



## MIDDLE MIOCENE MESOTHERIINE DIVERSITY AT CERDAS, BOLIVIA AND A RECONSIDERATION OF *PLESIOTYPOTHERIUM MINUS*

Beth Townsend and Darin A. Croft

### ABSTRACT

We describe a large collection of mesotheriid notoungulate specimens, including a well-preserved cranium, from the early to middle Miocene locality of Cerdas, Bolivia. We attempt to classify the specimens into dental wear groups (i.e., ontogenetic groups) based on tooth size, morphology, and position of the posterior mental foramen, and we compare these specimens to those from other middle-latitude localities in Chile (Chucal) and Bolivia (Achiri, Choquecota, Quebrada Honda, and Nazareno). Our metric analyses, using bivariate plots and coefficients of variation (CVs), indicate that nearly all Cerdas specimens pertain to a single species. Our phylogenetic analysis indicates that this species, '*Plesiotypotherium*' *minus* Villarroel 1978, should be referred to a different genus, more closely related to *Altitypotherium* Croft et al. 2004 (Chucal) and/or *Microtypotherium* Villarroel 1974b (Choquecota). We do not refer '*P.*' *minus* to a new genus at this time, pending revision of other early to middle Miocene mesotheriids from Bolivia. A smaller species, represented by two specimens, may also be present at Cerdas.

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**Key Words:** Body Size, CV, Mesotheriidae, Notoungulata, *Plesiotypotherium*, South America, Tertiary

### INTRODUCTION

The middle Miocene fossil mammal record of Bolivia is incredibly rich, yet numerous localities have received little detailed investigation. Due to its central position in South America, Bolivia today is an important biogeographical transition area that encompasses varied ecozones (Altiplano, Amazon rainforest, Andean range, and Chaco) that shelter a great deal of biodiversity. In the past, Bolivia and other middle latitude areas may have been a center of diversity and/or origin for certain

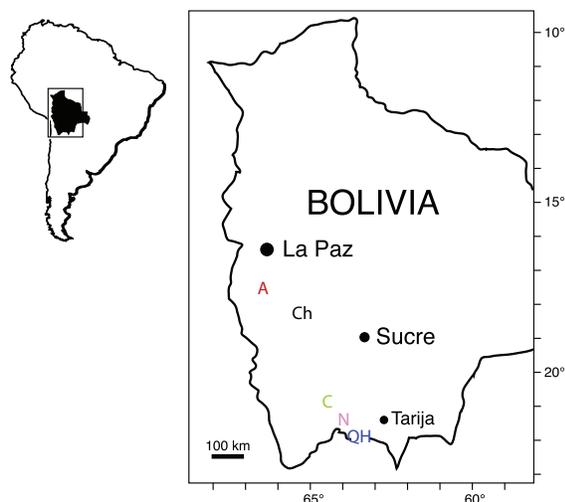
mammal groups including mesotheriid notoungulates (Marshall and Sempere 1991; Flynn and Wyss 1998; Cerdeño and Montalvo 2001; Croft et al. 2004, 2007, 2008; Flynn et al. 2005; Croft and Anaya 2006; Croft 2007).

Among notoungulates, mesotheriids are grouped within the suborder Typotheria, though their precise relationships within that clade are unclear (Simpson 1945; Cifelli 1993; Croft et al. 2004; Reguero and Castro 2004; Billet et al. 2008). Most typotheres are small notoungulates (< 10 kg;

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**FIGURE 1.** Map of Bolivia illustrating the localities Achiri (A), Cerdas (C), Choquecota (Ch), Nazareno (N), and Quebrada Honda (Q).

Elissamburu 2004) and are usually described as filling the small herbivore niche of modern rabbits, rodents, and small ungulates (Simpson 1967; Patterson and Pascual 1968; Cifelli 1985; Croft, 1999; Croft et al. 2003). Mesotheriids were among the largest of tyotheres and were likely semi-fossorial or fossorial (Shockey et al. 2007).

In Bolivia, mesotheriids are present in late Oligocene through late Miocene deposits throughout the Altiplano (Hoffstetter et al. 1972; Villarroel 1974a, 1974b, 1978; Hoffstetter 1986; Marshall and Sempere 1991; Oiso 1991; Marshall et al. 1992; Flynn and Swisher 1995; MacFadden et al. 1995; Hérail et al. 1996; Flynn et al. 2002; Croft et al. 2004, 2007; Croft 2007; Billet et al. 2008). Many of these occurrences pertain to *Plesiotypotherium*, a taxon first described from Achiri (Villarroel 1974a) and subsequently identified in other localities (Villarroel 1978; Oiso 1991; Croft 2007). Three species of *Plesiotypotherium* are currently recognized, two larger forms from Achiri (*P. achiriense* and *P. majus*) and a smaller one from Cerdas (*P. minus*; see below) (Figure 1). The generic status of *P. minus* has been unclear because it was diagnosed primarily on its small size rather than lack of derived character states. The species predates other members of the genus by some five million years.

In 1991, a team from the Florida Museum of Natural History recovered a large sample of mesotheriine craniodental material from Cerdas (MacFadden et al. 1995). Presumably because the holotype of *P. minus* had been collected from the

same general area as these specimens, most were referred to *P. minus*, including a well-preserved cranium; no detailed descriptions of the specimens were provided. The purpose of the present study is to: 1) describe the skull and other dental material collected from Cerdas in 1991 (supplemented by data from other collections; see below); and 2) evaluate the taxonomic validity of *P. minus* using these new specimens and data from other middle latitude mesotheriines from Chile and Bolivia (Table 1).

The Cerdas locality is situated in southern Bolivia about 60 km southeast of the city of Uyuni (21° 52' S, 66° 18-19' W; Villarroel 1978; MacFadden et al. 1995). Based on the “more specialized” morphology of *P. minus* relative to *Microtypotherium*, Marshall and Sempere (1991, p. 637) suggested the fauna might pertain to the Chasicuan SALMA (late Miocene). Subsequent radiometric dates and paleomagnetic correlations have demonstrated that Cerdas is considerably older (early middle Miocene, between 16.35 and 15.1 Ma; MacFadden et al. 1995), potentially corresponding to the Friasian SALMA *sensu stricto* (Flynn and Swisher 1995). Little has been published on the fauna collected at Cerdas—other than *P. minus*, only the small mesotheriine *Microtypotherium* cf. *choquecotense* and a specimen of *Plesiotypotherium* cf. *achirensense* have been reported (Villarroel 1978)—though investigations based on recent collecting efforts are currently underway (Croft et al. 2009).

## MATERIALS AND METHODS

The fossils described in this report are housed at the Florida Museum of Natural History in Gainesville, Florida, USA and the Facultad de Ingeniería Geológica of the Universidad Autónoma Tomás Frías, in Potosí, Bolivia. Measurements of these specimens were made to the nearest 0.1 mm using digital calipers. Comparative data were taken from the literature or gathered by DAC from original specimens. In addition to Cerdas, this study focuses on material from Choquecota, Quebrada Honda, and Nazareno in Bolivia and Chucal in Chile (Villarroel 1974b; Oiso 1991; Flynn et al. 2002; Croft et al. 2004, 2007; Croft 2007). In the following systematic review, single quotation marks are used to indicate uncertainty in taxonomic designations. We evaluated data on mesotheriines from both Choquecota and Quebrada Honda, but chose not to include them in these analyses because each locality has few or a single specimen.

**TABLE 1.** Temporal and geographical distribution of Bolivian Mesotheriinae.

Taxon	Locality	Location	Age Constraints	SALMA	REFERENCES
<i>Plesiotypotherium achirense</i>	Achiri	17°16'S, 69°01'W	7.6 Ma to 10.35 Ma	Huayquerian	Villarroel 1974a; Marshall et al. 1992
<i>Plesiotypotherium majus</i>	Achiri	17°16'S, 69°01'W	7.6 Ma to 10.35 Ma	Huayquerian	Villarroel 1974a; Marshall et al. 1992
<i>Plesiotypotherium minus</i>	Quebrada Honda	21°57'S, 65°25'W	11.96 ± 0.11 Ma to 12.83 ± 0.11 Ma	Laventan	Croft et al. 2004, 2007; MacFadden et al. 1990
<i>Plesiotypotherium</i> sp.	Nazareno	21°40'S, 65°35'W	9.58 ± 0.11 Ma to 20.9 ± 0.6 Ma	?Colloncuran	Oiso 1991; Héail et al. 1996; Horton 1998
<i>Microtypotherium choquecotense</i>	Choquecota	18°6'S, 67°55'W	14.2 ± 0.4	?Colloncuran	Villarroel 1974b; Marshall and Sempere 1991
<i>Plesiotypotherium' minus</i>	Cerdas	21°52'S, 6°18-19'W	15.10 ± 0.07 Ma to 16.36 ± 0.07 Ma	?Friasian s.s.	MacFadden et al. 1995, present study
<i>Microtypotherium</i> cf. <i>choquecotense</i>	Cerdas/Atocha	20° 55'S 66° 13' W	16.5-15.3 Ma	?Friasian s.s.	Villarroel 1974b; MacFadden et al. 1995
<i>Plesiotypotherium minus</i>	Cerdas	20°83 S, 66°4' W	16.5-15.3 Ma	?Friasian s.s.	Villarroel 1978; MacFadden et al. 1995
<i>Altitypotherium paucidens</i>	Chucal	18°32'S, 69°10'W	17.4 ± 0.4 Ma to 21.7 ± 0.8 Ma	Santacrucian	Croft et al. 2004, 2007; Riquelme 1998; Bond and Garcia 2002
<i>Altitypotherium chucalensis</i>	Chucal	18°32'S, 69°10'W	17.4 ± 0.4 Ma to 21.7 ± 0.8 Ma	Santacrucian	Croft et al. 2004, 2007; Riquelme 1998; Bond and Garcia 2002
<i>Eotypotherium chico</i>	Chucal	18°32'S, 69°10'W	17.4 ± 0.4 Ma to 21.7 ± 0.8 Ma	Santacrucian	Croft et al. 2004, 2007; Riquelme 1998; Bond and Garcia 2002

### Phylogenetic Analyses

To assess the phylogenetic position of the mesotheriine material from Cerdas (presumably *P. minus*), UF 133803 (the well-preserved skull) and mandibular specimens were added to the character-taxon matrix of Croft et al. (2004). Ordering of character states followed Croft et al. (2004). We corrected an error in the taxon list of Croft et al. (2004), repeated from Cerdeño and Montalvo (2001), listing *Pseudotypotherium hystatum* as *Mesotherium hystatum*. Recently studies (e.g., Cerdeño and Montalvo 2001; Reguero and Castro 2004) support the referral of this species to *Pseudotypotherium*, following Cabrera's (1937) original description. Trees were generated using the heuristic search option in PAUP 3.11 for the Macintosh computer, and character evaluation was performed in MacClade for the Macintosh. OTUs

with multiple character states were considered polymorphic. Multiple specimens were used to code each species, when possible.

### Metric Analyses

Dental dimensions (length and width of M1 and m2) were used to evaluate size variation among specimens. These data were evaluated visually using bivariate plots and statistically using the coefficient of variation (CV), calculated as the standard deviation divided by the sample mean, multiplied by 100 (Sokal and Rohlf 1995). Because the coefficient of variation is biased to underestimate relative variation, a correction factor was used for small samples (i.e., those < 10; Sokal and Rohlf 1995):

$$CV^*(1+1/4n)$$

### Viewing the Specimen On-line

We have provided three QuickTime movies illustrating dorsal (Movie 1), palatal (Movie 2), and laterally rotating (Movie 3) views of UF 133803, accessible at:

[http://www.palaeo-electronica.org/2010\\_1/192](http://www.palaeo-electronica.org/2010_1/192)

These movies are a dynamic means of viewing characters that might be less apparent in a photograph. These movies were built using Easypano Modelweaver and are imbedded in a program that allows the viewer to virtually manipulate the specimen.

### Abbreviations and Definitions

GB, Servicio Geológico de Bolivia; SGO PV, vertebrate paleontology collections, Museo Nacional de Historia Natural, Santiago, Chile; UATF, Universidad Autónoma Tomás Frías, Potosí, Bolivia; UF, Florida Museum of Natural History, Gainesville; cm, centimeter; Ma, megannum; mm, millimeter; SALMA, South American Land Mammal "Age"; upper case letters (e.g., M1) refer to maxillary dentition; lower case letters (e.g., m1) refer to mandibular dentition. Length refers to mesio-distal length, and width refers to bucco-lingual width.

### MESOTHERIINES OF BOLIVIA

It is only within the past 35 years that mesotheriines have been known from the Bolivian Altiplano (Marshall and Sempere 1991). In contrast, this group has been recognized in Argentina for nearly 150 years (Shockey et al. 2007). Most Bolivian mesotheriines are Miocene in age and all have been referred to two genera: *Microtypotherium* Villarroel 1974b and *Plesiotypotherium* Villarroel 1974a (but see Flynn et al. 2002 regarding a specimen from Micaña, Bolivia). Prior to the discovery of three new mesotheriines from the Santacrucian Chucal locality of Chile, these Bolivian genera were thought to be the basal-most members of the subfamily (Villarroel 1974a, 1974b, 1978; Marshall et al. 1983; Cerdeño and Montalvo 2001).

