightly higher than the dorsal margin of the orbit. Consequently, the frontonasal horns and nasal process are situated in a plane dorsal to the orbit. The anteroposterior length of the nasal incision appears to increase with age. In the juvenile skull (SDSNH 93246; Figure 8), the posteriormost edge of the nasal incision is above dP2. In the holotype skull, from an adult with only moderately worn permanent teeth, the posterior margin of the nasal incision is above the posterior edge of P3 (Figure 4a). In the remaining adult specimens with more advanced dental wear, the nasal incision extends to a point posterior to the paracone of P4 or, when the tooth is not preserved, its corresponding alveolus (Figures 5a and 7a). In *Parvicornus* the overall shape and proportions of the nasal incision and relative position of the frontonasal horns and nasal bone with respect to the orbits are similar to those of *Protitanotherium*, *Diplacodon*, and most members of the Brontotheriita except *Duchesneodus*, *Notiotitanops*, and *Megacerops*, whose lateral nasal incisions are anteroposteriorly shorter.

The orbits of adult skulls of *Parvicornus* are positioned above the posterior portion of M1 and the anterior portion of M2. The anterior portion of the bony rim of the orbit is directly above the anterolateral root of M1. *Diplacodon* and most Brontotheriita have similarly positioned orbits. The orbits of *Notiotitanops* and *Mega-*

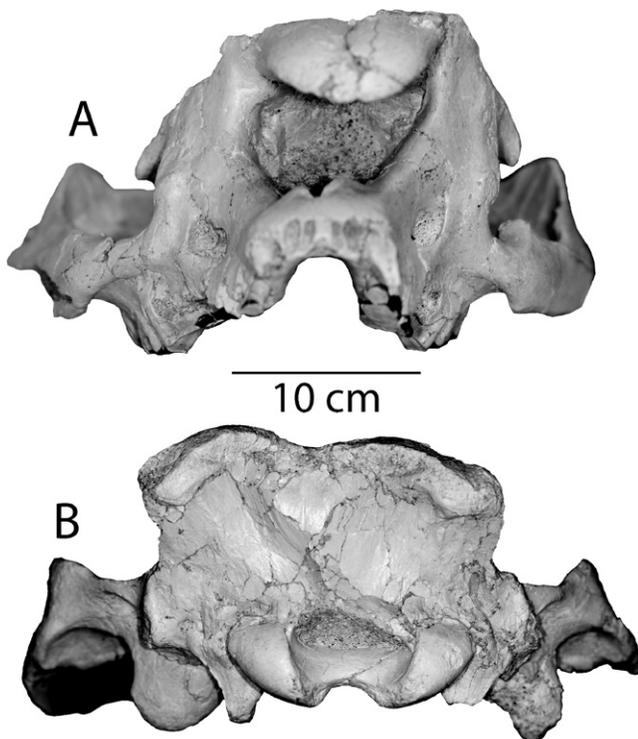


FIGURE 6. Skull (SDSNH 93245) referred to *Parvicornus occidentalis*. (A) Anterior view, (B) posterior view.

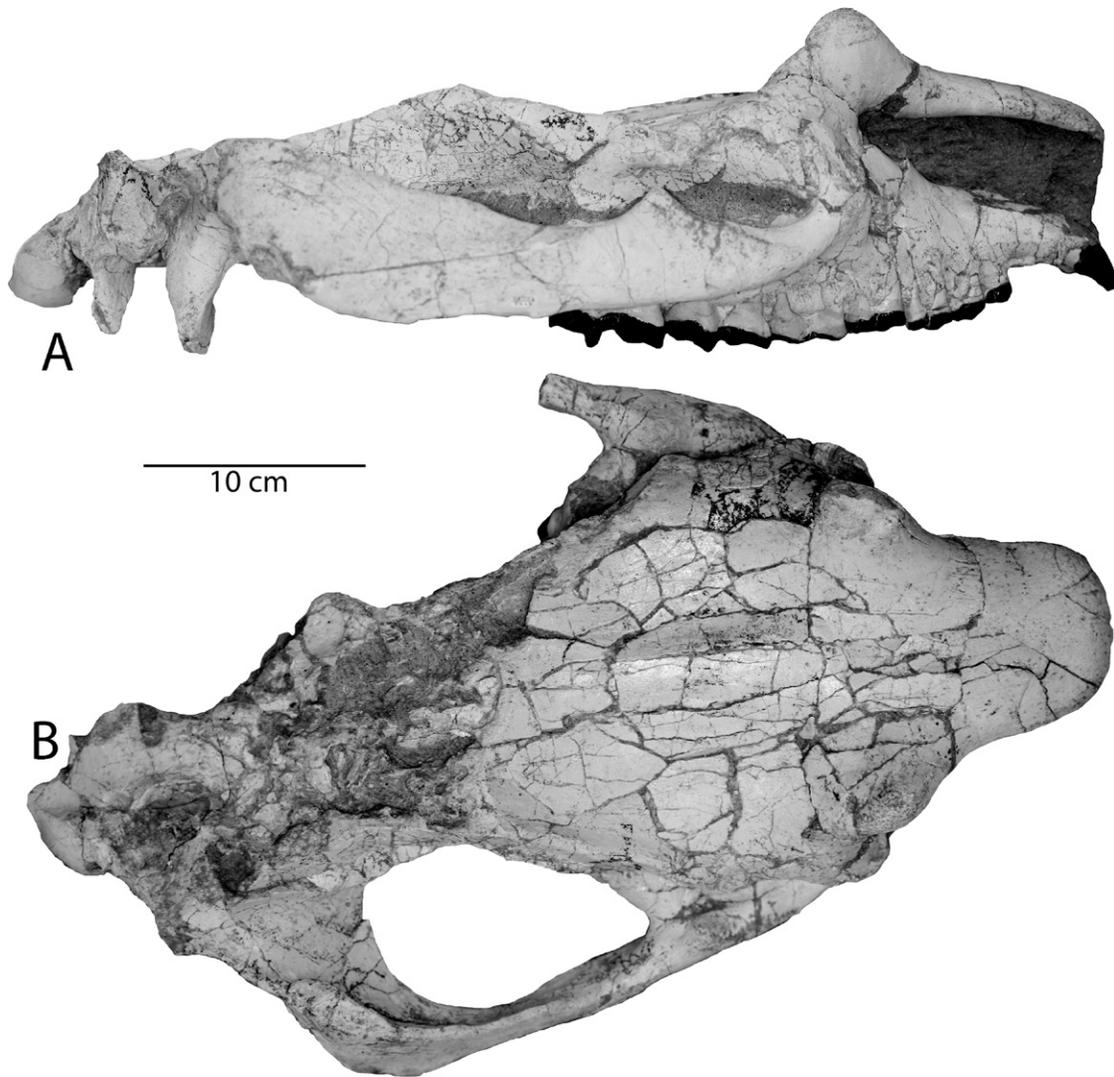


FIGURE 7. Skull (SDSNH 92050) referred to *Parvicornus occidentalis*. (A) Right view, (B) dorsal view.

cerops are positioned more anteriorly, with the anteriormost portion of the bony orbital rim entirely anterior to M1. The orbit of *Protitanotherium* is positioned more posteriorly than that of *Parvicornus*, with M1 being primarily anterior to the orbit.

In the adult and juvenile skulls of *Parvicornus* the premaxillo-maxillary rostrum tapers anteriorly dorsoventrally. The premaxillo-maxillary suture is most evident on the left side of the holotype skull (Figure 4b). The maxillary process of the premaxilla terminates on the dorsal surface of the rostrum and does not contact the nasal bone. Lack of a premaxilla–nasal contact is a derived condition seen in all brontotheriids except *Eotitanops*, the earliest true brontotheriid, in which the more plesiomorphic premaxilla–nasal contact is retained. The premaxilla of the holotype skull (SDSNH 107677) extends anterior to the canine (which is rooted in the maxilla), whereas in other Brontotheriita the premaxilla does not extend significantly anterior to the canine. In this sense, *Parvicornus* resembles *Protitanotherium*, *Diplacodon*, and other brontotheres outside the Brontotheriita, which retain unreduced premaxillae, relatively large incisors, and arched incisor rows (see description of upper incisors below).

Like nearly all horned brontotheres, the skull of *Parvicornus* has a characteristic saddle shape due to its concave dorsal surface from the

tips of the horns to the dorsal edge of the occiput. The dorsal surface of the skull is nearly flat in the transverse direction. The dorsal surface of the skull, from the orbital process of the frontal to the lateral wing of the occiput, forms an acute angle with the side of the skull. The parasagittal ridges formed by this angle are best preserved on SDSNH 93245 (Figure 5a, b). In a dorsal view of the skull, the parasagittal ridges remain widely separated throughout their length and constrict the transverse width of the posterodorsal cranial surface only moderately.

The zygomatic process of the jugal is horizontal, while the squamosal portion of the zygomatic is angled posterodorsally, giving the zygomatic arch a distinct curvature when viewed laterally. In dorsal view, the zygomatic arches of *Parvicornus* appear to be straight, thin, and strongly angled posterolaterally. There is some variation in overall zygomatic thickness; for instance, the zygomatic arches of SDSNH 92050 (Figure 7) are slightly thicker than those of SDSNH 93245 (Figure 5). None of the skulls of *Parvicornus* has the thick, laterally projected zygomatic swellings seen at the junction of the jugal and squamosal in *Dianotitan*, *Protitanops*, *Duchesneodus*, or *Megacerops*.

The occiput of the holotype (SDSNH 107667) is incomplete but better preserved on SDSNH 93245 (Figure 6). The occiput is wider

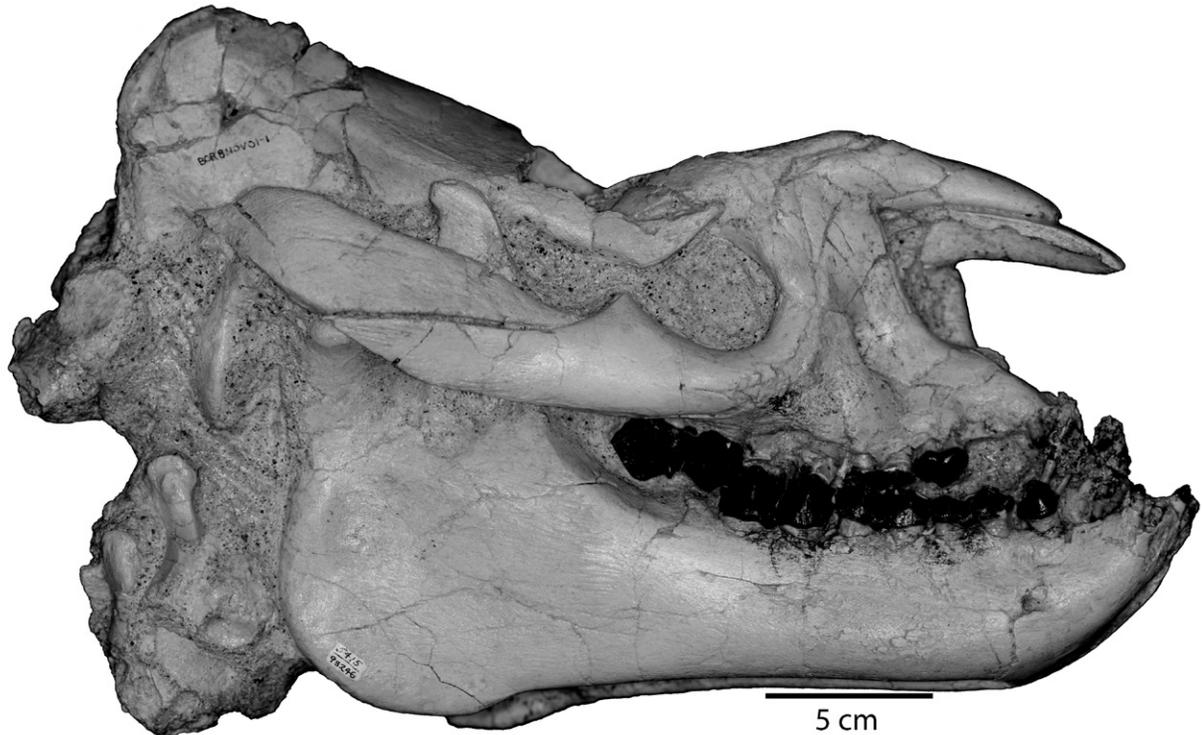


FIGURE 8. Juvenile skull and mandible (SDSNH 93246) referred to *Parvicornus occidentalis*.

in the transverse plane than in the dorsoventral plane. When viewed posteriorly, the occiput is nearly rectangular, although the middle of the occiput is transversely constricted. In lateral view, the posterior margin of the occiput arches posterodorsally, giving the occiput a backward-sloping appearance (Figure 5). In dorsal view, the posterior margin of the occiput is more deeply concave than in *Protitanotherium* and *Diplacodon* but similar to that of *Duchesneodus*. The nuchal crest is not as sharply notched as that of *Protitanops* or *Eubrontotherium*. The nuchal crest varies in thickness among the skulls of *Parvicornus*. The nuchal crest of SDSNH 93245 is comparatively quite thick (Figure 5), but another unfigured skull, SDSNH 93322, has a nuchal crest less than half as thick. The thickness of the nuchal crest in other brontotheres, such as *Eubrontotherium*, also varies, probably because of sexual dimorphism.

The position of the posterior nares in *Parvicornus* varies. On most of the adult skulls (SDSNH 107667, SDSNH 92050, SDSNH 92054, and SDSNH 93464), the anteriormost border of the posterior nares is situated between the M2s, as in *Eubrontotherium* and *Dianotitan*. In contrast, SDSNH 93245 has more posteriorly situated posterior nares, with the posterior margin slightly behind the protocones of the M3s (Figure 5c); this position more closely resembles that of *Protitanotherium*, *Diplacodon*, *Parabrantops*, *Protitanops*, and *Notiotitanops*. Other specimens we refer to *Parvicornus* have the posterior nares in an intermediate position with the anterior margin between the anterior edges of the M3s. Intraspecific variation in the position of the posterior nares is not unique to *Parvicornus*. For instance, *Duchesneodus uintens* varies to a similar degree.

Many brontotheres, including *Parvicornus*, have a distinct horseshoe-shaped bony emargination surrounding the anterior and lateral sides of the posterior nares on the ventral surface of the skull. Among the skulls of *Parvicornus*, the emargination is widest on SDSNH 93245 (Figure 5c). Other skulls, including the holotype (SDSNH 107667), have similar but narrower emargination (Figure 4c). *Diplacodon*, *Duchesneodus*, and *Dianotitan* have less emar-

gination or lack it entirely, while *Protitanotherium*, *Parabrantops*, *Eubrontotherium*, *Protitanops*, and *Notiotitanops* share similar emarginations.

Most aspects of the basicranium of *Parvicornus* are typical for brontotheriids. The postorbital portions of brontothere skulls are so elongate that the posterior nares form a pair of elongate narial canals on the ventral surface of the skull that are partitioned at the midline by an elongated vomer. In most brontotheres, including *Parvicornus*, this ventral narial canal becomes shallower posteriorly and typically runs into the sphenoid bone, extending as far posteriorly as the foramen ovale. Both SDSNH 107667 and SDSNH 93245 show this typical configuration (Figures 4c and 5c). The vomers of both specimens are incomplete, although portions of them can be seen within the sandstone matrix filling the narial canals of each skull. In *Parvicornus*, the narial canal extends about 5 mm past the foramen ovale and encroaches into the sphenoid. Enlarged ventral sphenoidal fossae, however, like those of *Diplacodon*, *Protitanops*, *Metatitan*, and *Sphenocoelus* are absent. The foramen lacerum and foramen ovale are widely separated. The transverse width of the basicranium, measured across the post-tympanic (mastoid) processes, is similar to the transverse distance across the M3s (measured from the buccal surfaces). In this respect, the proportions of the basicranium resemble most other brontotheriids with the exception of *Metatitan*, whose basicranium is extremely widened and anteroposteriorly shortened. The external auditory pseudomeatus enters the skull mediolaterally. As in most other horned brontotheres, the post-tympanic process angles anteroventrally toward the postglenoid process, occasionally making contact with it, resulting in an external auditory pseudomeatus that is either constricted ventrally or fully enclosed.

Upper Dentition—The upper dental formula of *Parvicornus* is 2/1/4/3. In Figure 9 the anterior dentitions (incisors and canines) of SDSNH 93322 (Figure 9a–b) and SDSNH 107666 (Figure 9c) are shown in close-up views along with two isolated upper incisors associated with the skull SDSNH 92056 (Figure 9d–e).

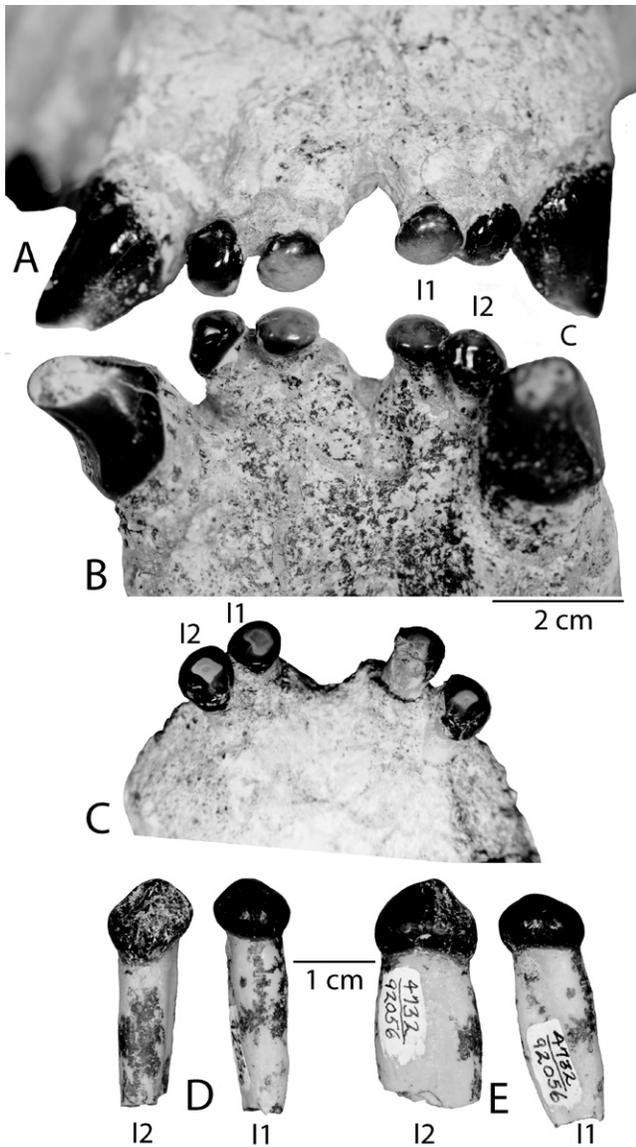


FIGURE 9. Upper incisors and canines of *Parvicornus occidentalis*. (A) Labial view of SDSNH 93322, (B) lingual view of SDSNH 93322, (C) lingual view of SDSNH 107666, (D) lingual sides of I2 and I1 associated with SDSNH 92056, (E) lateral sides of I2 and I1 associated with SDSNH 92056.