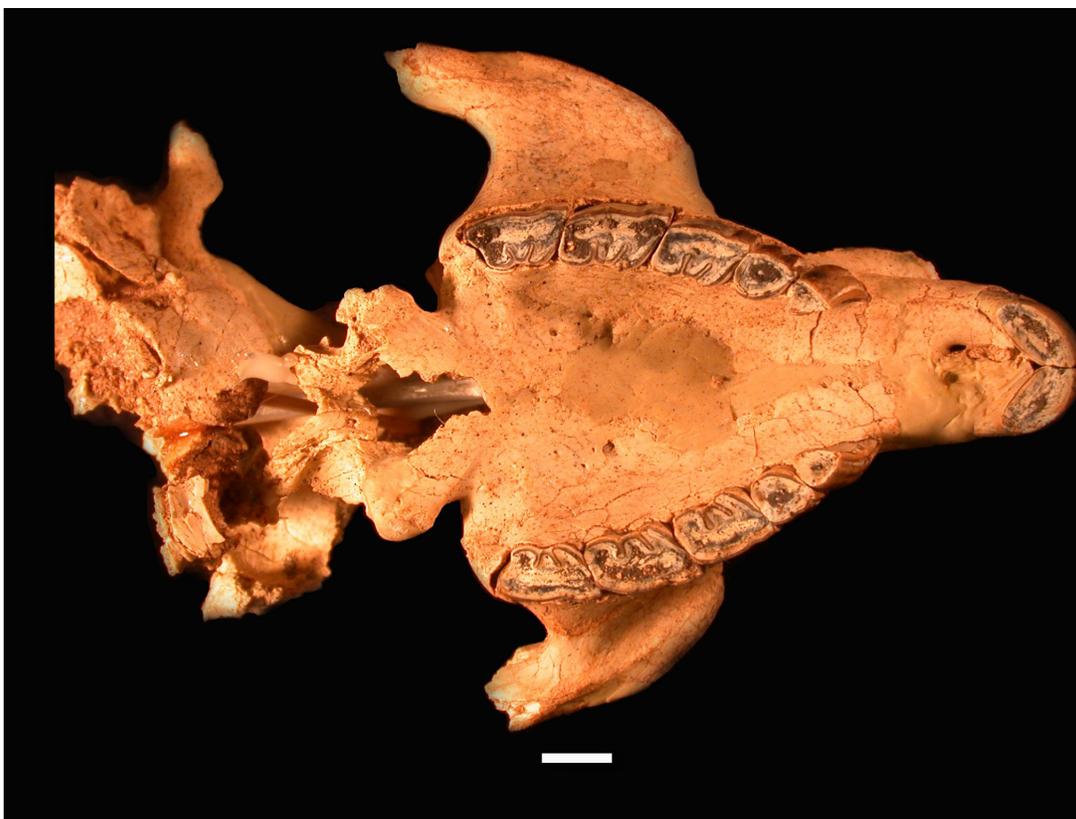
*Plesiotypotherium minus*, the smallest species of the genus and the subject of this report, is known only from two described specimens: the holotype (a left mandible from Cerdas preserving the full dentition and isolated right i1 and p4; Villarroel 1978) and a pair of mandibles from the late middle Miocene locality of Quebrada Honda (Croft 2007; Figure 1). MacFadden et al. (1995, p. 8160) collected "about 50 dentitions, mostly *Plesiotypotherium minus*" from Cerdas, but this paper—which focused primarily on geology and tectonics—did

not provide any detailed comparisons or descriptive data for the specimens. This UF collection includes both maxillae and mandibles and, as noted above, a well-preserved cranium (lacking only the anterior neurocranium, the nasal bones, and most of the dorsal portion of the skull; Figure 2). Recently, DAC and colleagues from UF, UATF, and U. of Rochester returned to the Cerdas locality (see Croft et al. 2009) and collected many additional mesotheriine specimens, including a partial skull with full dentition; these will also be evaluated in this report.

Some small mesotheriines from Nazareno have been referred to *Plesiotypotherium* based on general resemblance (Oiso 1991), but have not been described in detail; they have been considered to represent the smallest and oldest specimens of *Plesiotypotherium* (Oiso 1991) and may therefore be referable to *P. minus*. The dental dimensions reported by Oiso (1991) indicate a rather consistent size range for most of the sample, other than an outlier that is smaller than the smallest and most basal mesotheriine, *Eotypotherium chico* (Croft et al. 2004). The Nazareno specimens were evaluated in our study using data from Oiso (1991); we have not had the opportunity to view the material directly.

In addition to *Plesiotypotherium*, *Microtypotherium choquecotense* from the Choquecota locality is the only other mesotheriine from Bolivia. Until the discovery of the older Chucal fauna from Chile, this tiny mesotheriine was thought to be both the smallest and most primitive member of the subfamily (Villarroel 1974b). The holotype is a right maxilla bearing P4-M3 (and the alveolus for P3), and associated m2-m3 (Villarroel 1974b). Specimens from Cerdas (a posterior cranium, upper incisors, the lingual half of a left M2, and radius) also have been referred to *Microtypotherium* (Villarroel 1978).

Variation in dental morphology in *Plesiotypotherium* and *Microtypotherium* is not clearly understood. This is primarily due to a paucity of referred specimens and a relative absence of published measurements for those few specimens that have been referred to as recognized species. Villarroel (1974a) noted that the sample of *P. achirensense* from Achiri was highly variable, possibly indicating the presence of more than one species or sexual dimorphism, but did not explore this issue further. Other than a comparison of the Quebrada Honda specimen of *P. minus* with the holotypes of *P. minus* and *P. achirensense* (Croft 2007), no metric comparisons between *Plesiotypotherium* holotypes and any other specimens have been published.



**FIGURE 2.** UF 133803, '*P. minus*' from the Cerdas locality; a partial cranium bearing right I1, right P3-M3 and left I1, left P3-M3. Palatal view. Scale equals 1 cm.

This is surprising given that size is an important character for distinguishing species of mesotheriines, particularly when other dental characters (e.g., enamel sulci, lobe shape) are subtle or highly variable (Francis 1965; Villarroel 1974a, 1974b; Cerdeño and Montalvo 2001; Croft et al. 2004).

The phylogenetic relationships of *P. minus* are also unclear. Villarroel (1974a) suggested that the Bolivian mesotheriines from Cerdas and Choquecota (*Microtypotherium*) were more primitive than *Eutyptotherium* (from Argentina). He also proposed an anagenic mode of evolution for Bolivian mesotheriines with *Microtypotherium* as the basal-most form leading to *Plesiotypotherium minus*, then *Plesiotypotherium achirensis*, and finally to *Plesiotypotherium majus* (Villarroel 1974a, 1974b, 1978). Testing this hypothesis requires assessing: 1) metric variation within and among these forms; 2) variation in discrete dental characters; and 3) the identity of *Microtypotherium* cf. *M. choquecotense* from Cerdas. Croft et al. (2004) performed a cladistic analysis of dental and cranial characters for all known members of the subfamily, though *Plesiotypotherium* was coded at the generic level rather than as discrete species. Their results indicated

that *M. choquecotense* (from Choquecota) was basal to other Bolivian taxa and all Argentine species (Croft et al. 2004).

The relative abundance of mesotheriine specimens from Cerdas presents an opportunity to evaluate the validity of *P. minus* and the proper generic designation of this species. As detailed below, our analyses indicate that two groups of specimens can be distinguished at Cerdas based on size and dental characters of the lower molars. Neither shares an exclusive relationship with *Plesiotypotherium* (i.e., *P. achirensis*) and therefore should not be referred to this genus.

#### SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758  
 Order NOTOUNGULATA Roth, 1903  
 Suborder TYPOTHERIA Zittel, 1893  
 Family MESOTHERIIDAE Alston, 1876  
 Subfamily MESOTHERIINAE Simpson, 1945  
 '*Plesiotypotherium*' MINUS Villarroel, 1978  
*Microtypotherium* cf. *M. choquecotense* Villarroel;  
 Villarroel, p. 166, figs. 2, 3. v. 1974b

**Type Locality.** Cerdas, Department of Potosí, Bolivia.

**Distribution.** Cerdas beds, early middle Miocene, Friasian sensu stricto and/or Collorcuran SALMA, Department of Potosí, Bolivia (Villarrol 1978; Swanson et al. 1987; Marshall and Sempere 1991; MacFadden et al. 1995; Croft et al. 2009); Nazareno Formation, ?middle Miocene, ?Collorcuran SALMA, Department of Potosí, Bolivia (Oiso 1991; Hérail et al. 1996); Quebrada Honda, Honda Group, middle Miocene age, Laventan SALMA, Department of Tarija, Bolivia (Croft 2007).

**Referred specimens.** GB-223, left ramus bearing m1-3, right ramus bearing bases of p4-m3, half of a left mandibular corpus bearing i1-2 and dp3, and a palatal piece with the lingual halves of M2-3; UF 133803, partial cranium with complete maxillary dentition; UF 225690, complete left mandible with partial right (i1, p4); UF 225691, partial left mandible with p4-m3; UF 225692, left m1/2 and various bone fragments; UF 225693, right M2-3 and other tooth fragments; UF 225694, symphysis with bases of i1, right p4-m2, left m1, two partial lower molars; UF 225695, left M1/2; UF 225696, left mandible with m2-3, right mandible with partial m2; UF 225697, left mandible with m2 and partial m3; UF 225698, right M3 and partial left upper molar; UF 225699, left m3, partial mandible with right m2, partial m3, and partial symphysis; UF 225700, i1; UF 225701, left mandible with partial i2; right mandible with m2-3; UF 225706, lower incisor; UF 225709, right M1/2 and left P4-M1, various partial upper teeth; UF 225710, partial left mandible and symphysis including left i1-m2 and right i1-p4; UF 225711, partial left mandible with m3, various postcranial bones; UF 225713, two left M1/2, M3, i1, other tooth fragments; UF 225714, right mandible with p4-m3, numerous lower teeth/tooth fragments; UF 225721, various postcranial bones; UATF-V-000816, left M3; UATF-V-000839, right M2; UATF-V-000858, right M2-M3; UATF-V-000862, left M1-M3 and left M2 (isolated); UATF-V-000843 left P3, right P3-M3; UATF-V-000840, right and left P3-M3; UATF-V-000823, left dp3-4, m1-2; UATF-V-000827, right and left m1-m3; UATF-V-000879, right m1-m3; UATF-V-000844, left p4-m3; UATF-V-000815, left m1-m3; UATF-V-000847, right i1, m3, left p4, m3; UATF-V-000829, right m1; UATF-V-000835, left m1; UATF-V-000839, left m1; UATF-V-000837, p4; UATF-V-000874, m3; UATF-V-000845, left m1-m3.

### Revised Diagnosis of '*Plesiotypotherium*' minus

Differs from *M. choquecotense* in having an I1 that is ovoid, pointed distally with no lingual sulcus, and having a relatively wide post-palatal notch that does not extend to the level of M3. The molars increase in length from M1 to M3.

Differs from *P. achirensis* in presence of more ovoid P3 and rounder lingual edge of P4; '*P.*' minus is also smaller (based on dental measurements, approximately 30% smaller than *P. achirensis*).

Differs from *P. majus* in possession of shallower buccal sulci on premolars and presence of more ovoid premolars; also smaller in size (based on dental measurements, approximately 45% smaller than *P. majus*).

Differs from *Altitypotherium paucidens* in the presence of parallel maxillary diastemata, an elliptical first maxillary incisor (subtriangular in *A. paucidens*), presence of P3, and subparallel lingual lobes on lower molars.

Differs from *A. chucalensis* in the presence of parallel maxillary diastemata, a wider post palatal notch, an anteriorly placed buccal sulcus on P3, a more distinct buccal sulcus on P4, subparallel lingual molar lobes, and a large M1 middle lobe.

Differs from *Eotypotherium chico* in having a rounder P3, a more subtriangular P4, in M3 being the longest tooth, in having the root of zygomatic arch above M2, and in having the middle lobe well exposed in all three molars; it is also larger (based on dental measurements, approximately 40% larger than *Eotypotherium chico*).

Differs from *Eutypotherium* in the presence of parallel diastemata, a postpalatal notch that does not extend to level of M3, an ovoid I1 with no lingual sulcus, one labial sulcus on premolar ectolophs, and smaller size (approximately 20% smaller than *Eutypotherium lehmannnitschei*, based on dental dimensions).

Differs from *Typotheriopsis* in presence of a shallow suborbital fossa and an ovoid I1 with no lingual sulcus; also approximately 30% smaller based on dental measurements.

Differs from *Pseudotypotherium* in the presence of a postpalatal notch that does not extend to level of M3, a shallow suborbital fossa, one labial sulcus on premolar ectolophs, a lesser degree of molar imbrication, proportionally shorter teeth with little exposure of the middle lobes on the maxillary molars, and smaller size (based on dental measurements, approximately 20% smaller than *Pseudotypotherium exiguum*).

**TABLE 2.** Cranial metrics for UF 133803 '*Plesiotypotherium*' minus

Palate length	~84.02
I1-P3 diastema length	14.4
Maximum breadth of palate, internal (between borders of M3)	35.71
Maximum breadth of palate, external (between borders of M3)	48.91
Palate breadth at diastema	19.91
Width across zygomatic arches	~91.49 (slightly distorted)
Zygomatic arch height	21.78 below orbit to M2 alveolar edge

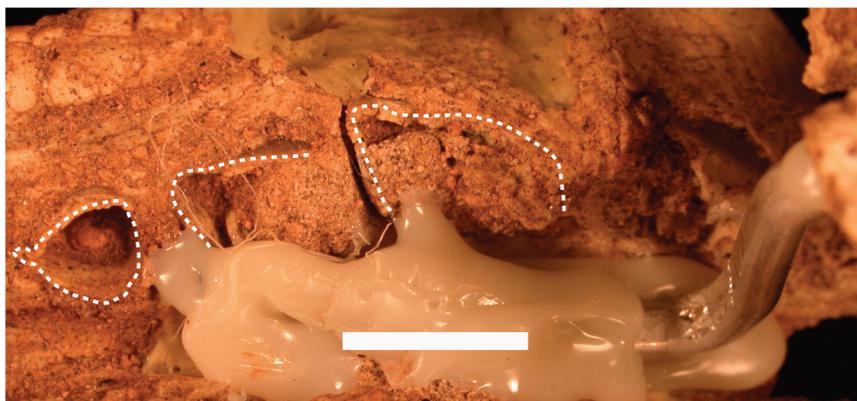
Differs from *Mesotherium* in the presence of shallow suborbital fossa, ovoid I1 with no lingual sulci, lack of lingual sulcus on P4 (*Mesotherium* has one), absence of elongate M1, and lesser degree of molar imbrication. '*P. minus*' is approximately 25% smaller than *M. maendrum*.

Differs from *Caraguatypotherium* in a more pronounced sagittal crest, a P4 without a lingual sulcus, lesser degree of molar imbrication, and smaller size (at least 20% smaller based on dental dimensions).

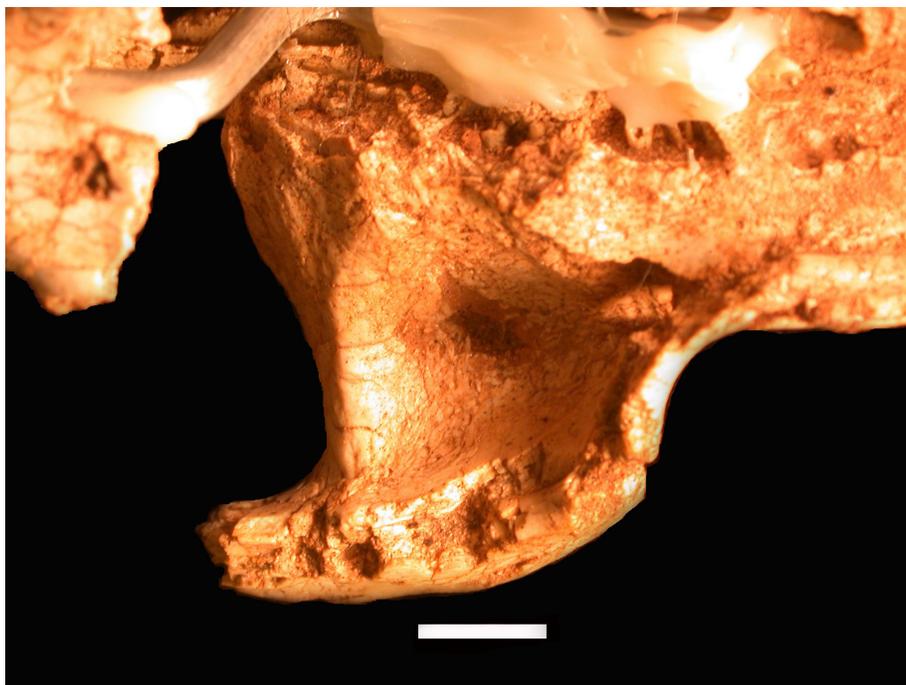
**Description.** Skull—The partial cranium of UF 133803 is in fair condition; the nasals, the anterior portion of the neurocranium, and the zygomatic processes of the temporal bone are not preserved. Much of the basicranium is missing except for portions of the right tympanic and the two pterygoids. The top of the neurocranium has the left and right parietals and squamosals, the sagittal crest, and a small portion of the frontal bone with an orbital process (right side only). The facial cranium preserves the right and left maxillae with full dentitions.

The palate exhibits some damage near the sagittal plane and restoration compound fills this damaged region. Many features of the palate are still intact, and at least six neurovascular foramina are present. It is apparent that UF 133803 had prominent incisive foramina; the left side is filled with restoration compound but the foramen is partially visible on the right and is approximately 7.5 mm long. The palate itself curves strongly toward the premolars and first two molars, then flattens slightly as it nears M3 (Figure 2). It is damaged on the left side between I1 and P3 (i.e., the diastema) but is plainly visible on the right. The diastemata are parallel and measure approximately 14.4 mm in length (Table 2). The palatal notch nearly reaches the level of the M3 and is acute (in contrast to the nearly 90° notch of *P. achirense*). The distance of the palatal notch from the back of the palate is much less than the width of the M3.

The nasal bones are missing, and the floor of the nasal cavity (typically formed by the maxilla) has been eroded away. This provides a view of the bases of the of the cheek teeth (Figure 3). The



**FIGURE 3.** Outlines of tooth crown bases (white broken lines) of specimen UF 133803. Right side of specimen, anterior to the left. Scale equals 1 cm.



**FIGURE 4.** UF 133803, 'P.' minus from the Cerdas locality. A dorsal view of the left suborbital fossa (pictured as right). Note the transverse strut of bone demarcating the posterior edge of the fossa. Scale equals 1 cm.

bases of the premolars and molars match the occlusal surfaces, indicating that these teeth are ever-growing (hypsodont), rootless, and would not have changed significantly with wear.

Both zygomatic arches of UF 133803 are intact but the right shows more damage on the distal aspect of the temporal process than is seen on the left. The zygomatic bones are quite broad and heavy, and each has its root perpendicular to the anterior edge of M1. The broad inferior surface present on both left and right arches apparently would have provided a large area for the origin of the masseter muscle. The suborbital fossa, present on the dorsal surface of the arch, is subtriangular and shallow, particularly in comparison with some other mesotheriines (e.g., *Tyotheriopsis*) (Figure 4). The major axis of the fossa is transverse. A transverse strut of bone demarcates the posterior border of the suborbital fossa. The infraorbital foramen is subcircular, of medium size (relative to other mesotheriines), and measures 4.3 x 4.1 mm (Table 3; Figure 5).

Only the posterior portions of the right and left frontals are present; the right orbital process that extends 13 mm posterolaterally to a broken distal edge. The frontals contact the parietals in an M-shaped suture; a thin tongue of the frontals extends posteriorly between the anterior exten-

sions of the parietals. The prominent sagittal crest is approximately 39 mm in length and shows some minor damage (Figure 6). The left parietal shares a partial sinuous suture with the squamosal that is ~16.9 mm in length. The squamosal portion of the right zygomatic arch has two distinct neurovascular foramina. The glenoid fossa on the right side appears to have been compressed in an antero-posterior direction.

Only the pterygoid wings and part of the basisphenoid are present on the sphenoid. Of the two sides, the left pterygoid complex is in better condition; although the lamina of the medial and lateral pterygoid plates are broken, the scaphoid fossa is preserved, which has been described as the origin of the tensor veli palatini muscle in toxodontians (Gabbert 2004). The right petrosal bulla is inflated but the entrance to the tympanic cavity has been crushed. The bulla is wider transversely than it is anteroposteriorly. The cerebellar aspect of the petrosal can be seen on both left and right sides. Due to damage of the neurocranium and basicranium, it is possible to see features of the petrosal bone inside the cranial cavity: the internal auditory foramen, subarcuate fossa, and the groove for the superior petrosal sinus (Figure 7).

Upper Dentition—In general, the teeth of UF 133803 are in excellent condition and exhibit few

**TABLE 3.** Comparison of suborbital fossa development and infraorbital foramen in *Plesiotypotherium minus* and other mesotheriines (based on Croft et al. 2004).

Taxon	Specimen	Suborbital fossa	Infraorbital foramen (mm)	M1 size (mm)	Relative size of Infraorbital foramen
<i>Altitypotherium paucidens</i>	SGOPV 4038	Shallow	10.5 x 5.5	12.5 x 8.6	0.42
<i>Eutypotherium chico</i>	SGOPV 5157	Shallow	4.0 x 3.5	9.5 x 6.4	0.18
<i>Eutypotherium lemannnitschei</i>	MLP 12-1701	Shallow	7.5 x 5.4	14.6 x 10.0	0.22
<i>Eutypotherium superans</i>	MACN 11079	Shallow	5.5 x 4.1	14.1 x 10.0	0.13
<i>Caraguatypotherium munozi</i>	SGOPV 4004	Shallow	6.5 x 4.9	16.5 x 10.0	0.15
<i>Typotheriopsis silveyrai</i>	MLP 36-xl-10-2	Deep	6.6 x 5.7	16.9 x 11.4	0.15
<i>Typotheriopsis</i> sp.	FMNH P14477	Deep	7.5x 6.2	22.5 x 14.5	0.11
<i>Plesiotypotherium' minus</i>	UF 133803	Deep	4.34 x 4.1	11.0 x 8.4	0.19
? <i>Pseudotypotherium</i> sp.	MACN 8010	Deep	14.2 x 12.4	23.8 x 11.0	0.53
? <i>Pseudotypotherium</i> sp.	MACN 1111	Deep	12.2 x 7.7	19.2 x 10.5	0.37
<i>Mesotherium cristatum</i>	MACN 2036	Absent	3.9 x 3.0	21.8 x 9.8	0.04
<i>Mesotherium pachygnathum</i>	MACN 1665	Absent?	9.4 x 5.8	24.4 x 11.4	0.15
<i>Mesotherium ?ugustirostrum</i>	MACN 6040	Absent	5.1 x 3.5	23.6 x 11.1	0.05

instances of breakage. Both left and right incisors are in excellent condition. They are elliptical with the major axis at approximately a 40-50° angle relative to the sagittal plane (Figure 6). No sulci or plications are present on the incisors. Incisors are hypselodont; the alveolus of each incisor is obvious because neither the nasal bones nor the floor of the nasal cavity is intact. A thin coat of cementum covers the lingual face of the incisor.

Both molars and premolars are hypselodont, as indicated by the open-ended bases of these teeth, which are visible due to the broken skull bones (Figure 3; Table 4). The length of the cheek tooth row is ~5 cm. The left P3 is completely intact, whereas the right P3 has a small chip missing from both the posterior lingual and posterior buccal faces. Based upon the complete left P3, this tooth is subtriangular with a strong anteriorly placed sulcus on the buccal face of the tooth, forming a distinct parastyle. A more shallow sulcus is found centrally on the buccal face of the P3. No cementum is present on the right P3 but the morphology of the left P3 suggests that it was present. This tooth is featureless on the occlusal surface. Enamel evenly covers the anterior, buccal, and lingual faces of the tooth. The P3 is wider than it is long (Table 5). The P4 is intact on both the left and right sides. The P4 is also subtriangular, but less so than the P3, as the protocone lingual face is

more rounded. A strong anterior sulcus is present on the buccal face of the P4, forming a parastyle. As in the P3, another sulcus is present on the central buccal face of the P4, but is not as pronounced. These sulci form the base of a prominent pillar evident in the occlusal outline of the P4. A thin coat of cementum is present on the buccal face of the tooth, and a much thicker coat is present on the lingual face. In an even coat, enamel covers the anterior, buccal, and lingual faces of the tooth, the posterior edge appears to be only covered in cementum. The P4 is wider than it is long (Table 5).

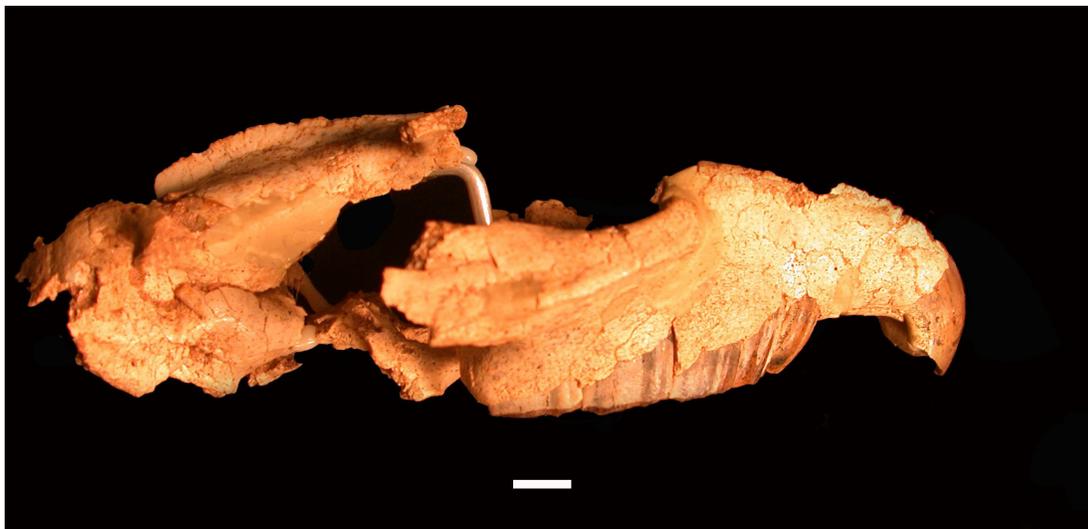
As with all mesotheriines, UF 133803 exhibits three lingual lobes on all molars (Figure 8). The length of the lingual lobes increases in size antero-posteriorly (i.e., the anterior lobe is the narrowest). The overall orientation of the molar lobes is subparallel, with the anterior lobe subtly directed posterolingually and the posterior lobe subtly directed more anteriorly in all molars. The molars increase in length mesiodistally, with M3 being the longest. Molar cementum is thicker lingually and thinner buccally. An even thickness of enamel is present on the anterior, buccal, and lingual faces of the molars. Other than the lobes themselves, no other occlusal features are found on these teeth, and no sulci or plications are apparent on the lingual surfaces of the molars.



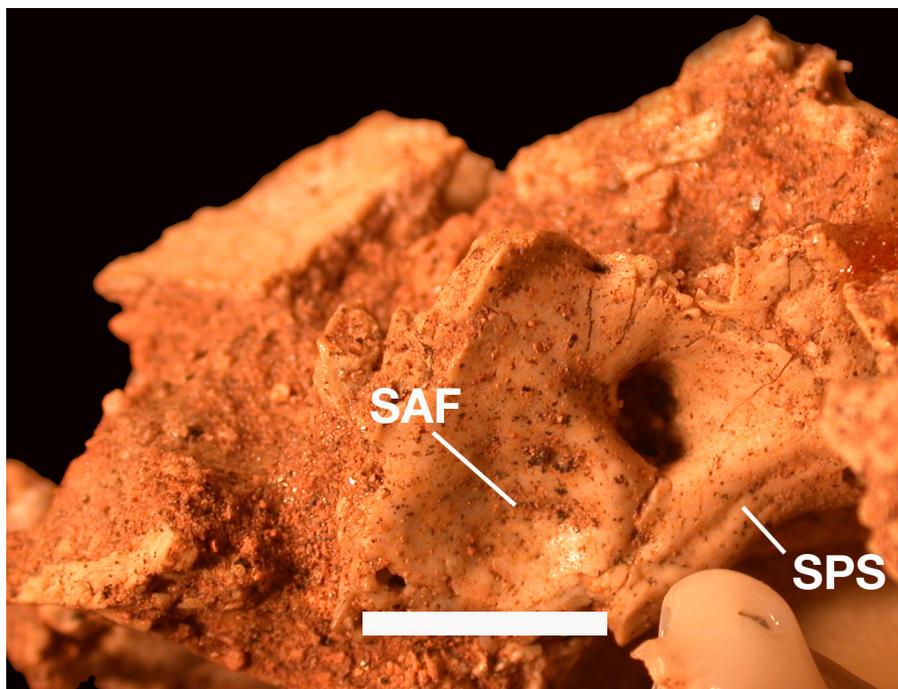
**FIGURE 5.** View of left infraorbital foramen of UF 133803 (pictured as right). Note the placement of the foramen and its subcircular shape. Scale equals 1 cm.