On most skulls of *Parvicornus* with partial or complete upper incisor rows the incisor rows are arched anteriorly, extending anteriorly beyond the canines. In this respect, *Parvicornus* differs from other Brontotheriida, whose incisor rows are weakly arched or straight. The skull of one specimen, however, SDSNH 93322, has an incisor row that is barely arched. The condition of this specimen more closely resembles that of other members of the Brontotheriida, whose incisor rows are typically straight and positioned either between the canines or extended only a slight distance anterior to them. The resemblance of SDSNH 93322 to other species of Brontotheriida may be significant, but it seems more likely that the “plastic” dorsoventral deformation that this skull has undergone might have deformed the shape of the incisor row.

All skulls of *Parvicornus occidentalis* have either two pairs of upper incisors or two pairs of alveoli, indicating that two pairs were

once present. The central incisors are separated by a mesial diastema that is typical of many brontotheres. The incisor roots are straight with an elliptical cross section that is longer labiolingually. The crown of the mesial incisor (I1) of SDSNH 93322 is short and globular, while the distal incisor (I2) retains a short subcaniniform cusp and a slight lingual cingulum (Figure 9a–b). Both the mesial and distal incisors of SDSNH 107667 have a small diamond-shaped wear facet, indicating that in an unworn state each incisor would have had a cusplike apex (Figure 9c). Finally, the isolated and unworn incisors associated with SDSNH 92056 show that each incisor had a slight cusplike apex more pronounced in the lateral incisor (I2; Figure 9d). In terms of shape, the upper incisors of *Parvicornus* are intermediate between the more subcaniniform I1 and I2 of *Diplacodon* and *Protitanotherium* and the amorphous globular upper incisors of *Duchesneodus* and *Eubrontotherium*. The mesiodistal widths of upper and lower second incisors (the more lateral incisor in *Parvicornus*) are plotted against lengths of the premolar row for a number of horned brontothere species in Figure 10. In the plot of upper dentitions (Figure 10a), *Parvicornus* falls near *Diplacodon*, *Notiotitanops*, *Duchesneodus*, and *Dianotitan* but forms a tight cluster that does not overlap with other species. Other species of Brontotheriida, including *Parvicornus*, *Duchesneodus*, *Eubrontotherium*, *Megacerops*, *Notiotitanops*, *Parabrantops*, and *Protitanops*, tend to group toward the left of the cluster along with *Diplacodon* and *Metatitan* because of their proportionally reduced incisors.

The upper canines of *Parvicornus occidentalis* are conical and posteriorly curved, usually with a weak lingual cingulum at the base of the crown. They are similar in size and shape to those of closely related species. As in most other brontotheres, the canines vary in size more than other dental elements, with measurements of canine crown diameter yielding a relatively high coefficient of variation (CV = 13.2) in comparison to other dental variables (Table 2). A precanine diastema (between the lateral incisor and the canine) is typically present but very short, no more than a few millimeters in length. The postcanine diastema is slightly longer than the anteroposterior length of P2. *Protitanotherium*, *Diplacodon*, and most species of Brontotheriida have postcanine diastemata of similar length, with the exceptions of *Duchesneodus*, *Megacerops*, and *Dianotitan*, whose postcanine diastemata are either very short or absent.

The premolars of *Parvicornus* are primarily described from SDSNH 105899, a crushed juvenile skull with a complete set of minimally worn upper premolars (Figure 11a). Details about premolar variation are provided by other specimens, including SDSNH 92050 (Figure 11b). An additional isolated P4 (SDSNH 105899) is shown in close-up from various angles (Figure 11d–g). Among brontotheriids, the premolars of *Parvicornus* are among the most molarized, yet they lack diagnostic traits differentiating them from those of closely related species. The semimolarized premolars have two pairs of lingual and labial cusps; however, the ectolophs are straight rather than W-shaped, and the lingual sides of the premolars retain a series of anteroposteriorly oriented lophs lacking on the true molars. The lingual cusps and crests of the premolars vary from specimen to specimen, while other aspects are more uniform. A similar pattern of intraspecific variation in premolars is found in numerous brontothere species (Mühbachler 2008).

The P1 is small with an ovoid outline and a small posteriorly shifted lingual shelf that gives the crown an oblique appearance. On the P1 of SDSNH 105899, there are two distinct labial cusps (paracone and metacone) connected by a short ectoloph. A short anterolingually angled parastyle extends from the paracone, while a short metastyle extends posteriorly from the metacone and arches lingually. On the lingual shelf a small elliptical protocone is embedded in a lingual crest that runs along the entire lingual margin of the P1 crown and connects to the metastyle at the posterolingual corner of the crown. A short protoloph connects the paracone to the protocone. The anterolingual corner of the P1 crown varies intraspecifically. In

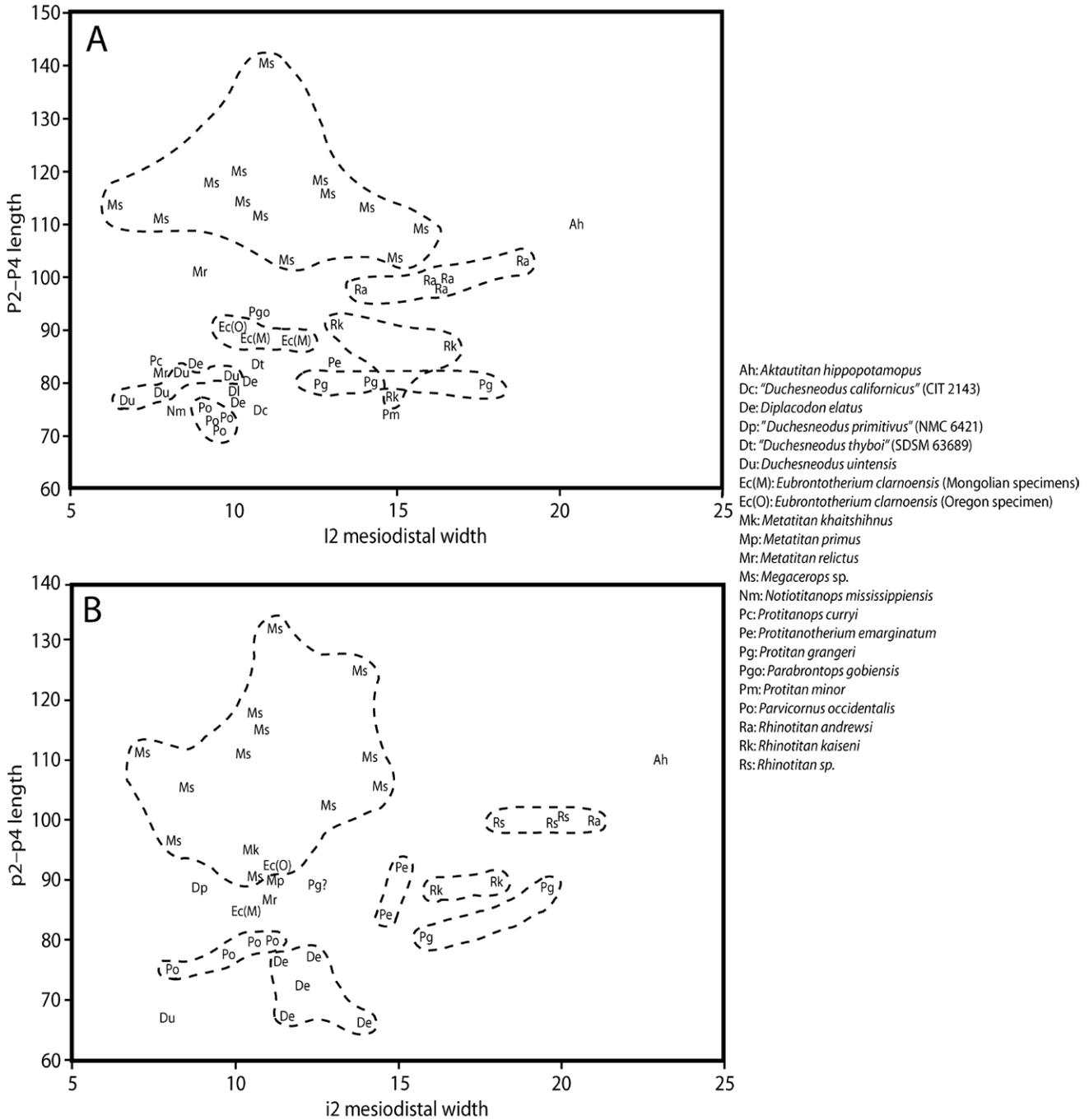


FIGURE 10. Width of second incisors plotted against total length of second to fourth premolars for various brontotheres. (A) Upper dentition, (B) lower dentition. Data for *Parvicornus occidentalis* are from Appendix 1. Data for other species are mostly from Muhlbachler (2008). All measurements are from the actual specimens except for "*Duchesneodus primitivus*," which was taken from a cast (AMNH 22450).

SDSNH 105899, the P1 has an additional crest with a well-developed wear facet on the anterolingual corner of the crown that is connected to the protoflop near its midpoint (Figure 11a). In other specimens, this additional crest appears as a simple continuation of the lingual crest that extends beyond the junction of the the protocone with the protoflop and lacks the connection with the protoflop at its midpoint. In other specimens (e.g., SDSNH 107670), the additional anterolingual crest is absent.

The P2, P3, and P4 have nearly rectangular outlines, although the lingual sides of these premolars are slightly narrower than the labial sides. The P2 parastyle of SDSNH 105899 is angled slightly lingually, giving the ectoflop of this tooth an appearance more rounded than P3 and P4 (Figure 11a). Parastyles of other specimens (SDSNH 92050) are straighter, giving the ectoflop a straighter appearance (Figure 11b). The P3 parastyle extends purely anteriorly in SDSNH 105899, but it can be angled more labially as in SDSNH 92050. The P4 para-

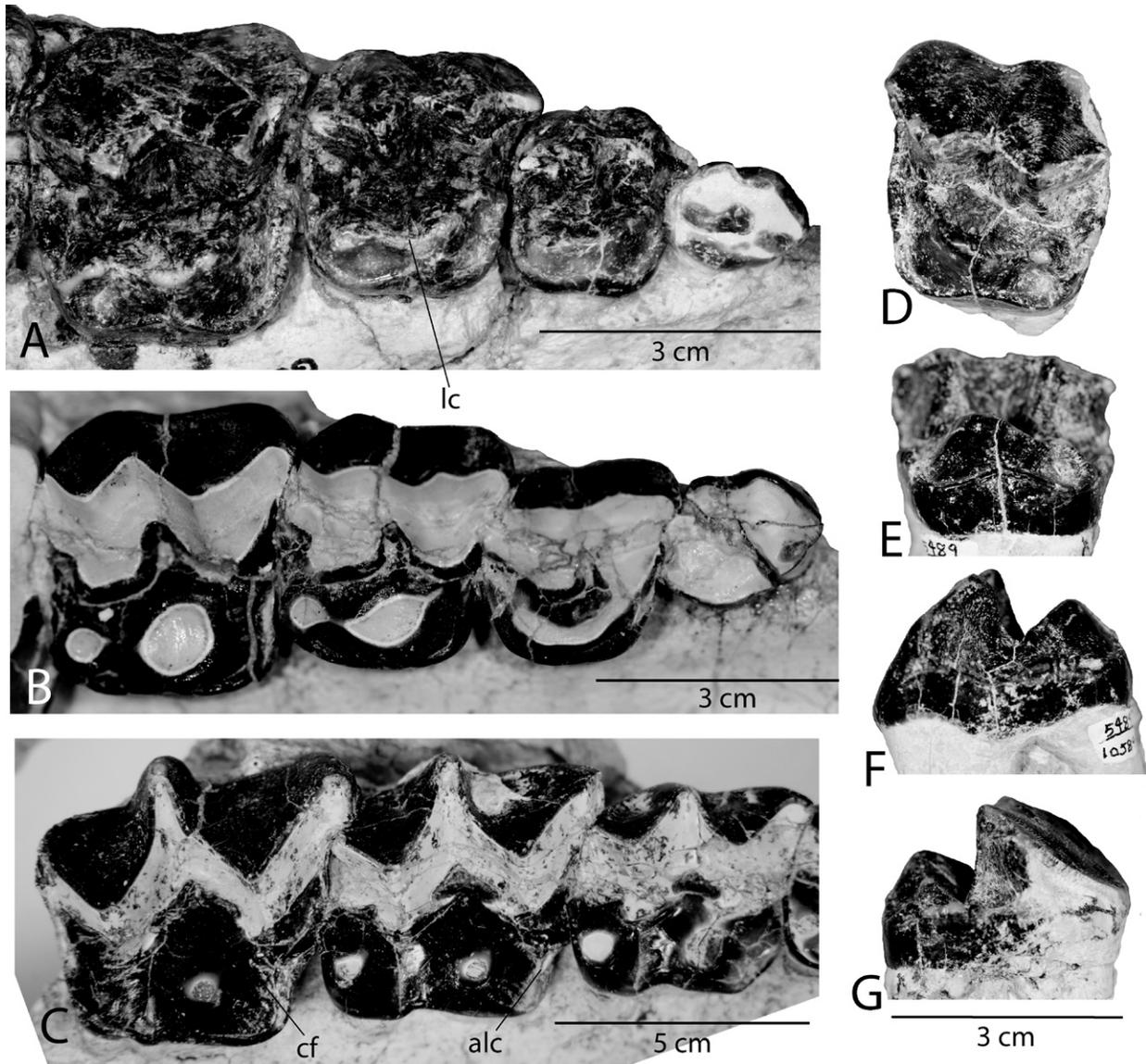


FIGURE 11. Upper cheekteeth of *Parvicornus occidentalis*. (A) Right P1–P4 of SDSNH 105899, (B) right P1–P4 of SDSNH 92050, (C) right M1–M3 of SDSNH 93322, (D–G) left P4 associated with SDSNH 105899 shown in occlusal, lingual, anterior, and posterior views.

styles of all specimens are strongly angled labially. The metastyles of P2–P4 are straight and not distinctly angled labially. The premolar ectolophs show a small but distinct paracone rib on the labial side of the paracone. The paracone rib tends to be strongest on the P2 and is progressively weaker and more indistinct on the P3 and P4. The premolars of SDSNH 105899 lack mesostyles, although weakly developed mesostyles can be found on the P4 of most other specimens of *Parvicornus*, including SDSNH 92050 (Figure 11b), SDSNH 92054, SDSNH 93322, SDSNH 107665, and SDSNH 107667. Although brontothere premolars generally lack mesostyles, they occasionally occur on P4s of many species without having become a fixed trait in any. *Parvicornus* is one of only two brontothere species, along with *Eubrontotherium*, in which a weakly developed P4 mesostyle occurs more frequently than not (Mhlbachler 2007, 2008).

The lingual sides of the P2, P3, and P4 vary more extensively, although there is always a protocone and hypocone on each of these premolars. Generally, the protocone and hypocone are most similar in

size to each other and strongly connected by a lingual crest on the P2. The hypocone becomes progressively smaller relative to the protocone and is less strongly connected to it in more posterior premolars. However, there is considerable intraspecific variation in these traits. The P2 protocone and hypocone of SDSNH 105899 are of about equal size and strongly connected by a lingual crest. The hypocone is progressively smaller on P3 and P4, and the lingual crest becomes thinner and lower, although it remains prominent in all three of these premolars (Figure 11a). In SDSNH 92050, the protocone, hypocone, and lingual crest are fused into a single structure that arches around the lingual side of the crown. This configuration largely has to do with the fact that the P2 of that specimen is worn; however, the hypocones of P3 and P4 of the same specimen are much smaller, and the lingual crest is weak (P3) or absent (P4). Most specimens of *Parvicornus*, including those with the premolars less worn, are most similar to SDSNH 92050 in terms of the relative sizes of the lingual cusps and the degree to which they are connected by a lingual crest. The

lingual sides of the premolars (P2–P4) of other specimens, such as SDSNH 107670, are morphologically intermediate between SDSNH 105899 and SDSNH 92050. They demonstrate that in *Parvicornus* the relative sizes of the lingual cusps, and the degree to which they are connected by a lingual crest, vary continuously.

Small preprotocristae are visible on the P2, P3, and occasionally on the P4 (most easily seen in Figure 11a). The preprotocrista is strongest on the P2 and fully connects the protocone to the lingual base of the paracone. There is generally a weak preprotocrista on the P3 that is only weakly or not at all connected to the paracone. A very weak preprotocrista is found on the P4 of some specimens (SDSNH 105889) but is altogether absent on others (SDSNH 92050). The anterior cingula of the premolars of *Parvicornus* are thick and higher in relief than the lingual or posterior premolar cingula. This is particularly evident on the P2, P3, and P4 of SDSNH 92050, where small wear facets are formed on the anterior cingula. A similar rise on the anterolingual cingula of the premolars is also seen occasionally in *Duchesneodus* and *Megacerops*. A similar rise in the enamel is seen near the midpoint of the lingual cingula of the premolars but not on their posterior cingula.

The molars of the holotype skull (SDSNH 107667) are shown in Figure 4c. An additional upper molar row (SDSNH 93322) is shown in Figure 11c. The molars have the W-shaped ectoloph characteristic of brontotheriids. Additionally, the molars of *Parvicornus* exhibit numerous characteristics typical of advanced brontotheres. The ectoloph is tall with a strong lingual vector to its angle. The labial ribs of the paracone and metacone are very weak. The band of enamel defining the lingual margin of the ectoloph is much thinner than that on the labial surface. The lingual margins of the paracone and metacone are wedge shaped; this feature is most evident on molars that are not heavily worn such as those of the holotype (SDSNH 107667). The anterior cingulum of the molars is thin and passes proximally to the distal peak of the parastyle. A central molar fossa is evident in the middle of each molar crown, and a distinct anterolingual cingular cusp can be seen on each just anterior to the protocone. As seen on the molars of SDSNH 93322, these anterolingual cingular cusps tend to develop small wear facets. In all specimens of *Parvicornus* the M3 hypocone is poorly developed, generally appearing as a small bump on the posterolingual corner of the tooth or as a raised ridge along the posterolingual cingulum.

Mandible and Lower Dentition.—The description of the jaw and lower dentition of *Parvicornus* is based primarily on SDSNH 105789 (Figures 12a–c and 13a–b), a complete mandible with a complete lower dentition. Figures 12 and 13 also show close-ups of the lower dentitions of two subadults with minimally worn teeth, SDSNH 107731 (Figure 12d–e and Figure 13c) and SDSNH 92056 (Figures 12f and 13d).

SDSNH 105789 is moderately compressed transversely. The sandstone matrix has been left between the right and left rami, but a small hole has been punched through anteriorly, revealing the posterior margin of the symphysis. The condyle and coronoid processes appear to be in good condition and are shaped typically for brontotheres. The mandibular symphysis of *Parvicornus* is proportionally similar to those of *Protitanotherium* and *Eubrontotherium* and transversely narrower than that of *Diplacodon*. The transverse width of the mandible of *Parvicornus* at the canines is similar to its transverse width at the p2s; in this *Parvicornus* differs distinctly from *Duchesneodus*, in which the width at the canines is much narrower.

In a lateral view of the mandible, the inferior margin of the symphysis is angled about 45° from the horizontal, and its convex surface transitions smoothly into the inferior (ventral) surface of the horizontal ramus. This aspect of the mandible of SDSNH 105789 strongly resembles that of *Diplacodon*. Most other mandibles of *Parvicornus* are very similar to those of SDSNH 105789 in this respect; however, a few specimens (e.g., SDSNH 92047) have a symphysis

with a much flatter inferior surface with a more abrupt transition. Similarly, the inferior surfaces of the symphyses of *Protitanotherium*, *Eubrontotherium*, and *Duchesneodus* tend to be flat or even convex in lateral view, with angular or abrupt transitions to the inferior surface of the horizontal ramus. The shapes of the inferior margins of the symphyses of the mandibles of *Megacerops* vary in this regard, with some having a convex surface transitioning smoothly into the horizontal ramus and others having flat or even convex surfaces with more abrupt transitions.

The posterior margin of the mandibular symphysis of *Parvicornus* is positioned between the anterior margins of the p4s (e.g., SDSNH 105789) or slightly more posteriorly, between the metaconids of the p4s (e.g., SDSNH 92048). Although the position of the posterior margin of the symphysis in *Parvicornus* varies slightly, it resembles that of *Protitanotherium* and most specimens of *Diplacodon*. In *Eubrontotherium*, *Duchesneodus*, *Notiotitanops*, and *Megacerops* the posterior margins consistently lie more posteriorly, between the p4 talonids or the m1 trigonids.

The mandibular dental formula of *Parvicornus* is 3/1/4/3. This species is one of only a few brontotheres, including *Eubrontotherium* and *Duchesneodus*, known to retain three pairs of lower incisors but only two pairs of upper incisors. In contrast, *Megacerops* has no more than two pairs of upper and lower incisors. The incisors of the Brontotheriita tended to fall out over the course of their lives. For instance, mandibles of *Duchesneodus* and *Megacerops* with extensive dental wear (indicating old age) usually have less than three or two incisors, respectively. *Parvicornus* too tended to lose incisors with age. A mandible (SDSNH 107733) with heavily worn dentition retains only two pairs (i1 and i2) of lower incisors.

Figure 10b is a plot of the mesiodistal width of i2 versus the length of p2–p4. *Parvicornus* forms a loose cluster that does not overlap with other species but lies near *Diplacodon*, *Eubrontotherium*, and *Duchesneodus*. The coefficients of variation of some lower-incisor variables are rather high (Table 3), probably because of small sample size ($n = 3$ or 4) and one specimen (SDSNH 107733) having excessively worn incisors.

The lower incisors of SDSNH 105789 form a distinctly arched row that extends anterior to the canines (Figure 13b). The subadult specimens, including SDSNH 92056 and 107731, appear to have the incisor row even more strongly arched (Figure 13c–d). In this character *Parvicornus* resembles *Diplacodon* and *Protitanotherium* but differs from other species of Brontotheriita, whose lower incisor rows are straighter and do not extend nearly as far anteriorly beyond the level of the canines. There are no significant diastemata between any of the incisors or between the i3 and canine. The i2 is distinctly larger than the i1 and i3, as in many advanced brontotheriids. The lower incisors of SDSNH 107731 and SDSNH 92056 are minimally worn, and each of the incisors has a wedge-shaped crown with a lingual cingulid and a thin vertical rib on the lingual surfaces of each incisor. These features are gradually eliminated with wear. The incisors of SDSNH 105789 are worn slightly, giving them a somewhat more bulbous appearance. Labial cingulids are not found on the incisors of any specimen.

Like the upper canines, the lower canines of *Parvicornus* vary in size more than the more posterior dental elements (Table 3), suggesting that they are sexually dimorphic. The postcanine diastema of SDSNH 105789 is slightly longer than the anteroposterior length of the p2. In this respect, it is most similar to that of *Eubrontotherium* and is distinctly longer than the very short postcanine diastemata of *Duchesneodus* and *Megacerops*.

The p1 is small and narrow, with a single cusp and a small simple talonid heel. The p2 trigonid and p2 talonid have nearly equal buccolingual widths. The p2 trigonid is anteroposteriorly longer than the talonid but not twice as long. The p3 and p4 trigonids are about the same length anteroposteriorly as their respective talonids, although

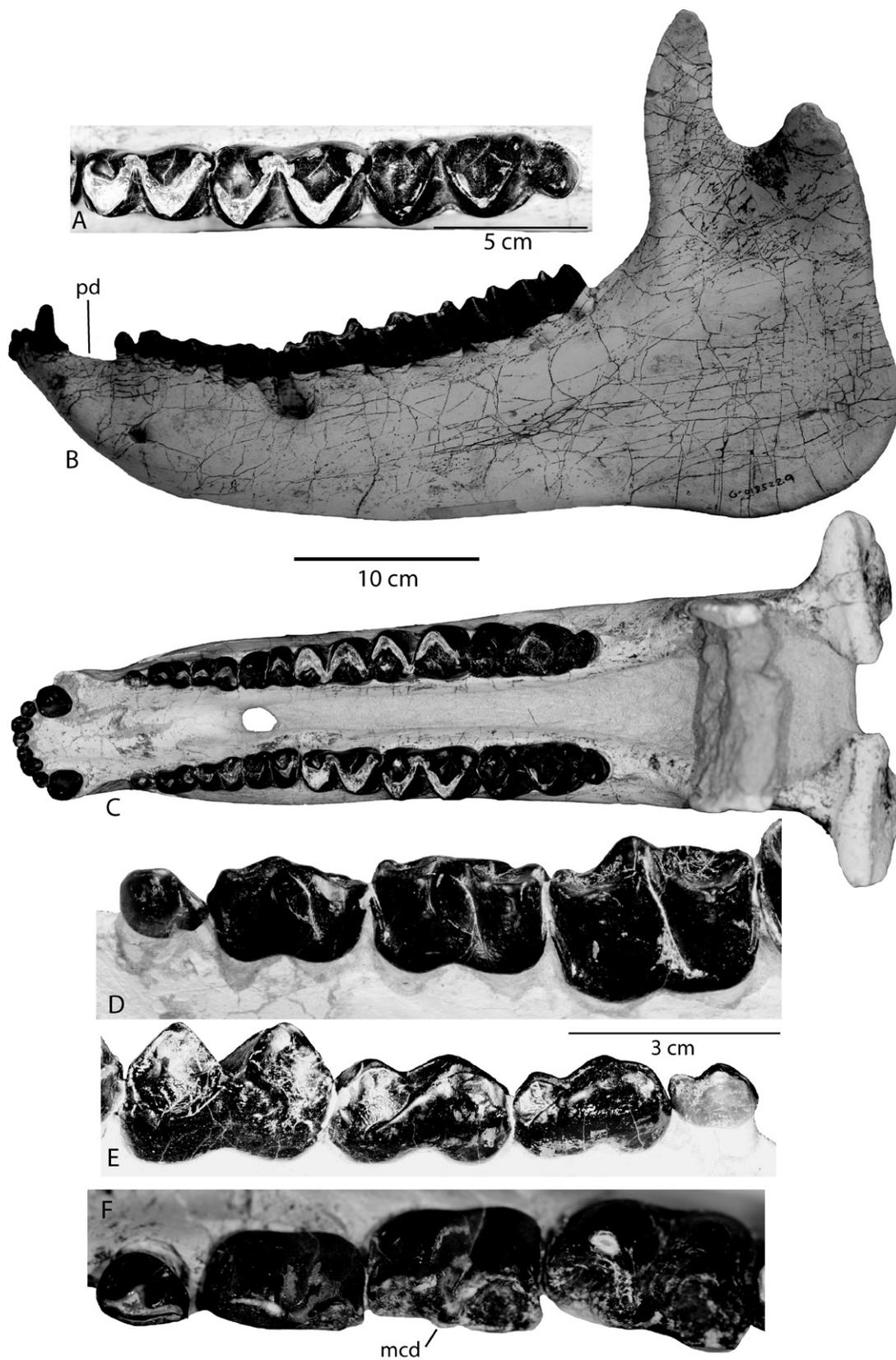


FIGURE 12. Mandible and lower dentition of *Parvicornus occidentalis*. (A) Left molars of SDSNH 105789, (B) left view of SDSNH 105789, (C) dorsal view of SDSNH 105789, (D) left premolars of SDSNH 107731 rotated to show labial side, (E) left premolars of SDSNH 107731 rotated to show lingual side, (F) right premolars of SDSNH 92056.

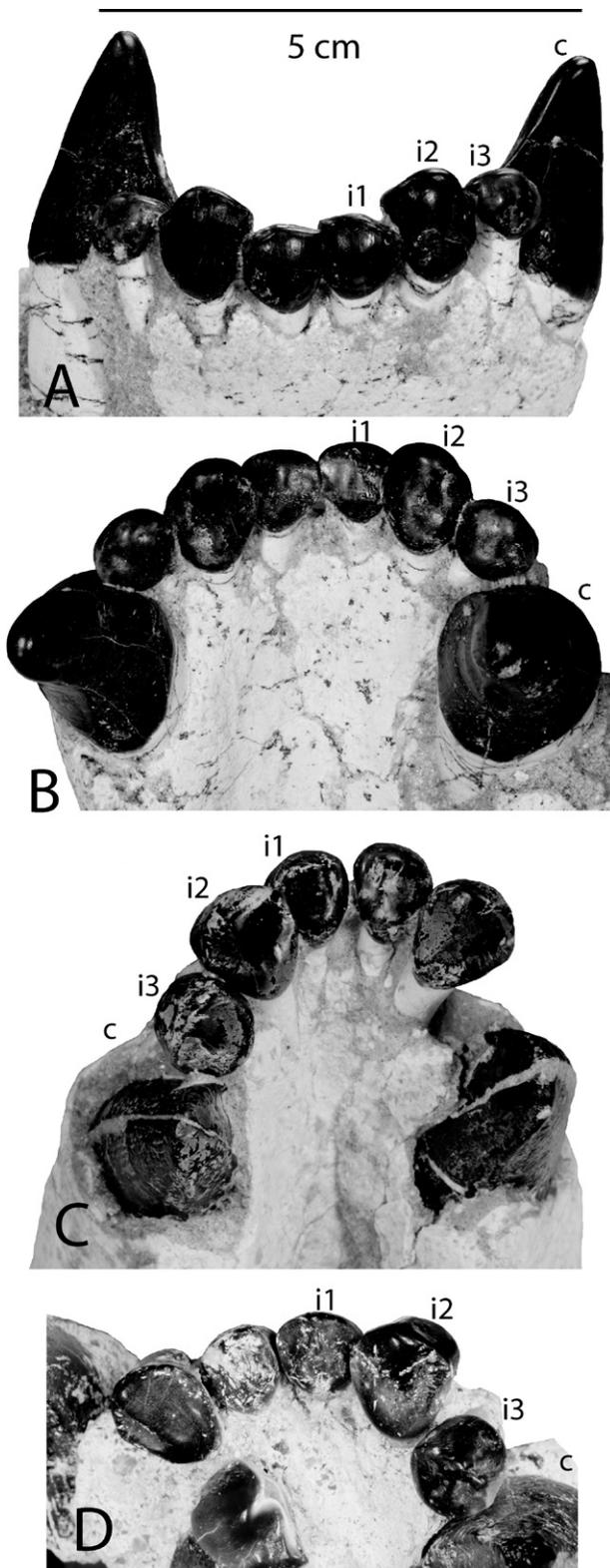


FIGURE 13. Lower incisors and canines of *Parvicornus occidentalis*. (A) Labial view of SDSNH 105789, (B) lingual view of SDSNH 105789, (C) lingual view of SDSNH 107731, (D) lingual view of SDSNH 92056.

the p3 and p4 talonids are buccolingually wider than their respective trigonids. The paralophid of p2 is nearly straight but arches slightly lingually, creating a small lingual trigonid notch. The p2 protolophid is straight but angled slightly lingually as well. The paralophid and protolophid of p3 are strongly angled lingually, creating a broad but shallow lingual notch. The paralophid and protolophid of p4 are longer and arch fully lingually. The talonid of the p2 has a short cristid obliqua and hypolophid with a shallow lingual talonid notch. In p3 and p4 the cristid obliqua and the hypolophid of the talonids are longer, with more molariform talonid basins. Labial and lingual cingulids are absent from the premolars. The premolars of *Parvicornus* are not clearly differentiated from those of *Diplacodon*, *Protitanotherium*, and *Eubrontotherium*. On the other hand, *Duchesneodus* and *Megacerops* tend to have more molariform premolars with a less elongate p2 trigonid, a wider p2 talonid, and more distinct labial cingulids.

In *Parvicornus*, a metaconid is always present on the p4, always absent on the p2, and usually absent on the p3 (e.g., SDSNH 107731), though a well-developed metaconid can be seen on the p3 of SDSNH 92056 (Figure 12f) at the junction of the protolophid and the cristid obliqua. One interesting aspect of variation in brontotheriid premolars is the presence or absence of a p3 metaconid. Most basal hornless brontotheriids lack it, while many more advanced horned species have it well developed. However, in a number of taxa, including *Metarhinus* (a hornless early Uintan genus) and *Rhinotitan* (a horned Sharamurian central Asian genus), a p3 metaconid may be either present or absent. *Parvicornus* is also polymorphic in this character. *Protitanotherium* and *Eubrontotherium* are not known to have a p3 metaconid, but as these species are known from rather small samples, such a polymorphism cannot be ruled out. On the other hand, *Diplacodon*, *Duchesneodus*, and *Megacerops* all express a p3 metaconid consistently.

The lower molars of *Parvicornus* (Figure 12a) are not different from those of other advanced brontotheriids. Typical characteristics include shallow occlusal basins, thin lingual enamel, and an elongate m3. Lingual cingulids are absent, while labial cingulids tend to be weak and discontinuous around each labial cusp.

Vertebrae.—SDSNH 107694 includes an associated atlas (Figure 14a–d) and axis (Figure 14e–f). Both elements are uncrushed, although the atlas is missing the dorsal arch and most of the right transverse process. Though incomplete, the dorsal tubercle of the atlas appears to have been rather low. The dorsal tubercles of *Diplacodon* (CMNH 2859), *Eubrontotherium* (PIN 3109-92), *Rhinotitan* (IVPP V3254-1), *Aktautitan* (KAN N2/875), and (cf.) *Embolotherium* sp. (PIN 3110-13) are generally taller. However, at least some specimens of *Megacerops* (YPM 12048) have a rather low dorsal tubercle similar to that of SDSNH 107694. The ventral tubercle of the atlas of SDSNH 107694 has a very prominent ventral tubercle that protrudes posteriorly from the ventral arch. This feature resembles some specimens of *Megacerops* (CMNH 114), although it is less prominent in other specimens of *Megacerops* (YPM 12048). In *Rhinotitan andrewsi* (Osborn, 1925) (IVPP V3254-1), *Diplacodon elatus* (CMNH 2859), *Eubrontotherium clarnoensis* (PIN 3109-92) and *Aktautitan hippopotamopus* Muhlbachler et al., 2004b (KAN N2/875), the ventral tubercle is less prominent and protrudes more ventrally than posteriorly.