The M1 is the shortest in the molar series. The more centrally placed buccal sulcus is the strongest sulcus on this surface of the tooth. This sulcus forms the base of a prominent rib that forms

the paracone fold of the M1. The anterior lobe of M1 is the smallest of any of the molar teeth. The middle lobe is trapezoidal in shape. The M2 is longer than the M1 and also exhibits a prominent cen-



**FIGURE 6.** Lateral view of UF 130883, 'P.' minus. Note the angle of the incisors and the extent of the sagittal crest. Scale equals 1 cm.



**FIGURE 7.** View of right internal acoustic meatus of UF 133803 with exposed subarcuate fossa (SAF) and superior petrosal sinus (SPS). Note the SPS is positioned anteriorly. Scale equals 1 cm.

trally located sulcus forming the parastyle region, which is the largest of the three molar teeth. The M2 is the widest tooth in the cheek tooth series. The middle lobe is rounded and is the largest middle lobe of the three molars. The M3 is the longest and narrowest tooth in the cheek tooth series and has a trapezoidal outline due to the posterior projection of the ectoloph. The buccal sulcus is also apparent on the M3, but is less prominent than that on the previous two molars. The parastyle region is prominent on the M3. The middle lobe is the smallest and the most triangular in shape. The posterior ectoloph lobe is subtle in some teeth (e.g., UF 133803; Figures 2 and Figure 8), but more prominent in others (e.g., UF 225698; Figure 9).

UF 133803 exhibits a degree of imbrication of 1.12 (Table 4; Flynn et al. 2005). As mentioned above, the enamel is equally thick on all faces of the tooth where it is present, but there is none on the posterior surface of the cheek teeth and this is most obvious in M3. The cementum is thicker lingually and a thinner buccally. The cementum is thick on the middle lobes of the molars, particularly that of M3.

**Lower Dentition**—Although characters of mesotheriine lower dentition do not allow for clear discrimination among genera (Croft 2007), lower teeth have been used to diagnose '*P.* minus' (Villar-

roel 1978). From the Cerdas locality, 24 partial lower dentitions appear to pertain to '*P.* minus'. Measurements for these specimens are provided in Table 6. The sample represents the entire lower tooth row (Figure 10). The *i*1 is variable in shape, ranging from sub-ovoid to sub-triangular to trapezoidal. The enamel covers only the anterior face of the incisor and in one specimen (UF 225701), a sulcus is present on the medial surface of the tooth. The second incisor is elliptical in outline and less variable in shape, with enamel covering only the labial surface of the tooth. The *p*4 is triangular with a slight buccal sulcus demarcating the trigonid from the talonid; enamel is found on the buccal and lingual faces of the *p*4. The trigonid is smaller and narrower than the talonid. Both regions of the tooth show some variability in shape: the trigonid ranges from slightly ovoid to having a rounded point mesially; the talonid of the *p*4 ranges from rounded to more distally elongate. The three molars exhibit a buccal sulcus that nearly reaches the lingual edge of the tooth; a small isthmus of dentin persists between both lobes through later stages of wear. The molars also exhibit two lingual sulci, one along the posterior edge of the trigonid near the dentin isthmus and the other with various degrees of depth on the talonid near to where it tapers to its distal edge

**TABLE 4.** Index of imbrication for mesotheriine specimens (Croft et al. 2004; Croft unpublished data).

Species	Specimen	Imbrication
<i>Eutyotherium lehmannitschei</i>	MLP 12-1701	1.1
<i>Plesiotyotherium</i> ' (CERDAS)	UF 133803	1.12
<i>Altityotherium chucalensis</i>	SGOPV 4100	1.12
<i>Eotyotherium chico</i>	SGOPV 5157	1.12
<i>Tyotheriopsis</i> sp.	MLP 76-VI-12-68	1.16
<i>Altityotherium paucidens</i>	SGOPV 4038	1.16
<i>Tyotheriopsis</i> sp.	MLP 55-IV-28-12	1.19
<i>Eutyotherium superans</i>	MACN 11079	1.2
<i>Tyotheriopsis silveyrai</i>	MLP 36-IX-10-2	1.21
<i>Tyotheriopsis</i> sp.	MLP 76-VI-12-126	1.21
<i>Tyotheriopsis chasicoensis</i>	MLP 12-1666	1.27
<i>Tyotheriopsis</i> sp.	MLP 29-X-11-29	1.28
aff. <i>Eutyotherium</i> sp.	MLP 72-IX-2-8	~1.3
<i>Mesotherium 'angustirostrum'</i>	MACN 6040	1.3
<i>Tyotheriopsis</i> sp.	MLP 32-IV-20-5	1.3
<i>Tyotheriopsis</i> sp.	MLP 28-X-11-33	1.33
<i>Tyotheriopsis</i> sp.	MLP 28-X-11-69	1.36
<i>Mesotherium</i> sp.	MACN 2037	1.46
<i>Pseudotyotherium exiguum</i>	MLP 12-1683	1.46
<i>Mesotherium cristatum</i>	MACN 1113	1.5
<i>Mesotherium maendrum</i>	MACN 8010	1.5
<i>Pseudotyotherium pseudopachygnathum</i>	MLP 12-1691	1.55
<i>Mesotherium maendrum</i>	MACN 2648	1.6
<i>Pseudotyotherium pseudopachygnathum</i>	MLP 12-1695	1.6
<i>Mesotherium cristatum</i>	MACN 2036	1.68
<i>Mesotherium maendrum</i>	MACN 1111	1.72
<i>Mesotherium cristatum</i>	MACN 2280	1.8
<i>Pseudotyotherium pseudopachygnathum</i>	MLP 12-1692	1.8
<i>Mesotherium pachygnathum</i>	MACN 1665	1.83

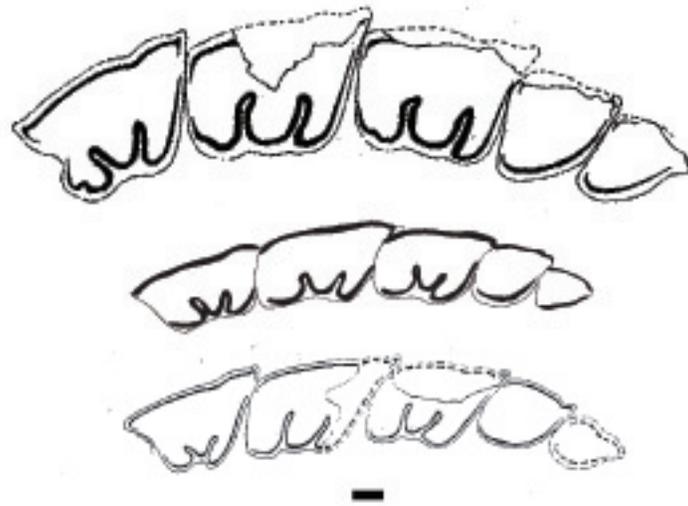
**Deciduous Lower Teeth.** Seven partial mandibles from Cerdas bear deciduous teeth. Only deciduous premolars (i.e., no deciduous incisors) are known at this time. The lower premolars resemble their adult counterparts although they are smaller in size. The dp3 (present on UF225704 and UATF-V-000823) is bilobed and resembles the adult p4 in having a triangular trigonid and a rounded talonid. The dp4 is also bilobate and resembles adult m1, but is smaller, with a trigonid more rounded than that of dp3. The talonid of dp4 is the most distin-

guishing feature of this tooth: the distal portion of the tooth is quite round, almost circular. In addition to size, distinction can be made among little worn adult m1s and dp4s by comparing talonid shape (dp4s have a very round distal end compared to p4s or m1s, which are more square; see Figure 11.1, 11.3) and the depth of the buccal sulcus (deeper on dp4s than on adult p4s).

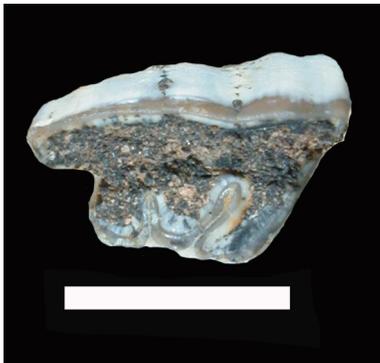
**Tooth Wear in 'P.' minus.** General wear trends seen in the Cerdas lower dentition sample include the obliteration of the enamel faces on the dp3 and

**TABLE 5.** Measurements of maxillary dentition for the skull of 'Plesiotypotherium' minus and other maxillary specimens from Cerdas, Plesiotypotherium achirensis, Plesiotypotherium majus, and Microtypotherium choquecotense. Data for P. achirensis, P. majus, and M. choquecotense from Villarroel (1974a, 1974b).

Taxon	Side	Adult/		I1		P3		P4		M1		M2		M3	
		Juvenile	I1	L	W	L	W	L	W	L	W	L	W	L	W
P. achirensis	holotype (ACH 26)	A	18.8	9.3	9.6	8.5	10.7	10	17	11	18.7	12.2	19.8	10.8	
P. majus	holotype (ACH 27)	A	21.6	10.5	13	10	13.7	12.3	20.8	12.8	21.8	12.9	24.6	12	
M. choquecotense	holotype (GB-002)	A			6.5	5.3	8.3	6.5	~12.1	~8.3	15.6	8.3	15.2	7.7	
	UF 225693	A								11.1	7.5	12.9	7.3		
	UF 225695	A							12	10.2					
	UF 225698	A											14.8	8	
	UF 225709	A					7.5	7.9		14	7.8				
	UF 225713	A	~10.5	~6.1					9.6	6.7	10.6	7.3	11.7	6.3	
	UATF 000816	L											13.0	7.6	
	UATF 000839	R									14.5	8.6			
	UATF 000858	R									12.4	10.5	15.2	9.1	
	UATF 000862	L							10.5	~9.4	14.0	8.9	14.5	8.1	
	UATF 000862	L									13.7	9.1			
	UATF 000843	L			6.1	7.7									
	UATF 000843	R			5.5	6.7	8.2	7.9	3.4	9.0	14.7	9.4	17.1	8.8	
Gen. et sp. indet	UATF 000840	L			5.8	4.5	7.1	5.3	9.5	5.8	10.0	~5.7			
Gen. et sp. indet	UATF 000840	R			5.9	5.3	7.2	5.5	9.4	6.1	9.7	6.4			
	P.' minus		5.88	6.38	5.65	6.95	6.8	7.37	10.96	8.4	13.37	8.92	13.75	7.7	



**FIGURE 8.** Occlusal outlines of maxillary dentitions of A. *Plesiotypotherium achirensis* (adapted from Villarroel 1974a), B. '*Plesiotypotherium*' minus, C. *Microtypotherium choquetotense* (adapted from Villarroel 1974b). Scale equals 2 mm.



**FIGURE 9.** UF 225698, right M3 showing posterior fourth lobe. Scale equals 1 cm.

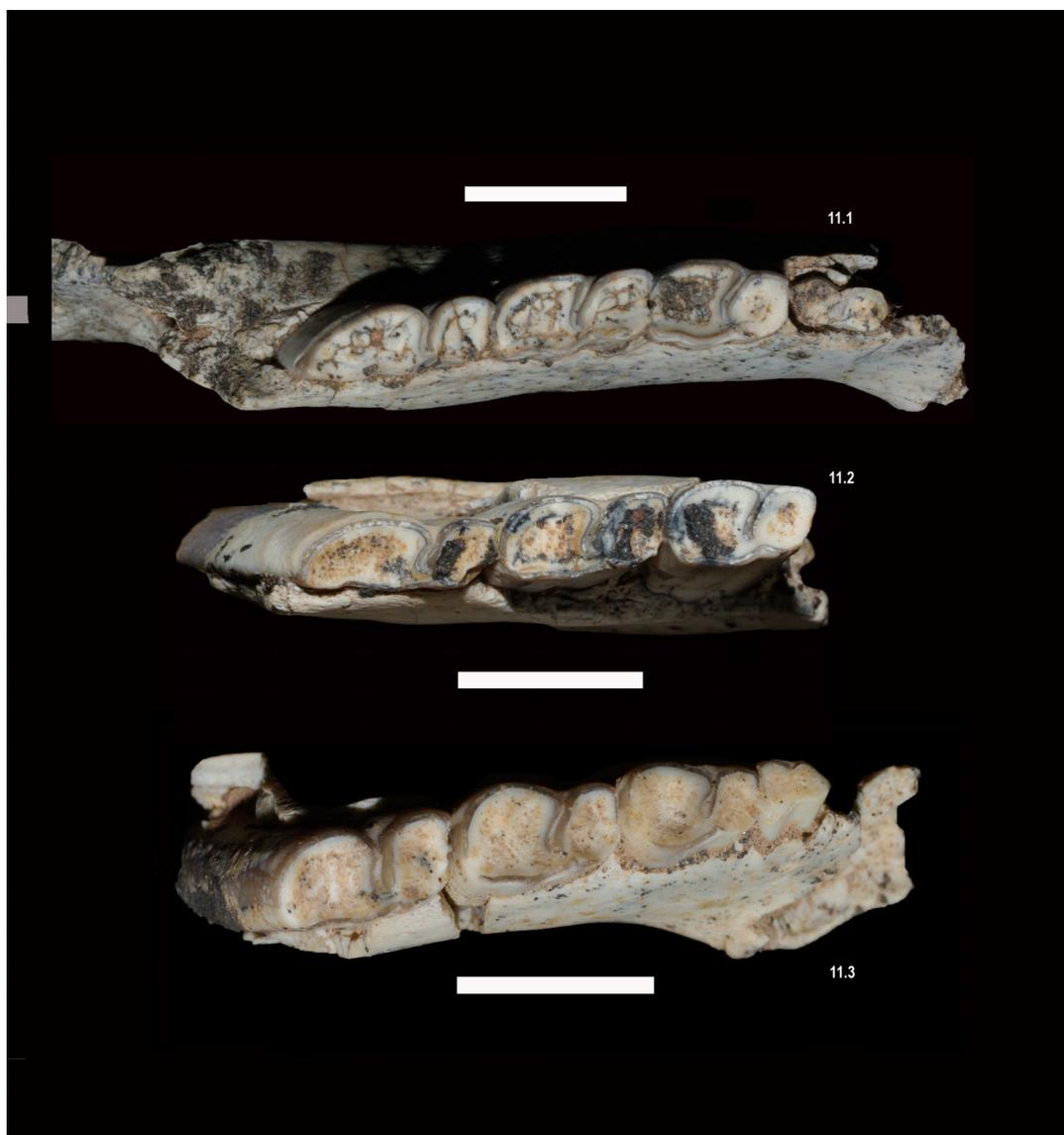
wear of the trigonid enamel on dp4. The only other noticeable features likely associated with wear are a deepening of the lingual sulcus on the distal edge of the talonid, and sharpening of the distal point of the m3 talonid. Billet et al. (2008) noted that the lingual sulcus deepens with wear in the deciduous teeth of trachytheriines. Although definitive wear categories could not be identified in the Cerdas material, specimens that exhibited both permanent and deciduous dentition had smaller adult teeth (shorter and narrower). Those specimens without associated deciduous teeth had larger (longer and broader) teeth, particularly in the first lower molar. The teeth associated with deciduous dentition and considered to be early wear are 10-15% shorter in



**FIGURE 10.** '*P.*' minus UF 225690, nearly complete left mandible and symphysis bearing i1-2, p4-m3 and right i1-2 and right p4. Note the two lingual sulci on the molars.