The atlas of SDSNH 107694 is perforated by three discernible foramina. The intervertebral foramen emerges from the vertebral canal and opens on the dorsal surface of the lateral mass, just posterior to the anterior articular cavity. Immediately lateral to the intervertebral foramen, a fully enclosed alar foramen can be seen. A similar alar foramen, which transmits portions of the first cervical nerve and vertebral artery, is seen in the atlas of *Equus* spp. (Sisson and Grossman 1953), but a fully enclosed alar foramen does not typically occur among brontotheres or other early perissodactyls. Instead, the

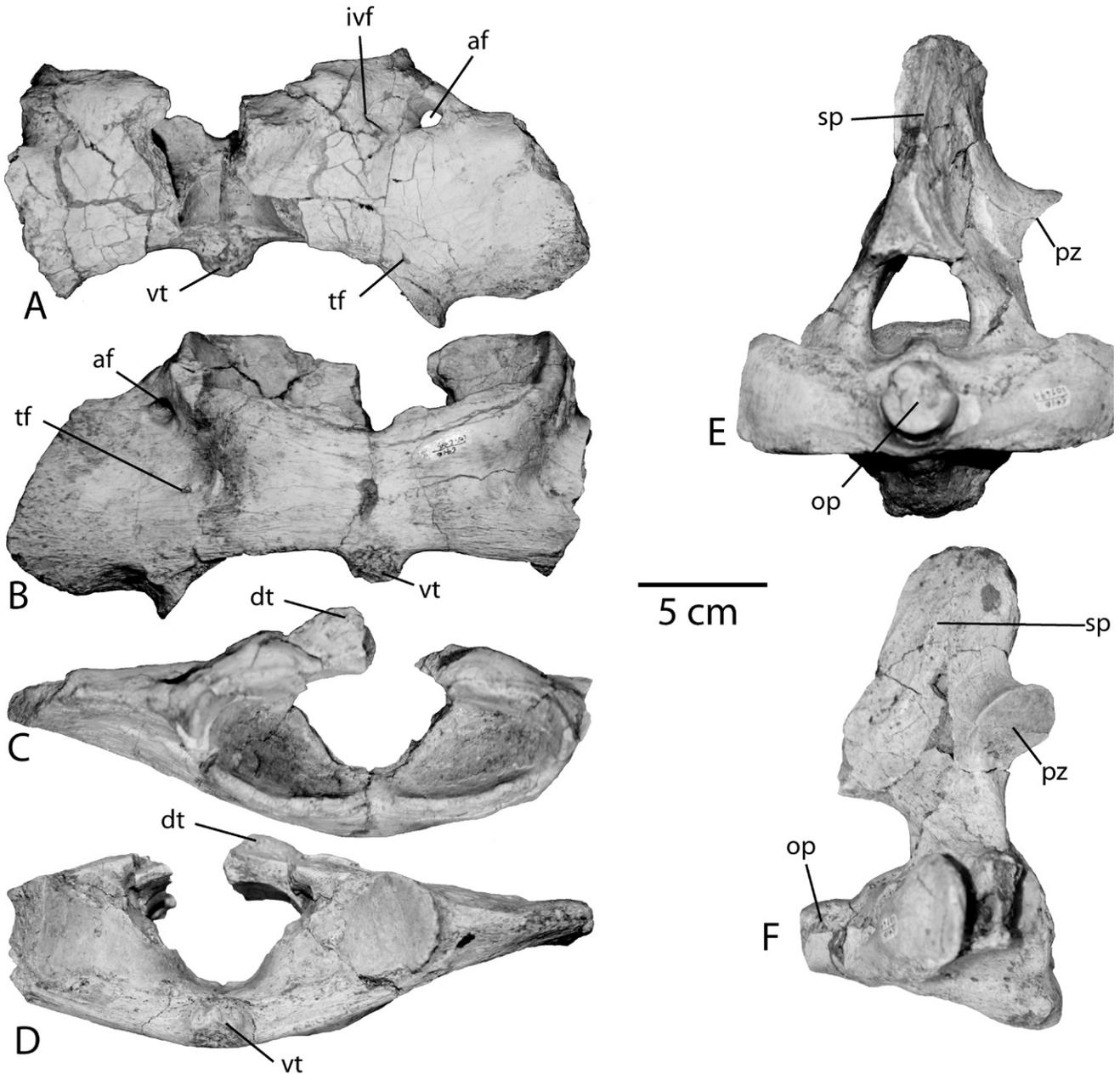


FIGURE 14. Atlas and axis of *Parvicornus occidentalis* (SDSNH 107694). (A) Dorsal view of atlas, (B) ventral view of atlas, (C) anterior view of atlas, (D) posterior view of atlas, (E) anterior view of axis, (F) left view of axis.

first cervical nerve and vertebral artery course through a deep notch rather than a fully enclosed foramen. At least one axis of *Megacerops* sp. (CMNH 114) is figured as having a fully enclosed alar foramen (Figure 621B in Osborn 1929), a condition duplicated in no other brontothere atlas, to our knowledge. It is unclear if the fully enclosed alar foramen of SDSNH 107694 represents a diagnostic species-level characteristic of *Parvicornus* or is only an anomaly. The third foramen is a small transverse foramen through both the dorsal and ventral surfaces of the right mass of the atlas of SDSNH 1107694. The transverse foramen of the atlas is large in more basal brontotheres, such as *Palaeosyops* and *Metatelmatherium* (Osborn 1929). The transverse foramen persists but is smaller in most advanced horned species, including *Rhinotitan* (IVPP V3254-1), *Diplacodon* (CMNH

2859), *Eubrontotherium* (PIN 3109-92), *Aktautitan* (KAN N2/875) and (cf.) *Embolotherium* sp. (PIN 3110-13). The transverse foramen is apparently absent in at least some specimens of *Megacerops* (e.g., YPM 12048; Osborn 1929). The transverse foramen persists in a diminished condition in the atlas of *Parvicornus*.

In comparison to contemporary amynodontid rhinocerotoids, the axes of brontotheres, including SDSNH 107694, are anteroposteriorly compressed because of a shorter odontoid process and shorter wedge-shaped centrum. However, the spinous process of the axis of SDSNH 107694 is rather tall and anteroposteriorly narrow in comparison to most other brontotheriid axes described in the literature. The spinous processes of the axes of *Diplacodon* (CMNH 2859), *Rhinotitan* (IVPP 3254-1), *Eubrontotherium* (PIN 3109-93),

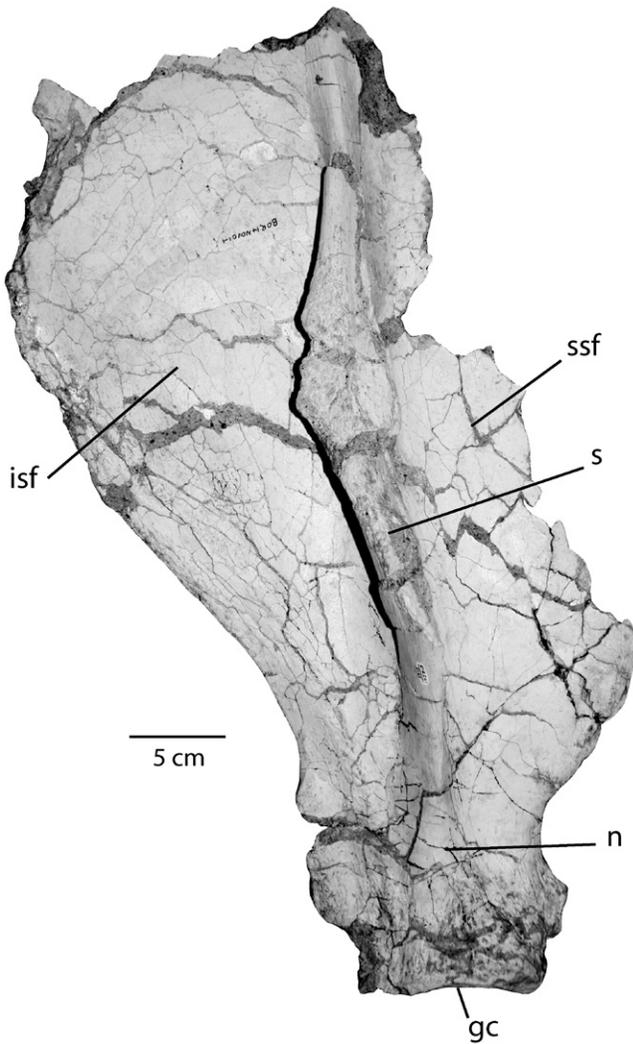


FIGURE 15. Partial right scapula of *Parvicornus occidentalis* (SDSNH 105813).

and *Megacerops* (e.g., YPM 12048) are anteroposteriorly wider and angled more posteriorly. The proximal bases of the spinous processes of the axes of *Rhinotitan* and *Eubrontotherium* extend as far or almost as far anteriorly as the tip of the odontoid process. The same seems to have been true of SDSNH 107694, though the anterior tip of the dorsal arch is broken, preventing a full assessment of this character. The spinous process of the axis of SDSNH 107694 does not greatly overhang the postzygapophyses. In this respect, it closely resembles the axes of *Rhinotitan* and *Eubrontotherium*. In contrast, axes of *Diplacodon* and *Megacerops* have spinous processes that overhang the postzygapophyses farther, in some cases by several centimeters.

Forelimb.—SDSNH 105813 is a partial but undistorted right scapula (Figure 15). There are few complete brontotheriid scapulae with which it can be compared, but in its overall proportions, SDSNH 105813 is similar to scapulae of *Aktautitan* (KAN N2/875) and *Metatitan* (PIN 3745-33) although not as broad as those of some specimens of *Megacerops* (e.g., NMNH 4262). The scapular neck is short and strongly notched anteriorly, while the proximal portion of the anterior edge of the scapula is rounded. These characteristics are typical of brontothere scapulae. The scapula reaches its greatest width

at a point about two-thirds of its length. In most other brontotheres, the posterior margin is pointed at this location, forming a roughly triangular infraspinous fossa. Although the posterior margin of SDSNH 105813 is damaged, it appears to have been more rounded or at least less distinctly triangular. The glenoid cavity is shallow, with its lateral edge forming only a slight concavity. The spine of the scapula thickens dorsally until about two-thirds of the way up, where the posterior margin forms a point that projects posteriorly. From that point the spine thins dorsally. The shape and thickness of the spine is not unusual for brontotheres of similar size, although much larger brontotheres, particularly the large specimens of *Megacerops* (e.g., YPM 12048), have much thicker and more rugose scapular spines.

Several humeri are attributable to *Parvicornus*. Only one of these, SDSNH 107698, preserves the complete length (Figure 16a–b). An additional partial humerus with a more complete and less distorted distal half (SDSNH 92080) is illustrated in Figure 16c–e. SDSNH 107698 appears to be atypically long and slender in comparison to other brontothere humeri, but this aspect of its appearance is partially artificial. Much of the deltoid crest of SDSNH 107698 is missing, and a portion of the lateral epicondyle has been displaced medially into the olecranon fossa. Though missing its proximal end, SDSNH 92080 has its distal half undamaged and indicates that the humerus of *Parvicornus* is proportioned like that of *Rhinotitan* (IVPP V3254-1) and *Diplacodon* (CMNH 2860) but somewhat more robust. It is much more elongate than that of *Aktautitan* (KAN 2/875) and more gracile than that of *Megacerops* (e.g., YPM 12048). The lateral tuberosity is not preserved on any of the humeri shown in Figure 16, but in one humerus of an adult *Parvicornus* (SDSNH 105819) the lateral tuberosity is anteroposteriorly wide, transversely narrow, and rises above the humeral head. Although the deltoid crest and/or tuberosity is broken or damaged in all available humeri of *Parvicornus*, the specimens all suggest that the deltoid tuberosity extended somewhat farther laterally than the deltoid crest, forming a small tubercle. This condition resembles that of most brontotheres, in which the deltoid tuberosity is continuous with the deltoid crest or forms a minor tubercle, but it differs from that of *Megacerops* (YPM 12048), in which the deltoid tuberosity is massive and projects laterally farther than the deltoid crest. The deltoid tuberosity of *Eubrontotherium* (PIN 3109-100) is much smaller and less pronounced than that of *Parvicornus*. The distal trochlea is asymmetrical; the medial condyle is larger than the lateral condyle. The undamaged lateral epicondyle of SDSNH 92080 is prominent, with a proximolaterally projecting tubercle at its apex. The medial epicondyle is less prominent. The lateral epicondyle of *Eubrontotherium* (PIN 3109-100) is much smaller and lacks the tubercle seen on the larger and more rugose lateral epicondyles of *Parvicornus* humeri. The olecranon fossa is proximodistally elongate, mediolaterally narrow, and angled distomedially. The narrow appearance of the olecranon fossa is attributable largely to the inward curvature of the lateral epicondylar margin, to a lesser extent to the medial condylar margin of the olecranon fossa. The distinctive tall and narrow shape of the olecranon fossa is shared with numerous brontotheres such as *Rhinotitan*, *Diplacodon*, and *Eubrontotherium*, while other brontotheres, including *Aktautitan* and *Megacerops*, appear to have much wider olecranon fossae.

Hindlimb.—Figure 17 depicts two femora of *Parvicornus*. SDSNH 105824 (Figure 17a–c) and SDSNH 107698 (Figure 17d–e). SDSNH 107698 preserves the complete length, although it is crushed anteroposteriorly, particularly at the distal end. The shaft of SDSNH 105824 seems artificially shortened, but it offers a complete and undistorted view of the distal end.

The femoral head is less rounded than the femoral heads of *Dolichorhinus* and other hornless brontotheres figured by Osborn (1929), as are those of other large brontotheres such as *Aktautitan* (KAN N2/875) and *Megacerops* (YPM 12048). The greater trochanter of SDSNH 107698 forms a distinct tuberosity that extends dorsally

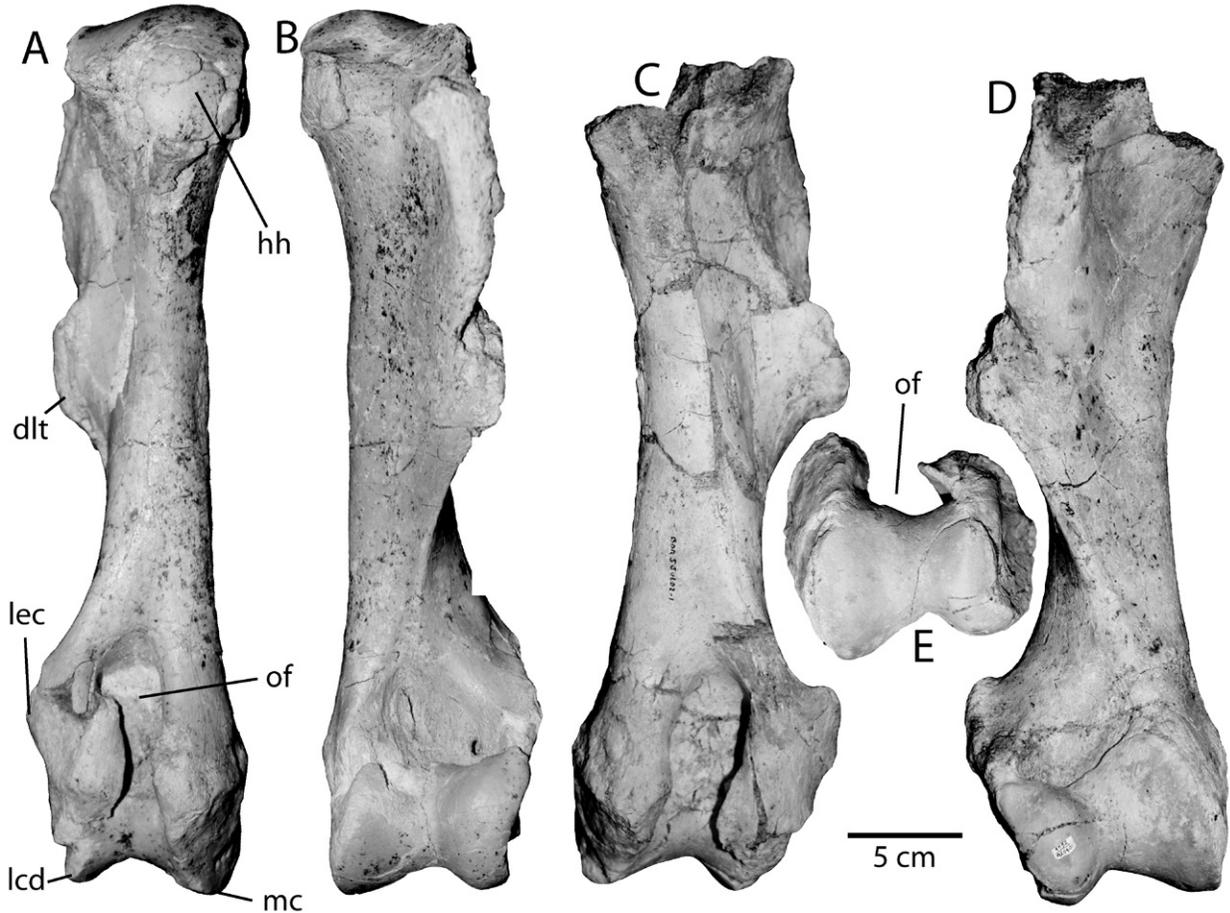


FIGURE 16. Humeri of *Parvicornus occidentalis*. (A) Posterior view of left humerus (SDSNH 107698), (B) anterior view of SDSNH 107698, (C) posterior view of right humerus (SDSNH 92080), (D) anterior view of SDSNH 92080, (E) distal view of SDSNH 92080.

higher than the femoral head. The greater trochanter of *Dolichorhinus* is larger but similar in height. On the other hand, the greater trochanter of *Megacerops* is similar to that of SDSNH 107698 but is more strongly angled medially. Among brontotheres, the lesser trochanter usually occurs on the medial side of the femoral shaft in a position slightly higher than the third trochanter. A lesser trochanter is not evident on SDSNH 107698. However, a 5.5-cm portion of the medial side of the femoral shaft has a broken surface in the approximate position where the lesser trochanter is expected, so it is possible that a poorly developed lesser trochanter was actually present. A small and incomplete lesser trochanter can be seen on SDSNH 105824. The third trochanter is positioned on the proximal part of the femoral shaft and is poorly developed in comparison to most perissodactyls but resembles that of other brontotheres. Many hornless brontotheres, such as *Palaeosyops* and *Dolichorhinus*, and very large horned brontotheres, such as *Megacerops*, have more prominent lesser and third trochanters, while *Aktautitan* has a third trochanter that is even more dramatically reduced than that of SDSNH 107698. In the size and position of the third trochanter and the reduction of the lesser trochanter *Parvicornus occidentalis* resembles *Rhinotitan* (IVPP V3254-1) and *Eubrontotherium* (PIN 3109-104). On the distal end of the femur, the medial trochlear ridge and medial condyle are larger than the lateral trochlear ridge and lateral condyle. This moderate amount of asymmetry is also found in the distal end of the femur of other brontotheres, such as *Aktautitan* (KAN N2/875; Mhlbachler et al. 2004b), but it never approaches the more extreme degree of asymmetry found among horses and rhinos (Hermanson and MacFadden 1996).

Juvenile Forelimb.—In addition to a juvenile skull, SDSNH 93246 includes an articulated right forelimb (Figure 18). The scapula and humerus are still largely buried in sandstone matrix, while the ulna, radius, and manus are almost completely exposed. Distal to the unfused distal epiphysis of the radius is a completely articulated set of carpals. The articulated condition of the carpals prevents a detailed description of the articular surfaces of each element; however, the articular relationships of the individual carpals do not seem to differ from those of other brontotheres. The carpus is proportionally taller and more slender than those of other large-bodied horned brontotheres (*Megacerops*, *Aktautitan*, and *Embolotherium*) for which an articulated manus is available (Osborn 1929, Yanovskaya 1980, Mhlbachler et al. 2004b). *Parvicornus* is more similar in this regard to smaller hornless brontotheres such as *Mesatirhinus* and *Dolichorhinus* (Peterson 1924, Osborn 1929), but this resemblance may simply reflect the specimen's juvenile condition.

Partial Skeleton of cf. Parvicornus occidentalis.—SDSNH 105766 (Figure 19) is a crushed skull and partial skeleton from the Duchesneau *Harpagolestes* quarry (SDSNH locality 5721), which is stratigraphically lower than the Bone Sands localities containing *Parvicornus* (Figure 2). This specimen is also considerably larger than any of the individuals we refer to *Parvicornus*. Given the specimen's lower stratigraphic position and larger size, its taxonomic identity is questionable. The skull is too damaged to be identified as *Parvicornus* or another species, such as *Eubrontotherium*, *Protitanops*, or *Notiotitanops*. Nonetheless, given the rarity of associated cranial and postcranial material for most species of Brontotheriita, we have

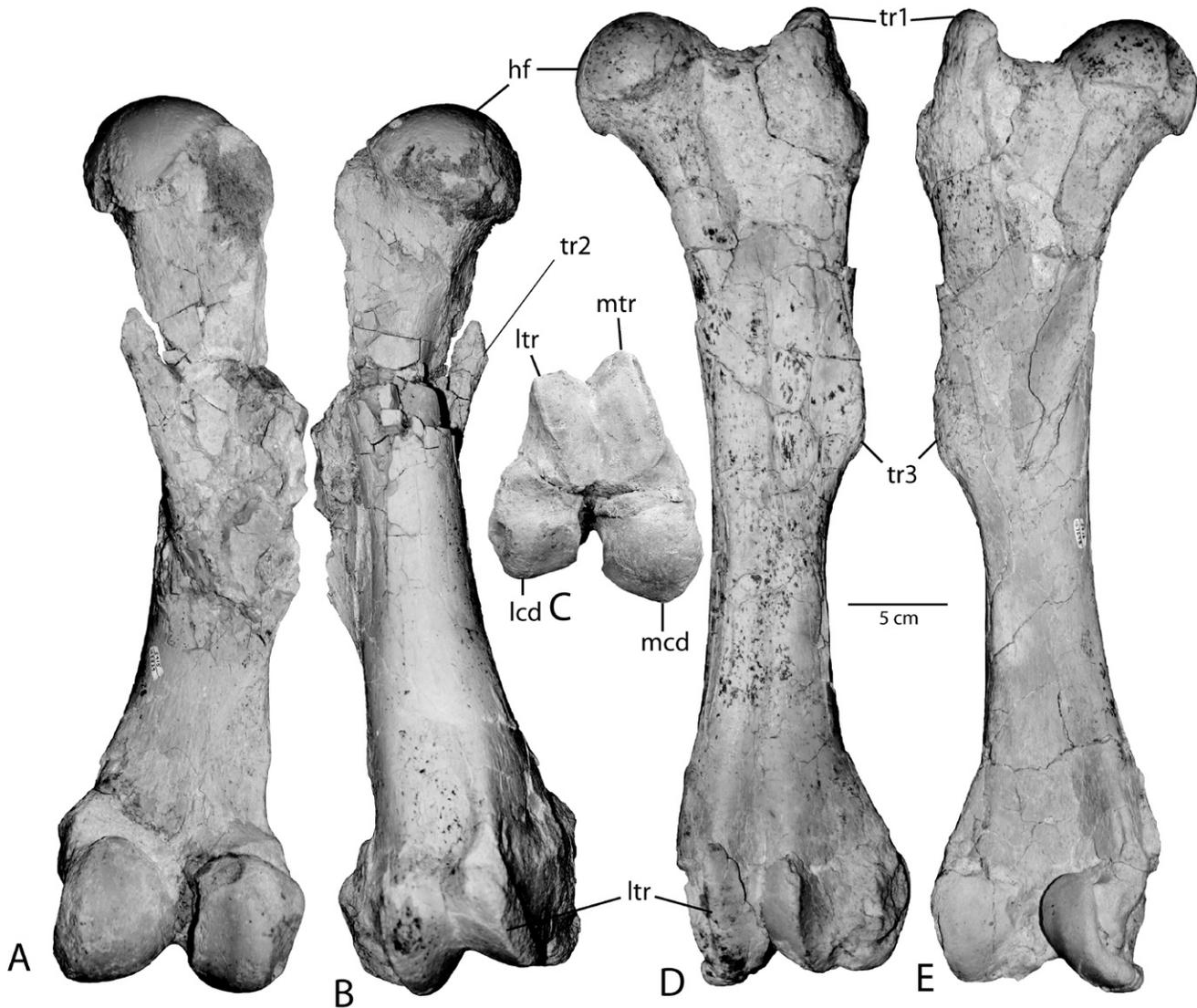


FIGURE 17. Femora of *Parvicornus occidentalis*. (A) Posterior view of right femur (SDSNH 105824), (B) anterior view of SDSNH 105824, (C) distal end of SDSNH 105824, (D) anterior view of left femur (SDSNH 107698), (E) posterior view of SDSNH 107698.

figured, described, and provided measurements for many of the elements of SDSNH 105766 (Table 4).

The wide, distally tapering nasal bone and short triangular frontonasal horns of SDSNH 105766 (Figure 19a) resemble those of SDSNH 92050 (Figure 7). There are two pairs of upper incisors, but, in contrast to most skulls of *Parvicornus*, the upper incisor row is nearly straight. The straighter incisor row may indicate a different species, though the rostrum has been smashed against a portion of the mandible, possibly distorting the degree of curvature of the incisor row.

Other elements of SDSNH 105766 include fragments of the right and left scapula, a crushed pelvis, and all of the main limb elements including the podial elements of both the manus and pes. A number of carpals and tarsals are preserved but are crushed, complicating the identification of individual elements except the astragalus and calcaneum. The overall lengths of the limb segments and relative proportions are very similar to those of *Rhinotitan* and *Megacerops* (Mihlbachler et al. 2004b). The humerus of SDSNH 105766 (Figure 19b) has a deltoid tuberosity similar in size and shape to that of *Parvicornus* as well as a very similar olecranon fossa that is char-

acteristically long and narrow. The radius (Figure 19d) is relatively typical for brontotheriids and appears to lack taxonomically distinctive features. The ulna (Figure 19c) of this specimen resembles that of *Rhinotitan* (IVPPV 3254-1) in the curvature of the shaft and its anteroposterior thickness at the level of the olecranon notch and is intermediate between the more curved gracile ulnae of hornless brontotheres (figured by Osborn 1929) and the much thickened and straighter ulna of *Megacerops* (YPM 12048).

On the femur (Figure 19f), the lack of a discernible lesser trochanter, a poorly developed third trochanter, and a greater trochanter that is mediolaterally and slightly lingually angled compare well with the femora of *Parvicornus*. The patella (Figure 19g) is narrow, with a rounded superior margin, a prominent apex (on the inferior margin), a flat lateral margin, and a rounded mesial margin. These aspects of the patella fall within the range of variation of other brontotheres. In comparison to SDSNH 105766, some brontothere patellae have a more concave superior margin or slightly concave lateral and mesial margins. The tibia (Figure 19h) is smashed and appears to lack taxonomically distinctive features. The metapodials (Figure 19e, k) are very similar in size to each other and proportioned like those of

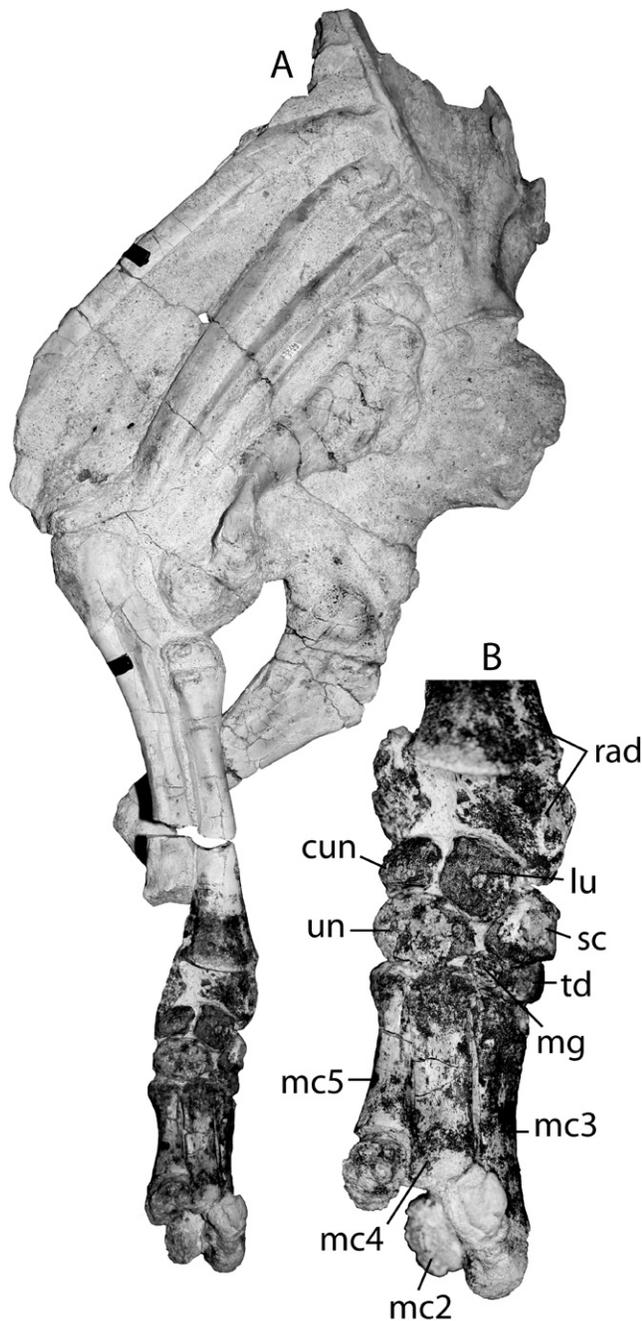


FIGURE 18. Juvenile right forelimb of *Parvicornus occidentalis* (SDSNH 93246). (A) Right forelimb with partial ribs, scapula, arm, forearm, and manus; (B) close-up of right manus.

other large-bodied brontotheres, indicating that each podial element had a significant role in bearing the animal's weight. (Note that the fourth metacarpal is transversely crushed and is artificially narrowed, as shown in Figure 19e.) The neck of the astragalus (Figure 19i) is much shorter than those of many hornless brontotheriids (see Osborn 1929), while the trochlea is not as deeply grooved. At the same time, the neck of the astragalus is not as shortened as that of *Megacerops* (YPM 12048), nor is the trochlea as shallowly grooved. The intermediate condition of the astragalus resembles that of *Rhinotitan* (IVPP V3254-1) and *Eubrontotherium* (PIN 3109-180). The proportions of

TABLE 4. Measurements of SDSNH 105766.

Variable ^a	Measurement (mm)
M3L	79.5
M3W	67.2
m1L	47.5
m2L	62.7
m3L	96.7
HL	~500
RL	440
UL	570
FL	650
TL	460
MC2L	178.9
MC2PW/DW	65.3/44.6
MC3L	189.8
MC3PW/DW	62.7/46.4
MC4L	179.5
MC4PW/DW	22.4/38.5
MC5L	165.9
MC5PW/DW	31.8/46.6
MT2L	170.5
MT2PW/DW	51.7/44.8
MT3L	165.1
MT3PW/DW	47.0/51.9
MT4L	153.7
MT4PW/DW	42.1/35.9

^aAbbreviations as in Appendix 2.

the calcaneum (Figure 19j) also resemble those of *Rhinotitan* (IVPP V3254-1) and *Eubrontotherium* (PIN 3109-182), with a long calcaneal tuber and a rather wide calcaneal shelf. The calcaneal shelf of *Megacerops* (YPM 12048) is considerably narrower.

PHYLOGENETIC ANALYSIS

Materials and Methods.—We added phylogenetic data for *Parvicornus* to the character matrix from Mhlbachler (2008) (Appendix 4), with a few corrections (see below). We analyzed an ingroup consisting of 48 taxa, all species of Brontotheriidae determined to be valid by Mhlbachler et al. (2004a), Mhlbachler (2008), and this study. We analyzed 87 cranial, dental, and mandibular characters representing 227 character states. Phylogenetic characters and their states are listed in Appendix 5 but explained more fully in Mhlbachler (2008). All ingroup taxa are included at the species level, except *Eotitanops* and *Paleosyops*, which are included at the genus level pending further review of their subgenus taxonomy. One unnamed operational taxonomic unit (“cf. *Eotitanops*” sensu Eberle 2006) represents a species distinct from any other species attributed to *Eotitanops* (Mhlbachler 2008). Two of the four outgroup taxa are the early hippomorph perissodactyls “*Hyacotherium*” (*Xenicohippus osborni* sensu Froehlich 2002) and *Pachynolophus*. The others are the brontotherioid *Lambdotherium popoagicum* Cope, 1880, and *Dangania pingi* Wang, 1995, an early Chinese perissodactyl suggested as an ancestor of the Brontotheriidae (Beard 1998, Hooker and Dashzeveg 2003).

The abundant fossil material of *Parvicornus occidentalis* reveals several ontogenetic effects on cranial and dental morphology. For instance, the anteroposterior depth of the nasal incision and the position of the anterior margin of the posterior nares appear to fluctuate somewhat with the degree of dental eruption and wear. Likewise, minor differences in horn size and overall cranial robusticity are most likely attributable to sexual dimorphism. These patterns of intraspecific variation are not unique to *Parvicornus* but are found in many

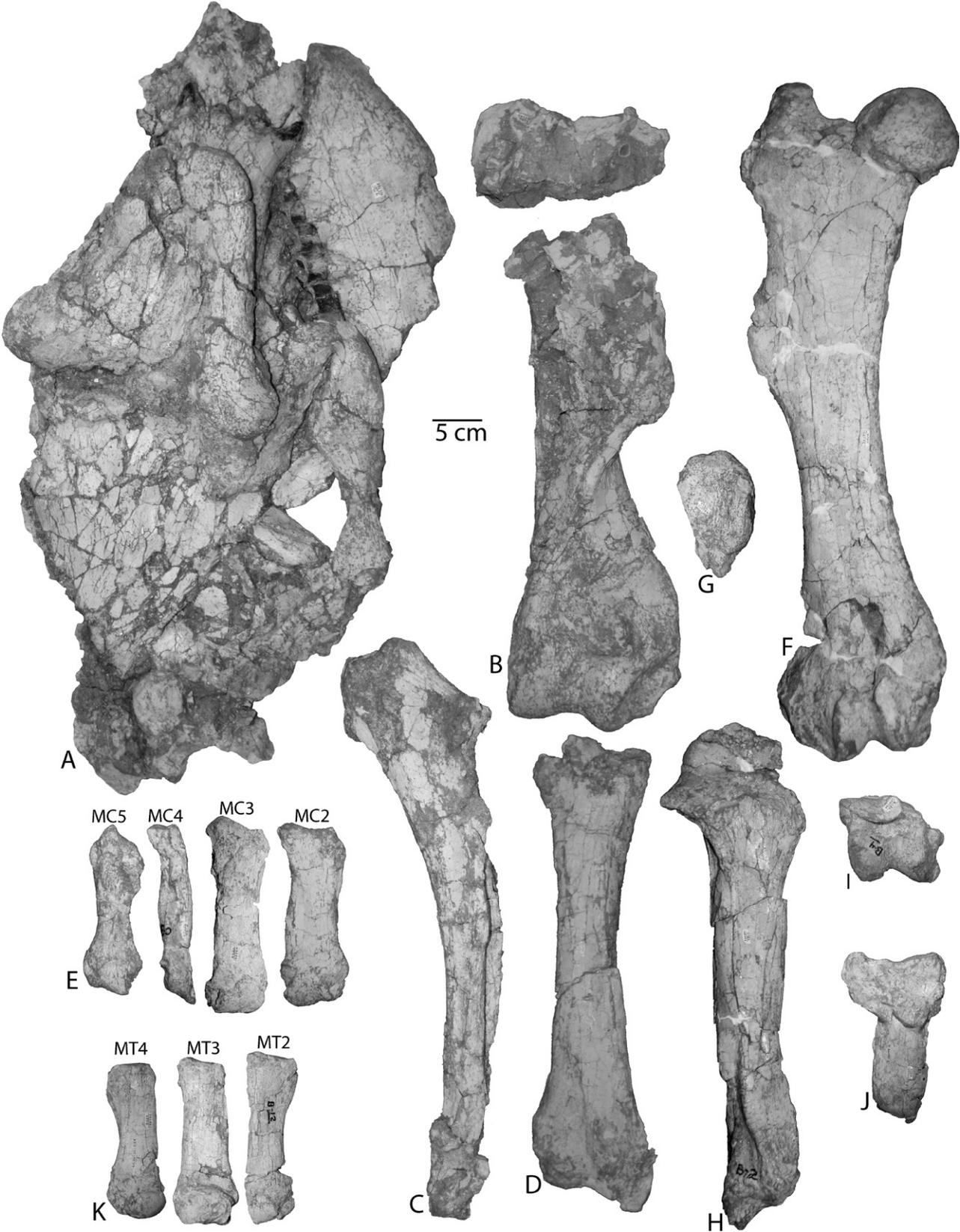


FIGURE 19. Partial skeleton of unidentified brontothere (SDSNH 105766) from the *Harpagolestes* quarry (SDSNH locality 5721). (A) Partial skull and mandible, (B) left humerus, (C) ulna, (D) right radius, (E) metacarpals of right manus, (F) right femur, (G) right patella, (H) right tibia, (I) right astragalus, (J) right calcaneum, (K) metatarsals of right pes.

brontotheres, such as *Duchesneodus* for which large quarry samples reveal similar patterns. For the most part, the phylogenetic characters we use are defined to accommodate intraspecific variation but still delimit clear and consistent differences between species. Inevitably, in *Parvicornus* and other brontotheres, occasionally variation within a species exceeds the limits of a single character state. Typically, specimens that are exceptional in this regard are juveniles or old adults. Therefore, when coding characters, we preferred specimens with the dentition fully adult but not extremely worn.