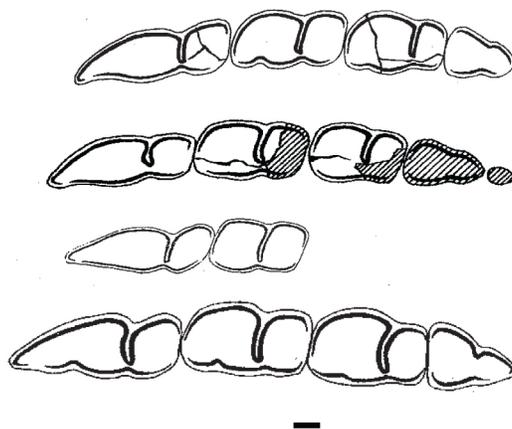


**FIGURE 11.** Three examples of deciduous and fairly unworn mandibular dentitions: 11.1 UAT-V-000879, dp4, m1-m3; 11.2 UATF-V- 000827, m1-m3; 11.3 UATF-V- 000823, a partial left mandibular ramus bearing dp3-4, m1-m2. Scale equals 1 cm.

length and ca. 5% narrower in width than those with a greater degree of wear (Table 6).

**Remarks.** We refer the maxillary specimens listed above to '*P.* minus based on dental similarities in maxillary tooth lobe shape and orientation and the following characters: relatively large infraorbital foramen; an angle of the major axis of the incisor near 50°; a low degree of imbrication; and slightly posterolaterally divergent diastemata. Villarroel (1974a) indicated that the genus *Plesiotypotherium* could exhibit slightly posterolaterally divergent diastemata, although the type exhibits parallel diastemata.

The assignment of mandibular specimens to '*P.* minus is based on similarity with the *P. minus* holotype in size and in morphology of the molar series (i.e., the presence of both an anterior and talonid lingual sulcus; Figure 12). As indicated by our phylogenetic analysis (below), the Cerdas sample does not share an exclusive relationship with specimens from Achiri that constitute the genus *Plesiotypotherium*; we thus cannot place the Cerdas sample in the genus *Plesiotypotherium*. The older age of the Cerdas sample is compatible with this assignment. However, further morphological and metric evaluation of the Cerdas sample in



**FIGURE 12.** From top to bottom: '*Plesiotypotherium*' *minus*, holotype; *Microtypotherium* cf. *M. choquetotense* (here referred to '*P.*' *minus*); *Microtypotherium choquetotense*, holotype; *Plesiotypotherium achirensense*, holotype. Note the two lingual sulci in '*P.*' *minus* and *P. achirensense*. Scale bar = 2 mm. Compiled from Villarroel, 1974a and 1978.

relation to the similarly aged Nazareno sample could clarify the taxonomic status of '*P.*' *minus*.

We refer the specimen assigned to *Microtypotherium* cf. *M. choquetotense* by Villarroel (1978) to '*P.*' *minus* because the specimen has no characters that uniquely suggest it pertains to *Microtypotherium* (e.g., m2 proportions > 1.60), or that suggest that it is more closely related to that species than to '*P.*' *minus*. Additionally, this specimen falls well within the size range of the '*P.*' *minus* sample (Figure 12).

Mesotheriinae, gen. et sp. indet.

Referred Specimens. UF 225707, right mandibular fragment bearing m2-3 (Figure 13); UATF-V-000840 partial rostrum with right and left I1, ?P4-M3 (left I1 and both ?M3 loose; see below for alternate interpretation of the tooth homologies; Figure 13).

Comments. These specimens are the smallest mesotheriines at the Cerdas locality (Figure 13). Both are clearly mesotheriine based on their dental morphology: UF 225707 exhibits no fosset-tids in either the trigonid or talonid (unlike trachytheriine mesotheriids), a slight lingual sulcus on the m2 talonid is present and the maxillary dentition exhibits imbrication (a feature of mesotheriines). Observation of dental and gnathic morphologies indicates that one specimen (UF 225707) is apparently an adult whereas UATF-V-000840 is a juvenile with a full adult tooth row other than an unerupted M3 (Figure 13). UF 225707 does not differ in morphology from unworn specimens of m2-3 seen in the '*P.*' *minus* sample: both teeth exhibit a rounded trigonid and a slightly pointed talonid, with the m3 exhibiting a more elon-

gate and pointed talonid. The lingual enamel face appears either worn or broken off in this specimen. The enamel that frames the labial sulcus is also worn or broken. The mental foramen of this specimen sits squarely underneath the trigonid of the m3. In Trachytheriinae, placement of the mental foramen underneath the distal m2 is suggestive of an advanced stage of development, such as adulthood (Billet et al. 2008). Villarroel (1974a) illustrated the posterior mental foramen on *Plesiotypotherium achirensense* (an adult specimen) beneath the right m2 trigonid, but mentioned nothing about it in the text. Since the position of the posterior mental foramen in adults of both *P. achirensense* and Trachytheriinae is beneath the m2, it is likely that UF 225707 represent an adult. UF 225707 exhibits a smaller m2 than any known specimen of *E. chico*, although the m3 falls within the range of the diminutive Chucal species, which is 20-25% smaller than the other species at Chucal (Figure 14.1). Such a significant size difference with an erupted m3 suggests that UF 225707 is a different species. Also, this specimen is considerably smaller than the adult dentitions associated with deciduous teeth in the '*P.*' *minus* sample (Figure 15).

UATF-V-000840 is more difficult to interpret, though we tentatively interpret it as including P3-M3 (only the dentition is described here, pending further preparation). In addition to the incisors, five cheek teeth are preserved on each side. The posteriormost are either unerupted or just recently erupted (Figure 13). The erupted maxillary teeth, particularly the molars, also resemble specimens of *Eotypotherium chico* in size and morphology



**FIGURE 13.** Left, UF 225707, a partial mandibular ramus bearing a right m2-3; the posterior mental foramen (PMF) is noted. Right, UATF-V-000840, a partial skull bearing left and right P3-M2, and a left I1. Scale equals 1 cm.

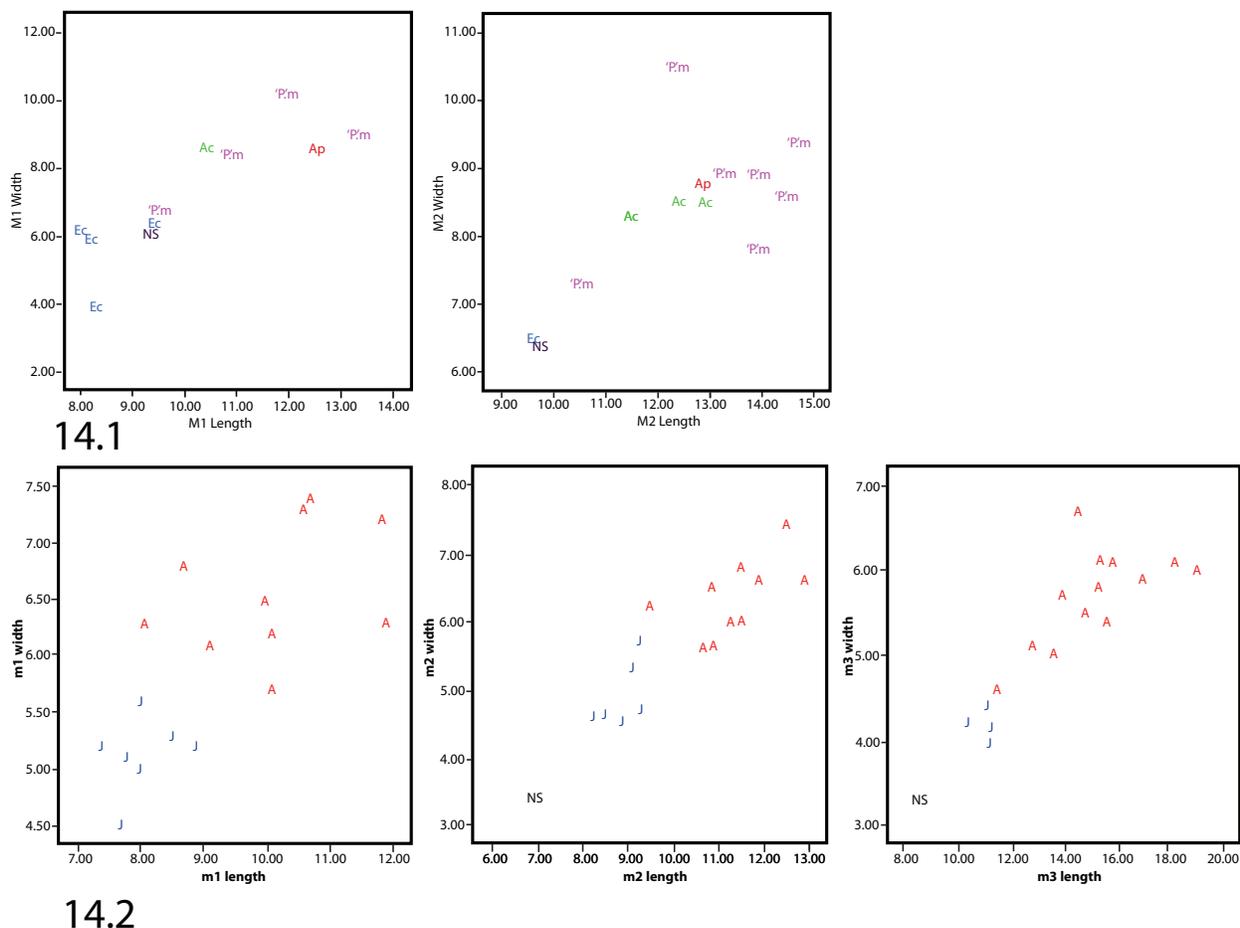
(Figure 14.2), including a fossette on the triangular P3, a quadrate P4 with an enclosed middle lobe, and extensive lingual exposure of the middle lobes of both M1 and M2.

The unworn M3s associated with this specimen clearly indicate it is an example of early wear. Plots of the M1 and M2 of UATF-V-000840 indicate that these teeth are much smaller than fully adult specimens from Cerdas. Based on dental dimensions, these upper teeth are 11-14% shorter in length than more worn teeth and 9% smaller in width than the teeth of UF 133803 (the skull).

Given the presence of a trilobed P4 and a fossette on the P3, it is also possible that UATF-V-000840 is a juvenile bearing dP3-4 and M1-3. Francis (1965) reported that the dP2-3 of *Pseudotypotherium* (his DM2-3) was subtriangular and that the dP4 was subquadrate, similar to the permanent P4. Francis (1965) also noted that the dP4

of *Mesotherium* was trilobed, similar to the permanent M1, although the deciduous tooth was much shorter than the adult molar. We favor an interpretation of P3-M3 for two reasons: first, the teeth interpreted as M1-2 are very similar in size; given the interpretation of Francis (1965) this would not be expected if the teeth were dP3-M1. Second, due to missing bone, the full lengths of the teeth are visible in buccal view and there is no indication of roots (suggestive of deciduous teeth in some typotheres) nor are replacement teeth evident in the teeth that could be interpreted as P3-4 (see Billet et al. 2008 and Billet et al. 2009 for remarks on deciduous typotheres teeth).

**Remarks.** These two unassociated specimens are substantially smaller than any others at Cerdas. They likely represent a second species, but it is also possible that at least UATF-V- 000840 is a



**FIGURE 14.** 14.1 Bivariate plots of first and second upper molar dimensions for Chucal mesotheriines with the addition of the unidentified mesotheriine of Cerdas, UATF-V- 000840. Note the position of the new mesotheriine relative to *E. chico*. 14.2 Bivariate plots of the first, second, and third lower molar dimensions for the mesotheriines of Cerdas including the new mesotheriine UF 225707 and those adult dentitions that have associated deciduous teeth. Ap = *Altitypothierium paucidens*, Ac = *Altitypothierium chucalensis*, Ec = *Eotypothierium chico*, 'P.'m = '*Plesiotypothierium minus*', NS = new Mesotheriinae from Cerdas.

juvenile of '*P.*' *minus*. Until more specimens are found, we cannot confidently interpret the identities of these teeth in this specimen.

#### Phylogenetic Position of '*P.*' *minus*

To evaluate the position of '*P.*' *minus* relative to *P. achirens*, we performed a phylogenetic analysis of mesotheriines based on the data matrix of Croft et al. (2004; Table 7 and Table 8), but coded '*P.*' *minus* separately from *Plesiotypothierium* from Achiri (= *P. achirens* and *P. majus*). The analysis resulted in 103 equally most-parsimonious trees of 77 minimum possible and 202 maximum steps. The strict consensus tree resembles that of Croft et al. (2004) for the younger mesotheriines from Argentina and Chile but shows less resolution near the base of the tree (Figure 15).

'*P.*' *minus* is part of a polytomy at node 4 that includes *Altitypothierium*, *M. choquecotense*, and a clade of all other mesotheriines except *Eotypothierium chico* (which is the basal-most mesotheriine). Character state changes at node 4 include: rodent-like rostrum shape (character #1:2), a very developed zygomatic plate (character #8:2), a subtriangular P3 (character #26:1), and a subtriangular and short P4, without a central fossette (character #19:1). For three characters (#3, 5, and 11) at least one member of the polytomy could not be coded. Seven characters (#1, 2, 4, 8, 19, and 26) are equivocal at this node; character state changes using ACCTRAN and DELTRAN optimization are reported in Table 9.

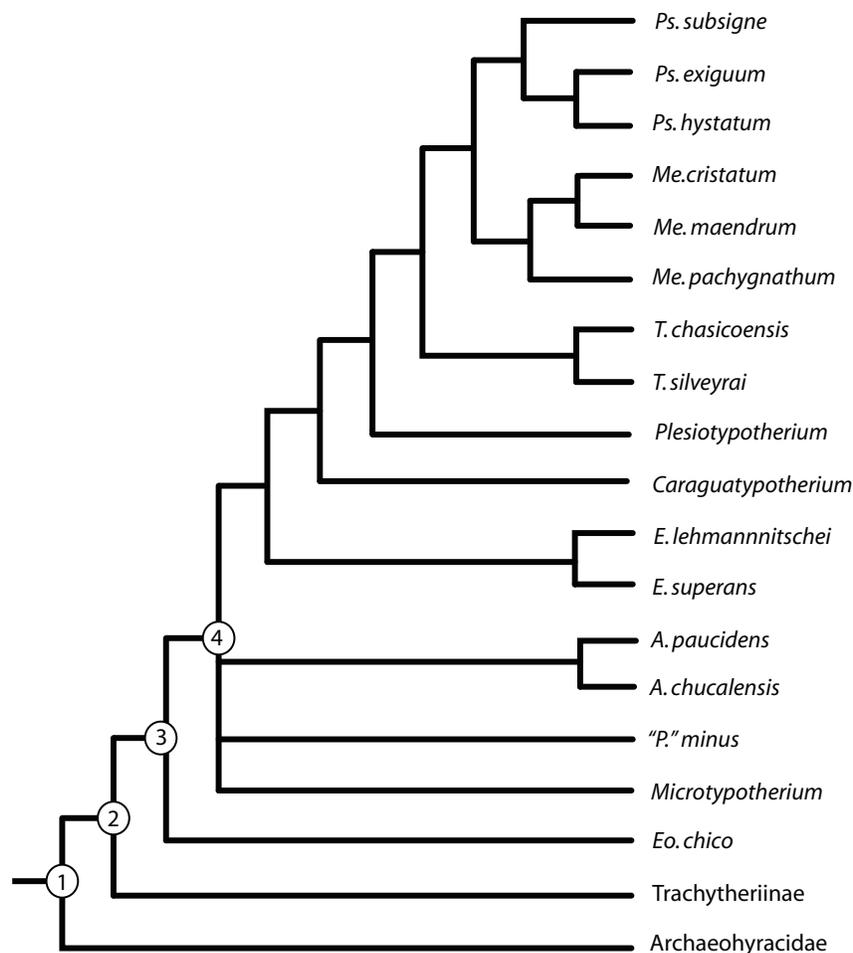
'*P.*' *minus* shares no derived character state with *Plesiotypothierium* (*P. achirens*). '*P.*' *minus*

**TABLE 7.** Characters and Character States (from Croft et al. 2004).

1.*	Rostrum: elongated and low (0); long and tall (1); short, rodent like (2)
2	Lengthening of premaxillae: absent (0); poorly defined (1); very pronounced (2)
3.*	Anterior rostral notch (premaxillae): very smoothly concave (0); forming obtuse angle (1); forming acute angle (2); tall, wide, "U" shaped (3)
4	Diastemata (upper and lower): absent or little developed (0); posterolaterally divergent (1); parallel or gently convergent (2); very convergent, convex (3)
5.*	Postorbital process: short (0); long and transverse (1); long, directed posteriorly (2)
6	Suborbital fossa: absent (0); poorly defined (1); well developed (2)
7.*	Root of zygomatic arch: posteriorly directed from the level of M1 or M2 (0); perpendicular to M1 (1); perpendicular to M1 with biconcave edge (2)
8	Zygomatic plate: absent or hardly developed (0); little developed (1); very developed (2)
9.*	Postpalatal notch: narrow, deep, and removed from M3 (0); wide and removed from M3 (1); deep to the level of M3 (2)
10	Occipital notch: absent (0); present (1)
11	Paraoccipital process: short (0), long (1)
12	Dentition: mesodont (0); protohypsodont (1); euhypsodont (2)
13	Upper molar imbrication (imbrication = width from M2 parastyle to M1 hypocone / width of M1 posterior face): <1.25 (0); between 1.25 and 1.50 (1); > 1.50 (2)
14	I1: with continuous enamel (0); with labial enamel only (1)
15	I1: obliquely implanted and not procumbent (0); obliquely implanted and procumbent (1); more transverse implantation and procumbent (2)
16.*	I1: oval (0); subtriangular, pointed distally, with mesial sulcus (1); wide, rounded, with lingual sulcus (2); wide and compressed labiolingually with two lingual sulci (3); subtriangular, pointed distally, with two lingual sulci (4)
17	I2-I3-C-P1/i3-c-p1: developed (0); reduced, at times absent in the adult (1); always absent (2)
18	P2: developed (0), reduced (1); absent (2)
19.*	P4: subtriangular, short, with central fossette (0); subtriangular, short, without central fossette (1); bilobed, with short and poorly defined lingual plication (2); bilobed, with well developed and patent lingual plication (3)
20	M1-M2: subtriangular with fossette (0); with anterior and posterior lobes convergent, enclosing a middle lobe that disappears with wear (1); with persistent middle lobe (2)
21.*	M3: subtriangular, with fossette (0); trilobed with little differentiated middle lobe (1); with short middle lobe, surrounded by the other two lobes (2); with the middle lobe less enclosed but still shorter than the others (3)
22	Ratio of i1/i2: < 1.50 (0); between 1.50 and 2.00 (1); between 2.00 and 3.00 (2), > 3.00 (3)
23.*	Section of i1: subcylindrical (0); rounded with little or no lingual sulcus (1); subtriangular with smooth sulcus (2); trapezoidal with well demarcated lingual sulcus (3); elliptical with smooth sulcus (4)
24	p3: present (0); absent (1)
25	Lower molars: with fossettes (0); without fossettes (1)
26.*	P3: subquadrangular (0); subtriangular (1); absent (2)
27	Premolar ectolophs: with two labial sulci (0); with one labial sulcus (1)
28	P4 proportions (length/width): < 1.50 (0); ? 1.50 (1)
29	M1 proportions (length/width): ? 1.30 (0); between 1.30 and 1.75 (1); ? 1.75 (2)
30	Anterior and posterior sides of M1 middle lobe: lingually convergent (0); subparallel (1); lingually divergent (2)
31	Lingual exposure of M1 middle lobe: little or none (0); extensive (1)
32.*	m2 proportions (length/width): between 1.60 and 2.30 (0); >2.30 (1); <1.60 (2)
33	Two pronounced lingual sulci on m3 talonid: absent (0); present (1)

TABLE 8. Character-Taxon Matrix.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33							
Archaeothyridae	0	0	0	0	0	0	0	0	0/1	0	0	0/1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	1						
Trachytheriinae	1	0	1	0	1	2	0	1	1	1	0	1	0	1	1	1	1	1	0/1	1	1	0	1	0	0/1	0	0	0	0	0	0	0	0	0	0					
Eutyotherium ehmannitchei	2	1	?	1	?	1	0	2	1	1	?	2	0	0	1	2	2	2	2	2	2	0	2	1	1	1	1	0	0	1	0	1	0	1	0	0				
Eutyotherium superans	2	1	2	1	?	1	0	2	1	1	?	2	0	0	1	2	2	2	1	2	3	?	?	?	?	0	1	0	0	1	0	1	0	1	?	0	0			
Typotheropsis chascoensis	2	1	?	2	2	2	0/1	2	0	1	1	2	0/1	0	1	2	2	2	1	2	2	1/2	2	1	1	1	1	1	0	1	1	1	1	1	0	0	0			
Typotheropsis silveyrai	2	1	2	2	2	2	1	2	0	1	1	2	0	?	1	?	2	2	1	2	2	?	?	?	?	?	1	1	0	1	1	1	1	1	?	0	0			
Pseudotyotherium subsigne	2	1	?	2	1	2	1	2	0/1	1	1	2	2	0	1	?	2	2	2/3	2	2/3	2	3	1	1	1	1	0	1	2	1	1	1	1	1	0	0			
Pseudotyotherium exiguum	2	?	?	?	1	?	1	2	1	?	?	2	2	?	?	?	?	?	?	3	2	3	2	?	1	1	1	0	1	2	1	1	1	1	1	0	0			
Pseudotyotherium nystatum	2	1	2	3	1	?	0	2	0	1	1	2	2	?	1	?	2	2	3	2	3	?	?	1	1	1	1	0	1	2	?	1	1	1	1	0	0			
Mesotherium cristatum	2	2	3	3	2	0	2	2	2	1	1	2	2	0	2	2	2	2	3	2	3	3	3	1	1	1	1	0	1	2	2	1	1	1	1	0	0			
Mesotherium pachynathum	2	1	?	2	2	0	1	2	2	1	1	2	2	0	2	2	2	2	3	2	3	3	?	1	1	1	1	0	1	2	2	1	1	1	1	0	0	0		
Mesotherium maendrum	2	2	2	3	2	0	1	2	2	1	1	2	2	0	2	3	2	2	3	2	3	3	4	1	1	1	1	0	1	2	2	1	1	1	1	0	0	0		
Plesiotyotherium achirensis	2	1	1	2	2	2	1	2	1	1	1	2	0	0	1	2	2	2	1/2	2	3	0	2	1	1	1	1	0	0	1	1	1	1	1	0	0	0	0		
Microtyotherium choquecotense	2	?	?	1	?	?	1	2	0	1	?	2	0	0	1	1	2	2	1	2	2	?	?	?	?	1	1	0	0	1	0	0	1	0	2	0	2	0		
Caraguatyotherium munozi	2	1	1	2	?	1	1	2	2	1	1	2	1	0	1	2	2	2	2	2	2	2	1	2	1	1	1	0	0	1	1	1	0	1	1	0	1	0	1	
Alityotherium paucidens	2	?	?	1	?	1	1	2	?	?	?	2	0	0	1	4	2	2	1	2	3	0	1	1	1	1	2	1	0	1	0	1	0	0	0	0	0	0	0	
Alityotherium chucalensis	?	?	?	1	?	?	?	?	2	?	?	2	0	0	?	4	2	2	1	2	2	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	
Eotyotherium chico	?	?	?	?	?	?	1	1	1	?	?	2	0	0	?	1	2	2	0	2	2	0	1	1	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	
P: minus	2	1	?	1	?	2	1	2	1	?	?	2	0	0	1	0	2	2	1	2	3	0/1	1	1	1	1	1	1	0	0	1	1	1	0	0	1	1	0	0	0



**FIGURE 15.** Strict consensus tree of mesotheriine relationships based on 45 trees of 88 steps. Node 4 indicates the polytomy that includes '*P.* minus'.

differs from *P. achirensense* in displaying primitive character states for six characters: diastemata shape (character # 4:1), shape of I1 and presence of sulcus (character # 16:0), shape of P4 and lack of fossette (character # 19:1; *P. achirensense* is polymorphic for this trait, exhibiting both states 1 and 2), the ratio of i1/i2 ('*P.* minus' is polymorphic for

this character (# 22), exhibiting both states 0 and 1), section of i1 (character # 23:1), and lingual exposure of M1 middle lobe (character # 31:0). '*P.* minus' is excluded from the clade of higher mesotheriines (including *P. achirensense*; node 5, Figure 13) by the absence of two derived character states: i1 subtriangular, trapezoidal or elliptical in section and

**TABLE 9.** Character optimization results for the polytomy at node 4.

Character	ACCTRAN	DELTRAN
1) rostrum length and shape	2 – short rodent-like rostrum	1 – long and tall rostrum
2) lengthening of premaxilla	1 – premaxilla poorly defined	0 – absence of lengthening
4) shape of diastemata	1 – posterolaterally divergent diastemata	0 – absent or little developed diastemata
8) development of zygomatic plate	2 – very developed plate	1 – little developed plate
19) morphology of P4	1 – subtriangular and short without a central fossette	0 – subtriangular and short with a central fossette
26) shape of P3	1 – subtriangular	0 – subquadrangular

exhibiting a lingual sulcus of varying depths (character # 23:2, 3, 4) and extensive lingual exposure of the M1 middle lobe (character # 31:1).

'*P. minus*' shares 21 derived states with both *Altitypotherium* species and 25 with *Microtypotherium*. '*P. minus*' differs from *Altitypotherium* in having a better-developed suborbital fossa (character # 6:2), an oval I1 (character #16:0), and subparallel sides of the M1 middle lobe (character # 30:1). '*P. minus*' differs from *Microtypotherium* in exhibiting m2 proportions between 1.60 and 2.30 (character # 32:0); *Microtypotherium* exhibits a unique state, with m2 proportions less than 1.60 (character # 32:2).

The '*P. minus*' sample from Cerdas does not pertain to the genus *Plesiotypotherium*, nor can it be referred to *Microtypotherium* or *Altitypotherium* based on this phylogenetic analysis. Rather, the sample appears to represent another branch within the radiation of small early to middle Miocene mesotheriines common in Bolivia and northern Chile. Additional craniodental material of this species and other early mesotheriines should help clarify relationships among these forms and potential links with later species.

#### **Variation in Small Mesotheriines: The Effects of Tooth Wear and Ontogeny on Taxonomy**

Sources of dental variation in small mesotheriines are not clear, making it difficult to determine whether differences in tooth size are due to size sexual dimorphism, ontogenetic change, or tooth wear. There are two potential models for variation in tooth size due to ontogenetic factors: 1) non-hypselodont mammals, where deciduous teeth are generally smaller than adult teeth and exhibit a unique morphology; and 2) euhypsodont rodents, which show variability in the size of their dentition throughout ontogeny, though the morphology of the deciduous tooth does not vary greatly from the adult tooth (Kramarz 2002).

Because our sample consists primarily of lower teeth and because they have few distinguishing features useful for taxonomy, we explored two potential sources of variation in the Cerdas '*P. minus*' sample: dental wear and ontogeny (potentially as indicated by posterior mental foramina placement). Wear has long been known to be a confounding factor in understanding taxonomic variation in mesotheriines. Francis (1965) noted that previous workers, such as Cabrera (1937, 1939), had remarked upon the widening of the molars during the extended development of mesotheriines: "...un franco engrosamiento dentario que

se prolonga durante todo el período de desarrollo del animal" (p. 8). Ontogenetic patterns (age of epiphyseal closure, dental eruption sequences) are not well documented for mesotheriines, although Billet et al. (2008) described an intriguing developmental sequence in the movement of the posterior mental foramen in trachytheriine mesotheriids. The position of the posterior mental foramen has been documented in other typotheres (see Simpson 1967), but Billet et al. (2008) demonstrated that as individuals of *Trachytherus* grow, this foramen moves from beneath the dp4 (in young individuals) to beneath the talonid of the m2 (in older individual).