We made three corrections to the character matrix in Mhlbachler (2008). We discovered that *Danjiangia pingi* was miscoded for characters 82 and 87 and corrected these errors in the current data matrix. We also found one error for an ingroup taxon, *Protitanops curryi*, initially coded as having a straight zygomatic arch (character 24, state 2). This assessment was based on the left zygomatic arch of the type skull (LACM/CIT 1854). When we reexamined the skull, we found that the left zygomatic arch appears to be damaged and partially reconstructed. The more intact zygomatic arch on the right side of the skull is weakly curved in a manner consistent with most other species of Brontotheriina (state 1) and so recoded the character.

Imposing a monophyletic ingroup and paraphyletic outgroup, we used Phylogenetic Analysis Using Parsimony, PAUP* version 4.0b10 (Swofford 2001) with the heuristic search algorithm to find the most parsimonious cladograms. All multistate characters, except 26 and 73, were ordered. For the latter, we constructed a special character-state tree in MacClade (Maddison and Maddison 2005; see Mhlbachler 2008 for clarification). Because the searches yielded large numbers of most parsimonious trees and poorly resolved strict consensus trees, we generated strict reduced consensus trees (Wilkinson 1994, 2003) with RadCon (Thorley and Page 2000) software, which identifies and removes unstable wildcards from all the most parsimonious trees *a posteriori*. RadCon generates a series of multiple reduced consensus trees with as many combinations of *a posteriori* taxon omissions as necessary to depict all of the phylogenetic information common to all of the most parsimonious trees. The complete series of strict reduced consensus trees produced by RadCon is not shown here. In the figured trees (Figures 20 and 21), the taxa omitted and remapped back onto the reduced consensus summary trees are those whose omission improved the trees' resolution (i.e., increased the number of nodes over that in the strict consensus tree). Any unstable taxon whose *a posteriori* removal did not, by itself, enhance tree resolution was left in the tree.

Results.—First we ran an analysis excluding *Parvicornus* but including the corrected data for *Danjiangia* and *Protitanops*. It yielded 7699 most parsimonious trees with tree length (TL) = 309, consistency index (CI) = 0.45, retention index (RI) = 0.81, and homoplasy index (HI) = 0.55. This analysis produced a strict consensus tree identical to that of Mhlbachler (2008). With the same taxa omitted *a posteriori*, the strict reduced consensus trees it produced were also identical, suggesting that these corrections had no effect on the resulting phylogenetic structure (Figure 20).

The second analysis, with *Parvicornus* included, yielded 283,336 most parsimonious trees with TL = 314, CI = 0.45, RI = 0.81, and HI = 0.55 (Figure 21). The addition of *Parvicornus* not only increased the number of most parsimonious trees greatly, it significantly reduced the phylogenetic resolution in the following ways:

(1) *Dolichorhinus* and the *Acrotitan–Desmatotitan* clade were previously basal to *Sphenocoelus* but now form a polytomy with *Sphenocoelus*.

(2) The subtribe Rhadinorhinina, a clade containing *Metarhinus* and *Fossendorhinus* previously supported by character 16, state 1 (a premaxillomaxillary rostrum that does not deepen proximally), is no longer supported and is potentially paraphyletic.

(3) *Microtitan* is much more erratic, taking multiple phylogenetic positions both within and outside of the tribe Brontotheriini, whereas

previously it nested within the Brontotheriini. Data on *Microtitan* are fragmentary; the character defining the Brontotheriini (character 5, state 1: possession of paired triangular processes of the frontal bone overlapping the nasal bone) is not preserved in extant specimens of *Microtitan*.

(4) Subtribe Telmatheriina, consisting of *Telmatherium validum* Marsh, 1872, *Wickia brevirohinus* Mhlbachler, 2008, *Metatelmatherium ultimum* Osborn, 1908, and *Qufutitan zhoui* Wang and Wang, 1997, supported in the previous analysis by a character reversal (loss of central molar fossa, state 0, character 65), is now collapsed into a polytomy along with *Sthenodectes incisivus* (Douglass, 1909), and subtribe Brontotheriina.

(5) In the first analysis, *Nanotitanops shanghuangensis* Qi and Beard, 1996, was problematic, taking numerous equally parsimonious positions within the Brontotheriina and just outside of it, as the possible sister taxon to *Epimanteoceras formosus* Granger and Gregory, 1943, or the Brontotheriina. In the second analysis, *Nanotitanops* remains a wild card but behaves even more erratically with equally parsimonious positions spread over a large portion of the tree, both within and outside the Brontotheriina. Cladistically, the Brontotheriina are defined by character 3, state 3 (conspicuous paired frontonasal horns). *Nanotitanops* is known only from teeth, so its questionable place within the Brontotheriina is due to missing data.

(6) The monophyly of the genus *Rhinotitan* is rendered questionable.

(7) Both analyses recover infratribe Embolotheriina, although the phylogenetic resolution within this clade is decreased in the second analysis. Previously, the *Aktautitan–Pollyosbornia–Gnathotitan* clade was found to be the sister clade to all other Embolotheriina, though this relationship is not strictly supported.

Phylogenetic Position of *Parvicornus occidentalis*.—Despite the decreased phylogenetic resolution outside of the Brontotheriina resulting from the introduction of *Parvicornus* into the analysis, this new species has no effect on the overall phylogenetic structure within the Brontotheriina, although *Parvicornus* nests within this clade. The phylogenetic position of *Parvicornus* is only partially resolved. It is not the most basal member of the Brontotheriidae, nor is it within the clade shared by the most derived members, including *Dianotitan*, *Duchenseodus*, *Notiotitanops*, and *Megacerops*. Instead, it resides in a polytomy with *Eubrntotherium clarnoensis* and *Protitanops curryi*.

DISCUSSION

Homology of Incisors among the Brontotheriina.—Among the Brontotheriina, only *Parabrntops gobiensis* retains three pairs of upper incisors, while all other known species of this infratribe, including *Parvicornus*, have lost at least one pair (Mhlbachler 2008). The incisors of *Megacerops* were interpreted by Osborn (1929) as I2 and I3, with the I1 presumed to have been lost. Given the small and practically vestigial condition of the incisors of *Megacerops* and other Brontotheriina, however, the homologies of the remaining incisors are unclear. The tiny and essentially vestigial incisors of *Megacerops* tended to fall out in life, leaving numbers of incisors in the same species to vary by individual. Many specimens exhibit partially remodeled alveoli for the incisors, indicating that the incisors did fall out in life. While two pairs appear to have been the normal initial number of upper incisors for *Megacerops coloradensis*, an anomalous specimen (USNM 4709) shows evidence of having had three upper incisors.

Specimens of *Duchesneodus uintensis*, another species known from a relatively large sample, bear one or two pairs of upper incisors. Both known skulls of *Parabrntops gobiensis* show evidence of having had three pairs. The skulls of *Eubrntotherium clarnoensis*, *Protitanops curryi*, *Notiotitanops mississippiensis*, and *Dianotitan luanensis* consistently show evidence of having had two pairs of

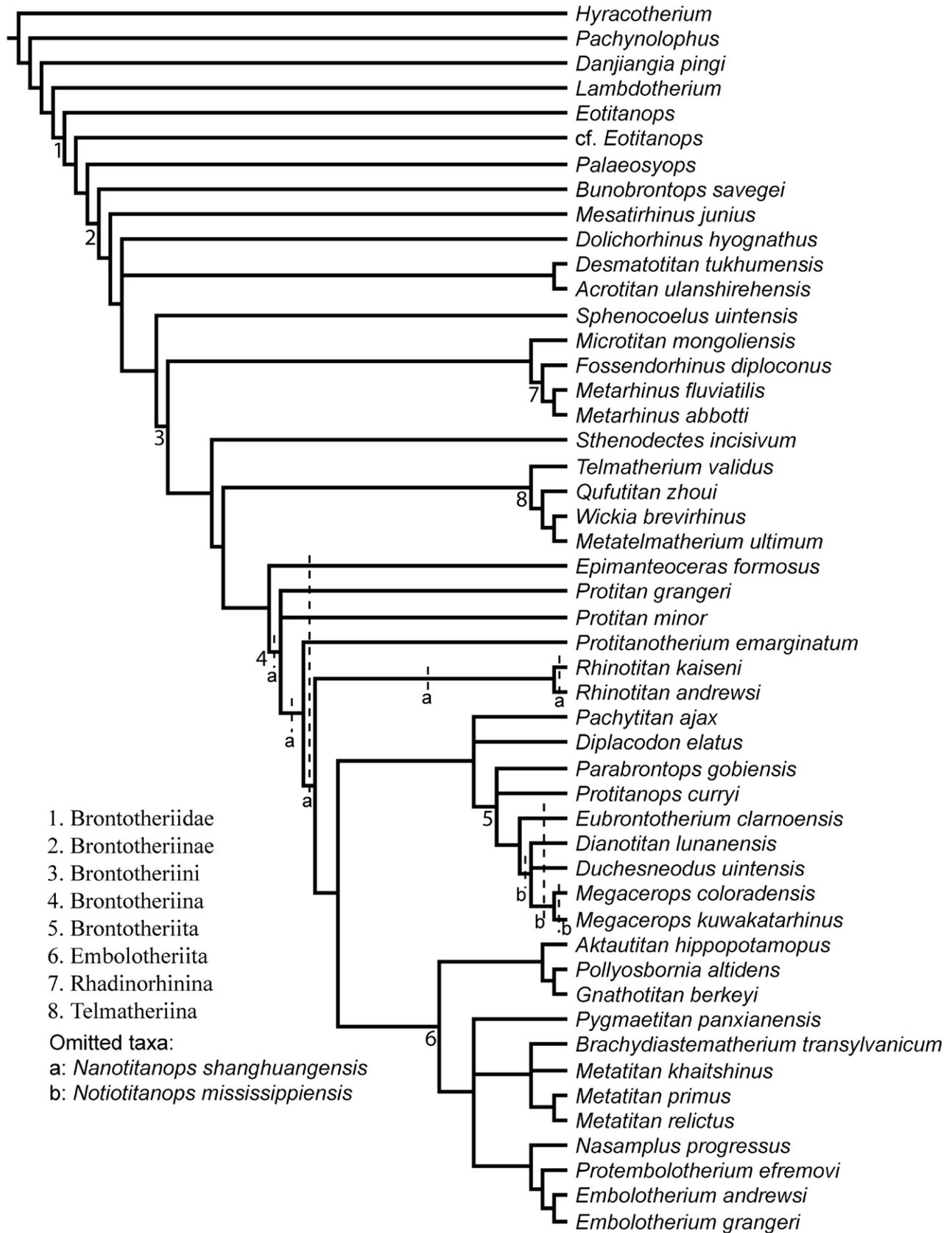


FIGURE 20. Strict reduced consensus of the Brontotheriidae and outgroups, *Parvicornus occidentalis* excluded. Branches intersected by dotted lines are equally parsimonious positions of omitted wildcard taxa.

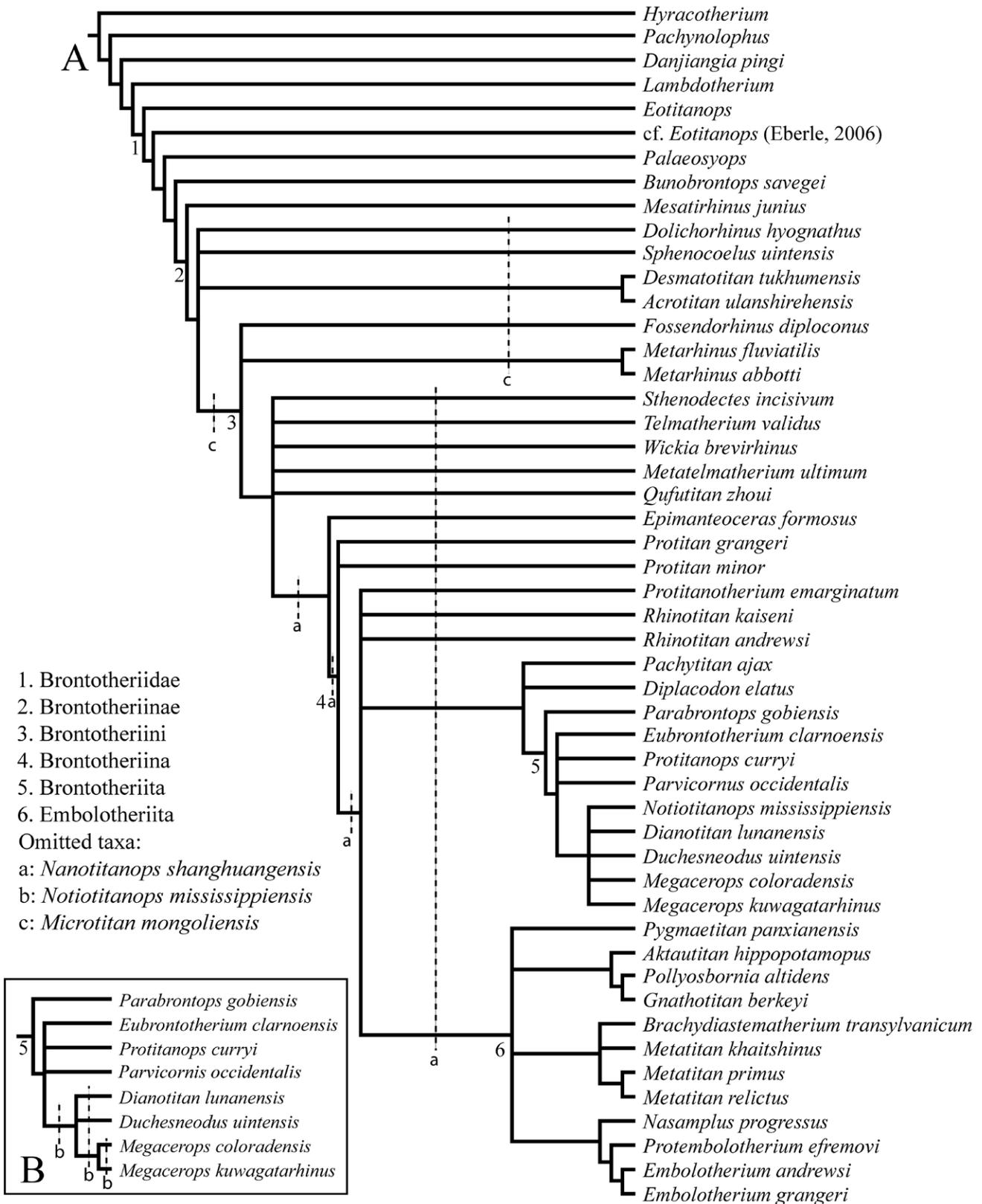


FIGURE 21. Strict reduced consensus of the Brontotheriidae with *Parvicornis occidentalis* included. (A) Strict reduced consensus of Brontotheriidae and outgroups. (B) Further reduced consensus of Brontotheriita with *Notiotitanops* removed *a posteriori*. Branches intersected by dotted lines are equally parsimonious positions of omitted wildcard taxa.

upper incisors. Likewise, two pairs are found consistently among specimens of *Parvicornus*.

The upper incisors of *Parvicornus* are small but less vestigial in appearance than those of other Brontotheriita and provide some clues regarding the homologies of the remaining incisors. The upper incisors of *Parvicornus* are morphologically intermediate between the tiny globular incisors of the other Brontotheriita and those of more primitive horned brontotheres such as *Protitanotherium* and *Diplacodon*. In *Diplacodon* and *Protitanotherium*, the I1 and I2 are small and subcaniniform, while the I3 retains a relatively large, tall caniniform shape. The incisors of *Parvicornus* are somewhat smaller than those of *Diplacodon elatus* but not reduced to the degree seen in *Megacerops coloradensis*. Likewise, the shape of the lateral incisor crown of *Parvicornus* retains a semidistinct conular aspect. The I1 and I2 of *Diplacodon elatus* and *Protitanotherium emarginatum* are very similar in appearance to the two remaining incisors of *Parvicornus*. None of the skulls of *Parvicornus*, however, has a larger and taller caniniform incisor like the I3 of *Diplacodon* and *Protitanotherium*. The simplest explanation is that the I3 has been lost while the I1 and I2 remain unchanged from an ancestral condition represented by more basal horned brontotheres. If this interpretation is correct, then the remaining incisors are I1 and I2, not I2 and I3 as Osborn (1929) had concluded.

The Ocean Ranch Brontothere as a Distinct Species.—*Parvicornus* lacks diagnostic autapomorphies but can be differentiated from all other brontotheres by its unique combination of character states. In the following discussion, where morphological distinctions relate to a phylogenetic character, that character's number is in bold type. Phylogenetic analyses suggest that *Pachytitan ajax* Granger and Gregory, 1943 and *Diplacodon elatus* are the immediate sister taxa of the Brontotheriita; it is therefore important to distinguish *Parvicornus* from these species. *Pachytitan ajax* is a poorly known species from the Shara Murun Formation (Sharamuruniian land mammal age, middle Eocene) of Central Asia, while *Diplacodon elatus*, from late Uintan NALMA (middle Eocene) deposits in the Uinta Basin of Utah, is much better known.