Until recently, tooth wear had not been classified into meaningful stages within a sample of typotheres. Croft et al. (2003) documented that wear has such a great effect on tooth dimensions in archaeohyracid typotheres that it must be considered prior to identifying specimens. These authors split the Tinguiririca sample into wear categories due to the high coefficient of variation in this single species sample as a whole. By splitting the sample into broad wear categories, the CVs were greatly reduced. Recently, Billet et al. (2008) recognized a series of eight ontogenetic/wear stages for a very large sample of trachytheriine mesotheriids from Salla, Bolivia. This study showed striking changes in tooth size due to wear for both maxillary and mandibular molars. The Croft et al. (2003) and Billet et al. (2008) studies have shown that wear has a profound effect on the size of teeth throughout the lifetime of an individual in certain typotheres. These studies suggest that dental wear can skew both the perception of dental variation and possibly the taxonomic composition of the total sample. When metrically evaluating a sample of typotheres dentitions, the effects of wear must be considered prior to any assessment of population variation (Croft et al. 2003).

Although the studies of Croft et al. (2003) and Billet et al. (2008) showed that dental dimensions changed with wear, the pattern presented by each was slightly different. Croft et al. (2003) found that M1-2/m1-2 of archaeohyracids became shorter and broader with wear, and that M3/m3 increased in length. Billet et al. (2008) noted that the trachytheriine M1 shortened with wear, and that the M3 lengthened with wear. These authors also reported that m1-2 broadened with wear and m2-3 lengthened (Billet et al. 2008).

In the Cerdas '*P. minus*' assemblage, similar wear-based trends were observed. We could only assess wear on mandibular molars because we did

not have a large sample of maxillary teeth. It is not possible to establish more than two wear categories with the Cerdas mesotheriines due to a lack of wear-related changes in occlusal features (e.g., fossettids) on the lower dentition. Fortunately, many specimens had both deciduous and adult teeth preserved in the lower tooth row; the presence of deciduous premolars can demonstrate the degree of wear present on adult molars based on age, the assumption being that if deciduous premolars are present in the tooth row, then the adult molars have erupted more recently and thus have less wear than those unassociated with deciduous teeth. This pattern of maintaining the dp4 with a fully erupted set of molars is a pattern seen in modern ungulates with rapid growth as a part of their life history pattern (Smith 2007). It is only after the full set of molars has erupted that the anterior dentition begins replacement (Smith 2007).

Two groups were identified within the 'P.' *minus* sample: adult molars associated with deciduous teeth or a newly erupted m3 and those without. Table 10 lists the univariate statistics for the 'P.' *minus* sample as a whole, as well as for the two wear groups. As for other typotheres groups, when wear is not considered, the CVs are very high for each tooth position. When those specimens are grouped by wear, CVs decrease substantially. Even these two wear groups still have very high coefficients of variation, however, suggesting that one or more unrecognized age/wear categories may be present.

In a plot of m1 dimensions (Figure 14.2), specimens with deciduous or newly erupted teeth are smallest, as would be expected. The remaining specimens are wider and longer. This trend is also apparent in m3 and less so in m2 (Figure 14.2). It should theoretically be possible to erect at least one more wear category for these mesotheriines that would be indicative of a middle phase of wear (Figure 14.2), but without occlusal features that vary with wear (as in archaeohyracids or *Trachytherus*), this may not be possible.

These data demonstrate that, as mesotheriid teeth undergo wear, they do change shape, a phenomenon reported for other typotheres (see Croft et al. 2003; Billet et al. 2008). In this sample, the m1s of juveniles (with less wear) were 26% shorter and 23% narrower than adult m1s, juvenile m2s were 19% shorter and narrower, and juvenile m3s were 22% shorter and 24% narrower (Table 6; Figure 14.2). Adult teeth associated with deciduous teeth or those that are newly erupted are the smallest overall (shortest and narrowest; e.g., UATF-V-

000879) for all tooth positions. Smith (2007) reported data for a series of ungulates showing that eruption patterns varied with life history patterns. She noted that in ungulates that had rapid growth rates, such as *Antidorcas* (the springbok), deciduous teeth are replaced only after permanent molars have erupted (Smith 2007). This pattern fits what is seen here in the 'P.' *minus* sample; in UATF-V-000879, dp4 is maintained through the eruption of m3. This suggests that 'P.' *minus* might have had a rapid growth as part of its life history, but without more data regarding the replacement of the anterior deciduous dentition, this remains speculative.

In addition to the lengthening and widening of teeth that occurs in more worn specimens, another dental feature emerges with wear: the presence of a sulcus on the lingual faces of the talonids. This feature is found on all three molars. It is absent or very subtle in younger specimens with less wear, but obvious on older individuals (Figure 16).

The posterior mental foramen is visible in six 'P.' *minus* specimens. Because it is visible in so few, we used it as a confirmatory method of relative age/development. No specimens from Cerdas have a posterior mental foramen below the m2 talonid (other than UF 225707, referred to *Mesotheriinae* indet.). In those specimens, in which the foramen is preserved, the most distal position in which it is found is below the m2 trigonid. In UATF-V-000823, a specimen with deciduous teeth, two mental foramina are present, the posterior under dp4, the anterior under dp3. Specimen UATF-V-000879, with retained dp4, exhibits the posterior mental foramen under the m1 talonid. Three specimens have the posterior foramen between m1 and m2 (UF 225690, 225691, and 225714). A very worn specimen, UATF-V-000815, has a mental foramen under the trigonid of m2 (with wear determined by presence of lingual grooves and overall larger size). Based on the work of Billet et al. (2008) and a specimen with deciduous teeth (UATF-V-000823), it is clear that mental foramina could be useful for establishing relative individual ages. When dividing the Cerdas sample into those specimens bearing deciduous dentition (with smaller permanent teeth) and those with only permanent dentition (larger teeth), an intermediate group appears (Figure 14.2). Those intermediate specimens also exhibit a posterior mental foramen at the m1-2 junction, indicating that they are not of advanced age (Figure 17). If it is true that these animals add adult molars before replacing the anterior deciduous dentition, it seems reasonable

**TABLE 10.** Measurements of adult mandibular and maxillary dentitions for 'Plesiotyotherium' minus from the Cerdas locality. Measurements are made to the nearest 0.1 mm. Coefficient of variation (CV) = 100 X (standard deviation/mean). A corrected CV [CVcorr = (CV X 1 + (1/4n))] is given for samples fewer than 10 (Sokal and Rohlf, 1995).

	M1			M2			M3			m1			m2			m3											
	L	W	N	L	W	N	L	W	N	L	W	N	L	W	N	L	W	N									
N	6	5	9	9	9	7	7	7	7	17	17	16	16	16	17	16	17	16									
Mean	10.98	8.08	13.00	8.55	14.29	7.94	9.26	5.98	10.41	5.73	13.94	5.41	0.80	1.52	1.68	1.76	1.22	1.72	0.91	1.43	0.88	1.44	0.90	3.14	0.80		
Std. Deviation	9.4-13.46.1-10.29.7-14.7			6.4-10.5			11.7-17.1			6.3-9.1			7.4-11.9			4.5-7.4			8.3-12.9			4.5-7.4			11.10-19		
Range	10.98-13.94			7.94-14.29			5.98-10.41			5.73-13.94			5.41-0.80			0.80-1.52			1.43-0.88			1.44-0.90			3.14-0.80		
CV	13.83	20.77	13.54	14.23	12.01	11.49	15.47	14.65	13.83	15.74	17.06	14.77															
CVcorr	14.41	21.81	13.92	14.63	12.44	11.90																					
<b>Lowers Associated With Deciduous Teeth</b>																											
N	7			7			7			7			5			2											
Mean	8.04			5.13			8.90			4.98			11.15			4.20											
Std. Deviation	0.51			0.34			0.47			0.50			0.07			0.28											
Range	7.4-8.9			4.5-5.6			8.3-9.3			4.6-5.7			11.1-11.2			4-4.4											
CV	6.29	6.54	5.27	9.98	6.73	6.52	6.77	5.53	10.48	0.71	7.58																
CVcorr	6.52	6.77	5.53	10.48	0.71	7.58																					
<b>Lowers Not Associated With Deciduous Teeth</b>																											
N	10			10			10			10			11			15											
Mean	10.11			6.58			11.09			6.07			14.31			5.58											
Std. Deviation	1.23			0.57			1.17			0.84			3.17			0.69											
Range	8.1-11.9			5.7-7.4			8.9-12.9			4.5-7.4			11.2-19			4.1-6.7											
CV	12.21	8.68	10.55	13.90	15.16	12.34																					
% difference between associated with deciduous and unassociated.																											
	20.4%	22.1%	19.8%	18.0%	22.1%	24.7%																					



**FIGURE 16.** Photograph of an older '*P.* minus individual, UATF-V- 000815 (top) and a younger individual (based on presence of dp4) UATF-V- 000823. Note that the lingual sulci are more pronounced in the older individual.

to assume that the posterior mental foramen would “move” further back as larger anterior teeth were added to the arcade.

**Comparisons with other Bolivian and Chilean Mesotheriines.** The Cerdas, Chucal, and Nazareno assemblages all have at least one striking similarity: at least one large and one small mesotheriine. At Chucal, the two species of *Altityotherium* overlap in size to some degree, but they clearly differ in morphology (particularly the presence of P3); *Eotypotherium chico* is markedly smaller, by 20-25%, compared to *Altityotherium* (Croft et al. 2004).

**Chucal.** Both *A. paucidens* and *A. chucalensis* exhibit low and consistent sample variation (Table 10), as typically characterizes single species samples (Table 10, Figure 18; Cope and Lacey 1992, 1995; Cope 1993, Plavcan and Cope 2001). *Eotypotherium chico* exhibits small CVs for all but three dental measurements: M1 and m1 width, and m3 length (Table 10, Figure 18). These high CVs are likely attributable to small sample size but wear also could be a factor (e.g., SGO PV 5158 exhibits a rather long m3; see Table 10). In general, the

overall low CV values for Chucal taxa lend support to the validity of these species.

**Nazareno.** The only published study from Nazareno is that of Oiso (1991), though we were able to study additional specimens from this locality in UATF collections. The UATF Nazareno sample is within the range of variation of the Oiso (1991) sample (Figure 19). We evaluated CVs from Nazareno in three ways: using the Oiso data alone, using the UATF data alone, and evaluating the combined samples. The Oiso (1991) data have very high CVs for all tooth positions (>10; Table 11). It appears that at least two taxa are present, one large and one small, and possibly more. Our reasoning for suggesting at least two taxa is that some of the smaller specimens have fully erupted third molars, indicating a later juvenile stage or adulthood. The UATF dataset has much lower CVs, all < 10, even when corrected for small sample sizes. The combined assemblage has very high CVs. The bivariate plot of m1 and m2 dimensions shows a size distribution pattern similar to that reported for Chucal and Cerdas: one large and one small size group (Figure 19), though the pattern is less apparent in the m3 plots.

## CONCLUSION

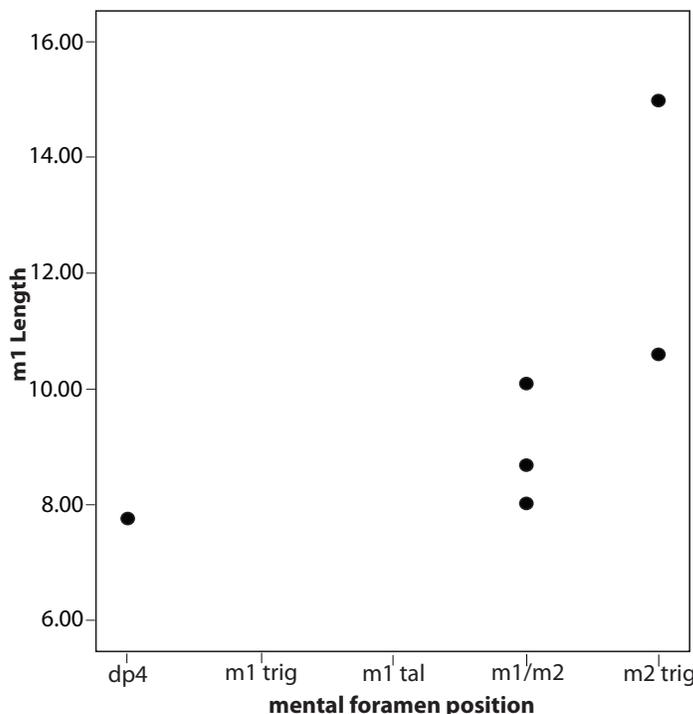
Based on the present study, the vast majority of specimens from Cerdas can be referred to as '*Plesiotypotherium*' *minus*, though two specimens may pertain to a second species. Our phylogenetic analysis indicates that the species '*P.*' *minus* do not belong in the genus *Plesiotypotherium*, but should be referred to another genus. Given that variation in *Microtypotherium choquecotense* is unknown – and that '*P.*' *minus* could potentially pertain to that genus – we refrain from creating a new genus at this time. We also refrain from naming a second species at Cerdas, given the uncertain dental homologies of at least UATF-V-000840 and the small sample size of this second morph.

The revised diagnosis of '*P.*' *minus*, the recognition of another diminutive form at Cerdas, plus the presence of similar forms at Quebrada Honda, Chucal, Choquecota, and Nazareno indicate that there was a greater diversity of basal mesotheriines from the middle latitudes of South America than previously imagined. It appears that these basal forms were rather conservative in morphology, particularly in size (Figure 20).