Parvicornus can be distinguished from both of these species by its slightly smaller incisors (43) and reduced number of upper incisors (42). *Pachytitan ajax* differs from *Parvicornus* in the following additional ways: lateral walls of the nasal process are strongly inrolled (11) and preprotocrista on P2 are more weakly developed (51). *Parvicornus* can be readily distinguished from *Diplacodon elatus* in the following ways: lateral edges of the nasal bone are not dorsally curved (10), large ventral sphenoidal fossae are absent (31), parasagittal ridges constrict the dorsal surface of the skull to a lesser extent (23), zygomatic arches are more strongly curved (24), lower incisors are more wedge-shaped (73), and upper premolar ribs are weaker (50).

There are currently nine diagnosable species of Brontotheriita, including *Parvicornus*. Although many of them are similar in overall size and generalized appearance, the number of character differences among them is a sufficient to define them conclusively as distinct species. Table 5 summarizes species-level character variation in the Brontotheriita. The strongly anteriorly arched upper and lower incisor rows (45) of *Parvicornus* most readily distinguish this species from other members of the Brontotheriita, including *Parabrontops*, *Eubrontotherium*, *Protitanops*, *Dianotitan*, *Duchesneodus*, *Notiotitanops*, and *Megacerops*. While other Brontotheriita have upper incisors with globular crowns, the upper incisors of *Parvicornus* retain a small peak like that of more basal brontotheres (44). *Parabrontops* differs by retaining three upper incisors (42) and having more weakly developed preprotocrista on P2 (51). The posterior margin of the mandibular symphysis of *Parvicornus* is situated more anteriorly than those of *Eubrontotherium*, *Notiotitanops*, *Duchesneodus*, and *Megacerops* (71). The zygomatic arches of *Protitanops*, *Dianotitan*, *Duchesneodus*, and *Megacerops* have lateral swellings at the junction of the jugal and squamosal bones that are not seen on *Parvicornus* (26). The lack of an upper postcanine diastema (46) and the absence of a bony emargination around the posterior nares (29) further distinguish *Duchesneodus*, *Dianotitan*, and *Megacerops* from *Parvicornus*. The conspicuous dorsal dome (21) that characterizes the crania of *Duchesneodus* and some specimens of *Megacerops*

TABLE 5. Characters diagnosing the species of Brontotheriita.

Trait	Species ^a									
	<i>n</i>	Po	Pg	Ec	Pc	Dl	Du	Nm	Mc	Mk
Frontonasal horns elongate	3	n	n	n	n	n	n	n	y	y
Horns bifurcated	—	n	n	n	n	n	n	n	n	y
Nasal incision extends posterior to P3	6	y	y	y	y	y	y	n	n	n
Cranial dome present	21	n	n	n	n	n	y	?	y/n	n
Lateral swelling on zygomatic arch	26	n	n	n	y	y	y	?	y	y
Anterior margin of posterior nares anterior to M3 protocones	28	y	n	y	n	y	y	n	n	y
Emargination of posterior nares lacking	29	n	n	n	n	y	y	n	y	y
Nuchal crest thick	39	n	n	n	n	y	n	n	y	n
Occipital pillars massive	40	n	n	n	n	n	n	n	y	y
Upper incisors (<i>n</i>)	42	2	3	2	2	2	2	2	2	?
Upper incisors globular	44	n	y	y	y	y	y	y	y	?
Incisor row strongly arched	45	y	n	n	n	n	n	n	n	?
Upper postcanine diastema	46	y	y	y	y	n	n	y	n	n
P2 preprotocrista strong	51	y	n	y	y	y	y	y	y	y
Molar metaloph present	67	n	n	n	n	n	n	n	n	y
Mandibular symphysis extends posterior to P4 trigonid	71	n	?	y	?	?	y	y	y	?
Lower incisors (<i>n</i>)	72	3	?	3	?	?	3	?	2	?
Mandibular postcanine diastema	76	y	?	y	?	?	y	?	n	?

^aDl = *Dianotitan lunanensis*; Du = *Duchesneodus uintensis*; Ec = *Eubrontotherium clarnoensis*; Mc = *Megacerops coloradensis*; Mk = *Megacerops kuwagatarhinus*; Nm = *Notiotitanops mississippiensis*; Pc = *Protitanops curryi*; Pg = *Parabrontops gobiensis*; Po = *Parvicornus occidentalis*.

is not apparent on any specimen of *Parvicornus*. *Megacerops* and *Notiotitanops* have anteroposteriorly shallower nasal incisions (6) and more anteriorly situated orbits (13). *Dianotitan* and *Megacerops* have thicker nuchal crests (39). Finally, *Megacerops* has longer horns (3), a much more massive occiput (40), and a reduced number of lower incisors (72).

Comparisons with *Nomina Dubia*.—We consider many named species of Brontotheriida *nomina dubia* because their holotypes (and closely associated specimens) lack diagnostic characters (Mhlbachler 2008, Janis et al. 2008). Specimens attributed to the majority of dubious species of Brontotheriida are from the classic White River Chadronian deposits of the high Great Plains and are most certainly representatives of *Megacerops*. Three dubious species of Brontotheriida, however, are of greater interest, and it is worth considering the possibility that they are the same as *Parvicornus*. These dubious taxa, all (probably incorrectly) attributed to the genus *Duchesneodus* by Lucas and Schoch (1982, 1989) include *Duchesneodus primitivus* (Lambe, 1908) from the Chadronian Cypress Hills Formation, Saskatchewan, Canada, *Duchesneodus californicus* (Stock, 1935) from the Duchesnean Sesse Formation of California, and *Duchesneodus thyboi* from the Duchesnean Slim Buttes Formation of South Dakota.

Mhlbachler (2008) concluded that *D. primitivus*, based on a single mandible (NMC 6421), is morphologically consistent with *D. uintensis* but that synonymy with either *Protitanops curryi* or *Notiotitanops mississippiensis*, two species whose mandibles are not known, is also plausible. In comparison to *Parvicornus occidentalis*, the incisors of NMC 6421 are proportionally smaller and more globular, and the anterior end of the mandibular symphysis is narrower. It seems unlikely that NMC 6421 is *Parvicornus*. Morphometrically, the proportions of the incisors and cheek teeth of NMC 6421 seem more similar to those of *Megacerops* or *Eubrontotherium* (Figure 10b), although NMC 6421 can be differentiated from these taxa in other ways.

Mhlbachler (2008) suggested that the dubious species *Duchesneodus californicus*, known from a large number of fragmentary specimens, could be either *Protitanops* or *Notiotitanops*. *Duchesneodus californicus* and *Parvicornus occidentalis* are very similar in overall size and have similar dentitions. Further comparison suggests that many of the numerous and mostly isolated incisors attributed to the former are proportionately smaller and more completely globular. The posterior margin of the symphyses of mandibles attributed to *D. californicus* is positioned more posteriorly than that of *Parvicornus*. A partial skull (LACM/CIT 2143) of unknown taxonomic identity originally assigned to *D. californicus* by Stock (1938) is more similar to *Parvicornus* in some respects, such as its proportionately larger (Figure 10a) and less globular incisors, but its nasal incision extends farther posteriorly than in skulls of *Parvicornus*. Although fossils attributed to *D. californicus* could represent multiple taxa, none of them are likely to be conspecific with *Parvicornus*.

The holotype of *Duchesneodus thyboi*, SDSM 63689, is an undiagnosable partial juvenile skull consistent with multiple species including *Eubrontotherium clarnoensis*, *Protitanops curryi*, and *Notiotitanops mississippiensis* (Mhlbachler 2008). In dental proportions it resembles *Parvicornus occidentalis*. Although it is somewhat larger overall (Figure 10a), conspecificity cannot readily be rejected. Bjork (1967) referred other specimens from several localities of the Slim Buttes Formation to *D. thyboi*. Like the type specimen, most of the referred specimens lack character sufficient for identification to species. Moreover, many of these specimens exhibit tiny (essentially vestigial) paraconules on the upper molars. Small paraconules are found in earlier hornless brontotheres from Bridgerian (*Palaesyops*, *Mesatirhinus*, *Telmatherium*) and early

Uintan (*Sphenocoelus*, *Dolichorhinus*) times, but, with the apparent exception of the Slim Buttes specimens, they are not observed in later brontotheriids.

Despite the somewhat perplexing nature of the Slim Buttes brontotheres, one specimen referred to *D. thyboi* by Bjork (1967), a portion of the premaxillomaxillary rostrum with a complete upper incisor row, a right upper canine, and P2–P3 (SDSM 63690; Figure 22), exhibits a suite of characters diagnostic of *Parvicornus*. Namely, the anterior dentition consists of two pairs of upper incisors with small semiglobular crowns forming a strongly arched row positioned completely anterior to the canines. In lateral view, this specimen also resembles *Parvicornus*, particularly in the angle and apparent anteroposterior depth of the nasal incision. Because the specimen lacks a complete premolar row it cannot be plotted in Figure 10a. A comparison of various measurements of premolars and incisors, however, indicates a size and proportions similar to those of *Parvicornus*. Given the fragmentary condition of SDSM 63690 and its occurrence at a locality other than that of the type of *D. thyboi*, we cannot be certain if this specimen belongs to the same species as SDSM 63689 (the type of *D. thyboi*). Nor can we determine with any clear certainty if it is conspecific with *Parvicornus* or if it represents a very similar yet insufficiently documented species. *Duchesneodus thyboi* remains a dubious species, but we can conclude that *Parvicornus* or a very similar species is present in the Duchesnean Slim Buttes deposits of South Dakota.

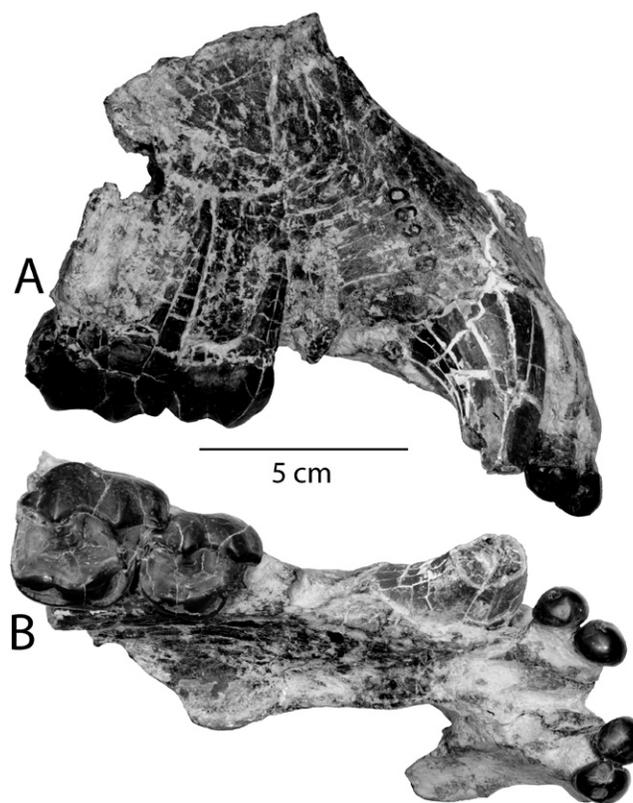


FIGURE 22. A portion of a maxilla and premaxilla (SDSM 63690) from the Slim Buttes Formation of South Dakota that may represent *Parvicornus occidentalis*. (A) Right side, (B) ventral view including right and left I1–2, right C, and right P2–P3.

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APPENDIX 1. (cont.)

SDSNH	i1L	i1W	i2L	i2W	i3L	i3W	cW	p1L	p1W	p2L	p2W	p3L	p3W	p4L	p4W	m1L	m1PW	m2L	m2PW	m3L	m3W	p2-p4	m1-m3	p2-m3	
92047							19.9	14.0	9.5	22.4	14.3	25.9	17.3	28.4	20.9							76.1			
92048										23.1	14.8														
92049										23.5	15.9														
92052										24.2	14.8	28.5	19.5	33.5	25.3	37.0	22.6	46.6	27.0		80.1	33.9	85.5	180.2	263.6
92053										23.4	15.5	28.4	15.5	30.4	18.4	43.0	28.3	56.8	35.1						
92056	9.3	9.8	10.8	13.7	10.0	11.0	24.4	13.5	10.5	21.9	14.1	26.9	17.6	30.4	21.8	44.9	26.5	55.3	31.5			79.7			
92058										26.4															
92059														31.5	20.1										
92060																43.9	26.5								
92061																43.3	23.6								
92062																		51.7	31.1						
93246																									
93465								12.2																	
105789	8.3	9.4	9.8	12.2	9.3	8.5	19.0	13.2	9.3	23.2	15.1	25.5	18.7	30.5	22.7	43.9	26.8	54.2	30.5	73.7	28.7	78.2	173.8	250.4	
105791																42.4	24.9	54.4	29.4	72.2	29.1	77.5	163.4	240.4	
105792																43.9	26.8	54.2	30.5	81.4	30.8				
105793																									
105794																38.9	25.8	49.3	30.0	69.2	29.6		155.8		
105795												23.8	14.4	27.7	19.3	40.2	24.4	50.4	28.2	66.7	28.5	75.3	155.0		
105796																43.5	26.9	55.9	31.2	70.8	27.7		178.3		
107675																45.1	23.1			77.7	31.3				
107677																40.0	25.6	48.9	30.1	70.0	29.9		161.1		
107730							23.9							29.4	19.9	40.0	25.6	53.8	32.2	72.2	29.9				
107731	8.4	10.0	10.9	12.4	10.5	10.2		13.3	9.4	23.5	13.8	26.9	16.6	31.1	19.9	43.2	24.7	55.9	30.0	76.8		79.6	169.9		
107732							27.3							30.4	21.9	40.0	26.1	54.0	32.3						
107733	8.0	6.9	8.0				25.8			22.0	12.5	23.5	16.2	30.1		40.4	49.7					75.1	174.5	247.9	

APPENDIX 2. Abbreviations for measurements. Upper-case letters refer to upper teeth, lower-case letters to lower teeth. More detailed descriptions of landmarks for dental measurements are given in Muhlbachler (2008).

1. I1L and i1L: Mesiodistal length of first incisor.
2. I1W and i1W: Labiolingual width of first incisor.
3. I2L and i2L: Mesiodistal length of second incisor.
4. I2W and i2W: Labiolingual width of second incisor.
5. I3L: Mesiodistal length of third lower incisor.
6. i3W: Labiolingual width of third lower incisor.
7. CL and cL: Maximum diameter of canine crown.
8. P1L and p1L: Anteroposterior length of first premolar.
9. P1W and p1W: Labiolingual width of first premolar.
10. P2L and p2L: Anteroposterior length of second premolar.
11. P2W and p2W: Labiolingual width of second premolar.
12. P3L and p3L: Anteroposterior length of third premolar.
13. P3W and p3W: Labiolingual width of third premolar.
14. P4L and p4L: Anteroposterior length of fourth premolar.
15. P4W and p4W: Labiolingual width of fourth premolar.
16. M1L and m1L: Anteroposterior length of first molar.
17. M1W and m1W: Labiolingual width of first molar.
18. M2L and m2L: Anteroposterior length of second molar.
19. M2W and m2W: Labiolingual width of second molar.
20. M3L and m3L: Anteroposterior length of third molar.
21. M3W and m3W: Labiolingual width of third molar.
22. P2–P4 and p2–p4: length of premolar tooth row, excluding P1 or p1.
23. M1–M3 and m1–m3: Length of molar row.
24. P2–M3 and p2–m3: Length of cheektooth row, excluding P1 or p1.
25. VL: Total length of skull measured on the ventral surface.
26. MVL: Length of skull measured from the P2 to the occipital condyle.
27. SW: Skull width measured across the maximum span of the zygomatic arches.
28. HL: Humerus length
29. RL: Radius length
30. UL: Ulna length
31. MCXL: Metacarpal length
32. MCXPW/DW: Metacarpal proximal width and distal width
33. MTXL: Metatarsal length
34. MTPW/DW: Metatarsal proximal width and distal width
35. FL: Femur length
36. TL: Tibia length

APPENDIX 3. Anatomical abbreviations used in figures.

af	alar foramen	mc3	third metacarpal
alc	anterolingual cusp of molar	mc4	fourth metacarpal
bs	basisphenoid	mc5	fifth metacarpal
C	upper canine	mt2	second metatarsal
c	lower canine	mt3	third metatarsal
cf	central fossa of molar	mt4	fourth metatarsal
cu	cuneiform	mcd	medial condyle
dt	dorsal tubercle of atlas	mg	magnum
dlt	deltoid tubercle	mtd	metaconid of lower third premolar
epn	emargination of posterior nares	mtr	medial trochlear ridge
fns	frontonasal suture	na	nasal
fo	foramen ovale	n	neck of scapula
fl	foramen lacerum	o	orbit
fr	frontal	op	odontoid process
eam	external auditory pseudomeatus	pd	postcanine diastema
gc	glenoid cavity	pgp	postglenoid process
hf	head of femur	pms	premaxillomaxillary suture
hh	head of humerus	pop	paroccipital process
I1	first upper incisor	ptp	post-tympanic process
i1	first lower incisor	pz	postzygopophysis
I2	second upper incisor	rad	radius
i2	second lower incisor	s	spine of scapula
i3	third lower incisor	sp	spinous process
ivf	intervertebral foramen	sc	scaphoid
isf	infraspinous fossa	ssf	supraspinous fossa
l	lacrimal	td	trapezoid
lec	lateral epicondyle	tf	transverse foramen
lc	lingual crest of premolar	tr1	greater trochanter
lcd	lateral condyle	tr2	lesser trochanter
lu	lunate	tr3	third trochanter
ltr	lateral trochlear ridge	un	unciform
max	maxilla	v	vomer
M2	upper second molar	vt	ventral tubercle of atlas
mc2	second metacarpal		

APPENDIX 4. Phylogenetic character matrix of Brontotheriidae and outgroup taxa.

	1	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	7777777778	8888888
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567
<i>Hyracotherium</i>	000-000001	0-10000000	0001000000	0000000000	1010000010	0000000000	0000000000	0000000000	00000000
<i>Pachynolophus</i>	000-0000?0	0-00000000	0001000100	001000000?	1010000000	0000000000	0000000000	0000000000	0201001
<i>Danjiangia</i>	?00-000000	0-1000?000	??????00?0	??????0?0?	?010000000	0001101000	1000000000	1000201000	0011002
						1			
<i>Lambdaotherium</i>	000-010000	?-10000000	0001?0010?	0010000000	1010000100	0011101000	1010011000	1000-0?000	0111001
		1							
<i>Eotitanops</i>	100-010001	0-00000000	0100?00?0?	0000000000	101?000101	1111101010	1011022021	101?200010	0010002
<i>cf. Eotitanops</i>	??????????	???????????	???????????	???????????	???????????	???????????	???????????	???????????	??100?2
<i>Palaeosyops</i>	100-020001	0-00000100	0100200000	0001000000	1011000111	1111101010	1012022021	1010200010	0010002
<i>Bunobrontops savagei</i>	???????????	???????????	???????????	???????????	???????????	???????????	???????????	???????????	??10002
<i>Mesatirhinus junius</i>	100-030001	0-00200200	0101000000	0000100000	1011000012	1111111121	1122022021	1010200010	0010012
<i>Desmatotitan tukumensis</i>	???????????	???????????	???????????	???????????	??1?0?0?0?	???????????	???????????	???????????	0010012
<i>Acrotitan ulanshirensis</i>	???????????	???????????	???????????	???????????	??1?0?0?0?	???????????	???????????	???????????	??2????
						2			
<i>Dolichorhinus hyognathus</i>	1110030001	0-00211200	0121000201	0100100000	1011000012	1111111121	1132133011	1020200010	0010012
<i>Sphenocoelus uintensis</i>	110-030001	0-00200200	010100000?	1100100000	1011000012	1111111121	1132143021	1010000010	0010012
<i>Microtitan mongoliensis</i>	?????2????	?0?0?00?0?	???????????	???????????	?????00013	1111111121	1132043001	1??0?0010	0010012
		3							
		4							
<i>Fossendorhinus diploconus</i>	100-?30????	0-11?10201	010000000?	0000000000	101?00?012	1121111121	113214300?	??20??????	0??????
<i>Metarhinus fluviatilis</i>	100-140000	0-12111200	0100100001	0000000000	1011000012	1111111121	1132143111	1020000010	0110012
<i>Metarhinus abbotti</i>	100-?40000	0-12111200	0100100001	0000000000	1011000012	1111111121	1132143101	1020000010	?110012
<i>Sthenodectes incisivum</i>	100-1100?1	0-11000201	010010000?	0000000000	1001010012	1111111121	1132143121	1020010010	0010012
<i>Telmatherium validus</i>	100-120001	0-10000201	0110100011	0000000000	1011000112	1111111121	1132033021	1020100010	0010012
<i>Wickia brevirhinus</i>	100-110001	0-10000201	011020001?	0000000000	1011000012	1111111121	1132033121	10?0000010	0010012
<i>Metatelmatherium ultimum</i>	100-110001	0-10000200	010020001?	0000000000	1011000012	1111111121	1132043121	1020100010	0010012
<i>Qufutitan zhoui</i>	??0-100001	0-10000210	??????01?	???????????	?023001012	1121111121	113204302?	???????????	?????????
		1							
		2							
<i>Epimanteoceras formosus</i>	1020120001	0-10000201	0120100111	0000000000	1011001012	1121111121	113214302?	???????????	?????????
<i>Protitan grangeri</i>	1030120102	0000000202	012210111?	1000000000	1011000012	1111111121	1132143021	2010000010	0010012
<i>Protitan minor</i>	1030130001	0010000202	01221011???	11000?0000	1011000012	1111111121	113214302?	???????????	?????????
<i>Protitanotherium emarginatum</i>	1030130112	0000000202	012210?11?	0001010000	1022001012	1111111121	1?32143021	2011000110	0010012
<i>Rhinotitan kaiseni</i>	1030121101	0010000201	014210011?	0101010000	0011001012	1121111121	1132143021	2011000110	0110012
<i>Rhinotitan andrewsi</i>	1030131102	1010000201	014210011?	0101011000	0012001012	1121111121	1132143021	2011000110	0110012
			2						
<i>Nanotitanops shanghuangensis</i>	???????????	???????????	???????????	???????????	??????1?12	1121111121	11321330??	???????????	??100??
<i>Pollyosbornia altidens</i>	???????????	???????????	???????????	???????????	??1?0?0?0?	???????????	???????????	20??0?0010	0210012
					2				
<i>Pygmaetitan panxianensis</i>	???????????	???????????	???????????	???????????	?010110102	1121111121	1132142101	?010?00???	??10112
					2				
<i>Gnathotitan berkeyi</i>	?????2????	?000000???	???????????	???????????	?01?001012	1121111121	1132143101	2021000010	0210012
		3							
		4							
<i>Aktautitan hippopotamopus</i>	1031132101	0010000202	013210011?	??1?0??00	1012001012	1111111121	1132143101	2021000110	0210012
<i>Brachydiastematherium transylvanicum</i>	???????????	???????????	???????????	???????????	??2?0?0?0?	???????????	???????????	3?11010110	02100??
<i>Metatitan primus</i>	1031132101	0000000201	014210122?	?0?1?1100	0?3?111012	1121111121	1132143121	3031010111	?210012
<i>Metatitan relictus</i>	1031142101	0000000201	014210122?	1001011100	1032111012	1121111121	1132143121	3031010111	1210012
<i>Metatitan khaitshinus</i>	1031142101	0000000201	014210112?	1001011100	002?011012	1121111121	1132143121	3011010110	0210012
<i>Nasampus progressus</i>	??321321?1	0010?0????	?1?????????	???????????	???????????	1131111121	11321?3???	???????????	?????????
<i>Protembolotherium efremovi</i>	1032?3301-	-110000202	014111022?	0101010010	1??00?013	1131111121	113214320?	???????????	?????????
<i>Embolotherium andrewsi</i>	1032134---	-110000212	014101022?	0101010011	2033011013	1131111121	1132143201	301?010110	1210112
<i>Embolotherium grangeri</i>	1032?44---	-010000212	014111022?	0101010000	2013001013	1131111121	1132143201	3011000110	1210112
<i>Pachytitan ajax</i>	??30?30112	1????0020?	???????????	???????????	?01100?01?	1131111121	1132143???	???????????	?????????
		1							
<i>Diplacodon elatus</i>	1030?31113	0010000202	012210010?1	001010000	1022001012	2131111121	1132143121	2011000110	02?0012
<i>Parabrantops gobiensis</i>	1030130112	0010000202	013210011?0	00?0?0000	?033101013	1131111121	113214310?	???????????	?????????
<i>Eubrntotherium clamoensis</i>	1030130112	0010000202	013110001?0	001010000	1133101013	2131111121	1132143111	3031000110	0010012
<i>Protitanops curryi</i>	1030?30112	0010000202	013111011?0	001010000	1133101013	2131111121	1132143121	???????????	??10012
<i>Notiotitanops mississippiensis</i>	10??2?1?1?	0?2000020?	0??11?0?11?	0010?00??	1133101013	2131111121	1132143101	3?????????	?210012
<i>Dianotitan lunanensis</i>	1030?30112	0010000202	013111000?0	001010010	?133111013	2131111121	113214310?	???????????	?????????
<i>Duchesneodus uintensis</i>	1030130112	0010000202	213111000?0	001010000	1133111013	2131111121	1132143101	3031000110	0210012
<i>Megacerops coloradensis</i>	1040120112	0020000202	11311101000	001010011	1133111013	2131111121	1132143101	3131010110	0210012
<i>Megacerops kuwagatarhinus</i>	1040?20112	0020000202	014111000??	0?1010001	1????1?0??	2131111121	113214210?	???????????	?????????
<i>Parvicornus occidentalis</i>	0030130112	0010000202	01311000101	001010000	1132001013	2131111121	1132143111	2031000110	0110012

APPENDIX 5. Phylogenetic characters.

- 1: Postorbital cranium: (0) not elongate, (1) elongate.
- 2: Overall skull proportions: (0) not elongate, length/width ratio ≤ 2.0 , (1) elongate, length/width > 2.0 .
- 3: Bony protuberance (horn): (0) absent, (1) small swelling primarily on nasal bone, (2) inconspicuous frontonasal swelling, (3) conspicuous paired frontonasal horns, (4) frontonasal horns extremely long.
- 4: Frontonasal horns: (0) widely spaced, (1) narrowly spaced, (2) fused into a single transverse crest.
- 5: Frontal bone: (0) does not overlap the nasal bone or intrude into the nasal bone, (1) overlaps the nasal bone or intrudes into the nasal bone.
- 6: Position of posterior margin of nasal incision: (0) anterior to the premolars, (1) between the anterior margin of P1 and the anterior margin of P2, (2) between the anterior margin of P2 and the posterior margin of P3, (3) between the anterior margin of P4 and the posterolateral root of M1, (4) positioned at the posterior margin of M1 or more posterior.
- 7: Nasal process: (0) originates from an unelevated position, (1) semi-elevated, (2) fully elevated, (3) sometimes present in elevated position, but very reduced, (4) lost or absorbed by the frontonasal process.
- 8: Nasal process: (0) narrow, (1) broad.
- 9: Distal edge of nasal: (0) thin, (1) thickened.
- 10: Lateral walls of the nasal process: (0) thin, shallow, (1) thin, deep, (2) thickened, (3) thickened with upturned lateral edges.
- 11: Lateral walls of nasal process: (0) not inrolled, (1) inrolled.
- 12: Frontonasal process (ram): (0) straight, (1) posterodorsally curved.
- 13: Position of anterior rim of orbit: (0) above M2, (1) above M1, (2) anterior to M1.
- 14: Orbits: (0) not laterally protruding, (1) moderately laterally protruding, (2) more extremely laterally protruding.
- 15: Infraorbital jugal process: (0) absent, (1) small, (2) large.
- 16: Premaxillomaxillary rostrum: (0) deepens proximally, (1) does not deepen proximally.
- 17: Premaxillomaxillary rostral cavity: (0) open dorsally and continuous with the nasal cavity, (1) sealed dorsally by a bony cover, separated from the nasal cavity.
- 18: Premaxilla: (0) thin, contacts nasals, (1) robust, does not contact nasals, highly constricted symphysis, (2) robust, does not contact nasals, longer symphysis.
- 19: Premaxillary symphysis: (0) angled with flat or convex anterodorsal surface, (1) vertical with concave anterior surface.
- 20: Dorsal surface of skull: (0) nearly flat above the orbits, strongly convex over the postorbital cranial region, (1) slightly concave above orbits and nearly flat over the postorbital cranial region, (2) entire dorsal surface of the skull is concave or saddle-shaped.
- 21: Dorsal cranial dome: (0) absent, (1) small, variably present, (2) present.
- 22: Postorbital width of skull (0) constricted, (1) not constricted.
- 23: Sagittal crest: (0) true sagittal crest, (1) parasagittal ridges converge closely but do not actually make contact, (2) parasagittal ridges remain separate, but the dorsal surface of the skull is strongly constricted, (3) dorsal surface of skull is moderately constricted, (4) dorsal surface of skull is constricted by parasagittal ridges minimally if at all.
- 24: Zygomatic arch: (0) strongly curved, (1) weakly curved, (2) straight.
- 25: Zygomatic arches: (0) nearly parallel, (1) posteriorly divergent, (2) strongly arched laterally.
- 26: Lateral swellings of zygomatic arch: (0) absent, (1) present.
- 27: Postzygomatic process: (0) absent, (1) present.
- 28: Position of anterior margin of posterior nares: (0) anterior to the protocone of M3, (1) usually between or somewhat behind the protocones of M3, (2) at the posterior margin or behind M3.
- 29: Emargination of posterior nares: (0) absent or very narrow, (1) present and of moderate width, (2) present and wide.
- 30: Maxilloturbinate: (0) not exposed in choanae of posterior nares, (1) extend behind the anterior rim of the posterior nares.
- 31: Ventral sphenoidal fossae: (0) absent, (1) present.
- 32: External auditory pseudomeatus: (0) mediolaterally angled, (1) posteromedially angled.
- 33: Foramen ovale: (0) not confluent with foramen lacerum, (1) confluent.
- 34: External auditory pseudomeatus: (0) not constricted ventrally, (1) highly constricted ventrally.
- 35: Occipital condyles: (0) small (1) large.
- 36: Proportions of occiput: (0) dorsal portion narrower than ventral portion, (1) dorsal portion as wide or wider than ventral portion.
- 37: Posterior end of skull: (0) narrow, (1) widened.
- 38: Basicranium: (0) normally proportioned, (1) shortened.
- 39: Nuchal crest: (0) thin, (1) thick.
- 40: Occipital pillars: (0) weak, (1) massive.
- 41: Tilt of occiput: (0) relatively vertical, (1) moderately to strongly tilted, (2) elevated.
- 42: Pairs of upper incisors: (0) three, (1) two.
- 43: Upper and lower incisors: (0) very large, (1) large, (2) small, (3) very small.
- 44: Upper incisors: (0) spatulate with flat or rounded apices, (1) all subcaniniform, (2) I1 and I2 semiglobular or globular; I3 subcaniniform, (3) all globular.
- 45: Shape of incisor row: (0) arched, (1) straight.
- 46: Upper postcanine diastema: (0) present, (1) absent.
- 47: P1: (0) simple (1) complex.
- 48: Diastema between P1 and P2: (0) absent, (1) present.
- 49: P2 metacone: (0) small swelling, (1) distinct cusp.
- 50: Labial upper premolar ribs: (0) paracone and metacone ribs large and equal, (1) paracone rib strong, metacone rib weak, (2) paracone rib narrow, metacone rib very weak, (3) all labial ribs very weak.
- 51: Preprotocristae and paraconules of P2, P3, and P4: (0) absent or very weakly developed on P2, strongly developed on P3 and P4, (1) weakly developed on P2, faint to absent on P3 and P4, (2) strongly developed on P2, weakly developed on P3 and P4.
- 52: Upper premolar postprotocrista: (0) present on P3 and P4, (1) absent.
- 53: Upper premolar lingual morphology: (0) lingual side of crown is narrow with cone-shaped protocone, (1) lingual side of crown is somewhat wider, protocone often associated with lingual crest, (2) small hypocones variably present, situated close to protocone, and connected by lingual crest, (3) well-developed hypocones always present and spaced more posteriorly from hypocone and variably connected by a lingual crest.
- 54: Upper molar parastyle: (0) low, (1) high.
- 55: Upper molar parastyle: (0) mainly anterior to paracone, (1) mainly labial to paracone.
- 56: Upper molar anterior cingulum (0) forms parastyle shelf, (1) does not form parastyle shelf.
- 57: Upper molar metastyle: (0) straight, (1) angled labially.
- 58: Upper molar ectoloph: (0) brachydont, (1) hypsodont.
- 59: Labial side of upper molar paracone and metacone: (0) erect, (1) linguallly angled and concave, (2) linguallly angled and convex.
- 60: Molar ribs (0) strong, (1) weak.
- 61: Upper molar mesostyle: (0) absent, (1) present.
- 62: Lingual margins of molar paracone and metacone: (0) rounded (1) wedged.
- 63: Thickness of the lingual enamel of the upper molar ectoloph: (0) equal in thickness to the labial ectoloph enamel, (1) thickened around the paracone and metacone, (2) moderately thinned between paracone and metacone, (3) thinner than labial ectoloph enamel throughout.
- 64: Labiolingual width of upper molar ectoloph: (0) narrow, (1) intermediate, (2) wide.
- 65: Central molar fossa: (0) absent, (1) present.
- 66: Upper molar protoloph and paraconules: (0) large, (1) reduced, but functional, (2) very small, (3) pinhead-sized paraconule variably present, (4) absent.
- 67: M1–M2 metaloph: (0) well developed, (1) small but distinct, (2) vestigial metalophlike ridge, (3) absent.
- 68: Upper molar anterolingual cingular cusp: (0) absent, (1) small, (2) large.
- 69: M3 hypocone: (0) present, (1) variably present and absent, (2) absent or very rare.
- 70: Shape of mandibular symphysis: (0) long and narrow, (1) short and robust.
- 71: Position of posterior margin of mandibular symphysis: (0) anterior to the premolars, (1) between the p2 talonid and p3 trigonid, (2) between the p3 talonid and p4 trigonid, (3) between the p4 talonid and m1 trigonid.

- 72:** Number of lower incisors: (0) three pairs, (1) two pairs.
- 73:** Lower incisor morphology: (0) thin and spatulate, (1) i1–i2 semispatulate, i3 subcaniniform, (2) all incisors subcaniniform, (3) all incisors short and wedge-shaped or globular.
- 74:** Relative size of lower incisors: (0) i2 about the same size as i3, (1) i2 larger than i3.
- 75:** Diastema between p1 and p2: (0) absent, (1) variably present, (2) present.
- 76:** Mandibular postcanine (c–p1) diastema: (0) present, (1) absent.
- 77:** Orientation of p1: (0) vertical, (1) rooted into the jaw at an oblique angle.
- 78:** Length of p2 trigonid: (0) much longer than talonid, (1) slightly longer than talonid.
- 79:** Cristid obliqua of p2: (0) absent, (1) present.
- 80:** Labial notch of p2: (0) broad, (1) narrow, deep.
- 81:** Metaconid of p2: (0) absent, (1) variably present and absent.
- 82:** Metaconid of p3: (0) absent, (1) variable, (2) present.
- 83:** Lower molar cristid obliqua: (0) low, (1) high.
- 84:** Molar metaconid: (0) single, (1) twinned.
- 85:** Lower molar occlusal basins: (0) shallow, (1) deep.
- 86:** Lower m3: (0) short, (1) long.
- 87:** Hypoconulid of m3: (0) connected labially, (1) middle, (2) lingually.