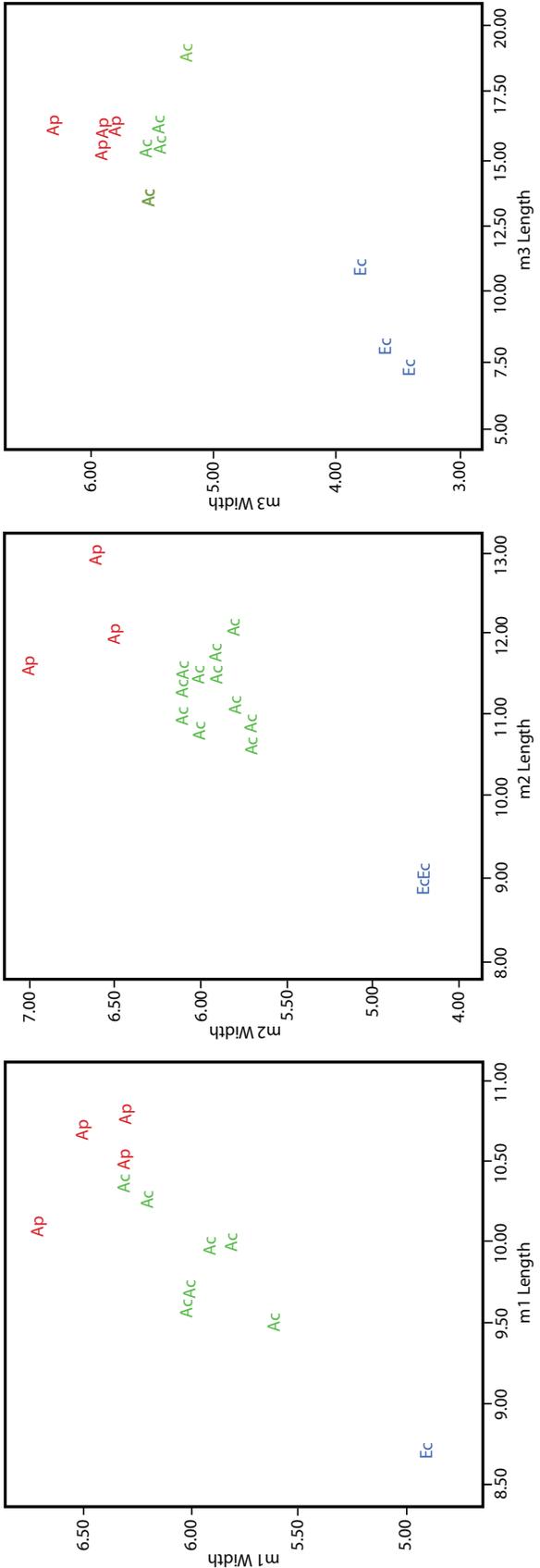
UF 133803 is the most complete cranium of a basal mesotheriine presently known (Movies 1-3)

and provides new insights into the anatomy of phylogenetically important regions such as the sub-orbital fossa and foramen, shape of the rostrum, and general morphology of the jugal region; other features such as the internal regions of the bony ear and the posterior neurocranium are now known for these early mesotheriines based on the cranial material from Cerdas. The other specimens from Cerdas provide additional insights into dental development and eruption patterns in this group.

A primary challenge in basal mesotheriine taxonomy is that the holotype of '*P.*' *minus* is a lower dentition, which is not usually diagnostic even at the generic level within Mesotheriinae (see also Croft 2007). Given the additional observations from our study indicating that lower cheek tooth dimensions are not stable over the lifetime of an animal, the use of size as a criterion for identifying species is called into question. The lack of distinguishing occlusal surface features such as fossettids make it difficult to assess wear states within a population. Although lower dentitions remain troublesome to classify, we have demonstrated that their dimensions relate closely to wear, and that the lingual talonid sulcus may be useful for assessing wear state, along with the position of the posterior mental foramen. Such factors should permit compari-



**FIGURE 17.** Bivariate plot of posterior mental foramina position under a specific tooth locus or between loci to m1 length; dp4 = under dp4, m1 trig = under m1 trigonid, m1 tal = under m1 talonid, m1/m2 = between m1 and m2 loci, m2 trig = under m2 trigonid.



**FIGURE 18.** Bivariate plots of m1-3 dimensions for Chucal mesotheriines. Ap = *Altitypotherium paucidens*, Ac = *Altitypotherium chucalensis*, Ec = *Eotypotherium chico*.

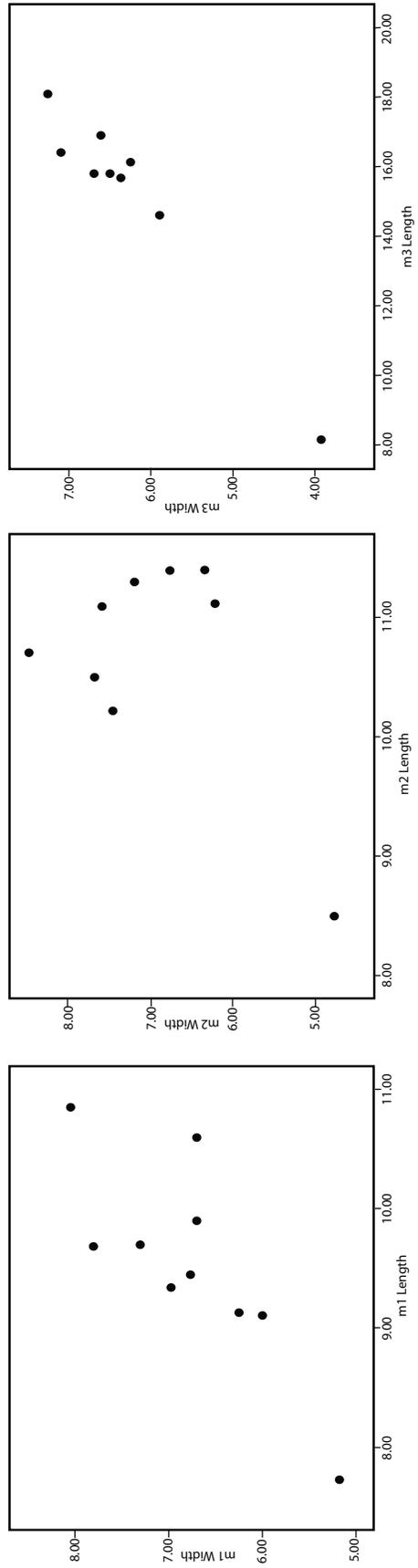


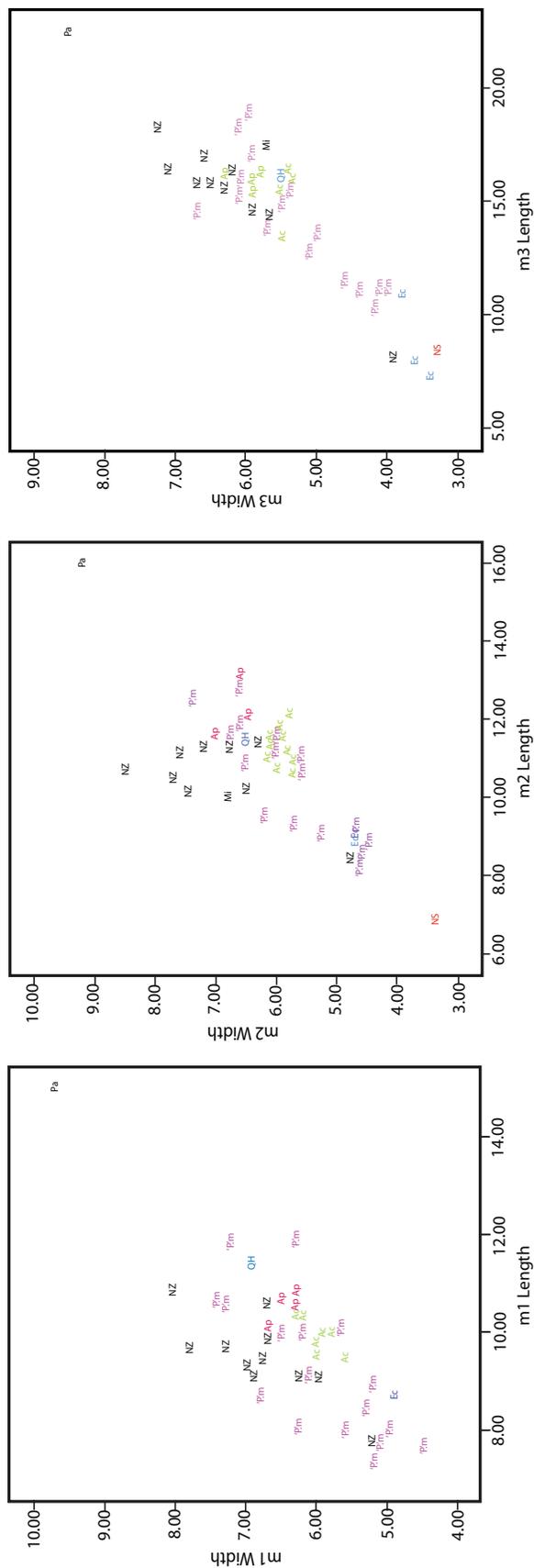
FIGURE 19. Bivariate plots of m1-3 dimensions for Nazareno mesotheriines.

**TABLE 11.** Measurements of adult mandibular and maxillary dentitions for the mesotheriines from the Nazareno locality. Measurements are made to the nearest 0.1 mm. Coefficient of variation (CV) = 100 X (standard deviation/mean). A corrected CV [CVcorr = (CV X 1 + (1/4n))] is given for samples lower than 10 (Sokal and Rohlf, 1995). Oiso data from his 1991 publication, UATF data taken by DAC. Combined assemblage from Oiso (1991) and UATF

	<b>M1</b>		<b>M2</b>		<b>M3</b>		<b>m1</b>		<b>m2</b>		<b>m3</b>	
	L	W	L	W	L	W	L	W	L	W	L	W
N	12	12	11	12	7	7	11	11	9	10	10	10
Mean	10.18	7.87	11.59	8.40	11.83	7.45	9.51	6.79	10.59	7.01	15.18	6.23
Std. Deviation	2.36	1.98	2.67	1.88	3.20	2.06	0.83	0.80	0.92	1.00	2.70	0.94
Range	3.45-12.44	2.66-10.16	4.5-14.68	3.23-10.06	5.13-14.63	3.21-9.4	7.73-10.84	5.19-8.04	8.49-11.4	4.78-8.49	8.13-18.09	3.93-7.25
CV	23.22	25.11	23.00	22.43	27.02	27.70	8.71	11.79	8.70	14.31	17.79	15.07
Oiso assemblage only.	M1		M2		M3		m1		m2		m3	
	L	W	L	W	L	W	L	W	L	W	L	W
N	10	10	9	9	6	6	7	7	6	7	6	6
Mean	10.23	7.90	11.66	8.36	11.92	7.49	9.32	6.85	10.40	6.79	14.87	6.02
Std. Deviation	2.61	2.18	2.97	2.13	3.49	2.26	0.92	0.96	1.08	1.14	3.54	1.14
Range	3.45-12.44	2.66-10.16	4.5-14.68	3.23-10.06	5.13-14.63	3.21-9.4	7.73-10.84	5.19-8.04	8.49-11.4	4.78-8.49	8.13-18.09	3.93-7.25
CV	25.52	27.66	25.46	25.44	29.30	30.14	9.86	13.95	10.36	16.84	23.77	18.96
CV corr	26.15	28.35	26.17	26.15	30.53	31.39	10.21	14.45	10.80	17.44	24.76	19.75
UATF assemblage only.	M1		M2		M3		m1		m2		m3	
	L	W	L	W	L	W	L	W	L	W	L	W
N	2	2	2	3	1	1	5	5	3	3	4	4
Mean	9.95	7.75	11.25	8.53	11.30	7.20	9.84	6.68	10.97	7.50	15.65	6.55
Std. Deviation	0.21	0.07	0.49	1.18			0.54	0.46	0.42	0.26	0.75	0.50
Range	9.8-10.1	7.7-7.8	10.9-11.6	7.8-9.9			9.1-10.6	6.0-7.3	10.5-11.3	7.2-7.7	14.6-16.4	5.9-7.1
CV	2.13	0.91	4.40	13.88	0.00	0.00	5.45	6.89	3.80	3.53	4.82	7.63
CV corr	2.40	1.03	4.95	15.04	0.00	0.00	5.73	7.24	4.11	3.82	5.13	8.11

sons of specimens of similar wear stage, lending greater accuracy to taxonomic interpretations. More work on identifying visible patterns of lower molar shape change with wear would certainly be useful (e.g., the posterior end of the m3 talonid appears to become more rounded with wear).

The '*P.* minus' sample from Cerdas provides yet another example of the importance of considering each individual specimen as a member of a once dynamic population. The great pitfall of identifying morphological species in the fossil record is an undesirable return to typology. Identifying and



**FIGURE 20.** Bivariate plots of m1-3 dimensions for mesotheriines of Cerdas, Chucal, Choquecota, Achiri, Quebrada Honda, and Nazareno. Ap = *Altitypootherium paucidens*, Ac = *Altitypootherium chucalensis*, Ec = *Eotypootherium chico*, MI = *Microtypootherium choquecotense*, NS = new Mesotheriinae from Cerdas, NZ = Nazareno specimens, Pa = *Plesiotypootherium achiriense*, 'P.'m = '*Plesiotypootherium' minus*, QH = Quebrada Honda, *Plesiotypootherium minus* specimen.



**MOVIE 1.** On-line movie of UF 133803, '*P.*' minus skull showing dorsal aspect of skull. The viewer can rotate the skull in this orientation.

**MOVIE 2.** On-line movie of UF 133803, '*P.*' minus skull showing ventral aspect of skull. The viewer can rotate the skull in this orientation.

**MOVIE 3.** On-line movie of UF 133803, '*P.*' minus skull showing a rotation of the skull through the anterior-posterior axis. The viewer can rotate the skull in this orientation.

NOTE: These movies are available online at [paleo-electronica.org/2010\\_1/192/index.html](http://paleo-electronica.org/2010_1/192/index.html)

attempting to quantify variation within a population can help prevent such an error. We have provided here a sizeable sample of metric data that illustrate variation for another group of typotheres notoungulates. We have also shown that an ontogenetic and ecological criterion, dental wear, must be evaluated prior to any taxonomic analysis. This finding supports prior investigations of other typotheres, suggesting it may be a characteristic of the clade. Further work on the sample from Nazareno must include an assessment of wear as a part of any systematic study.

We used CVs to evaluate the samples from Cerdas, Nazareno, and Chucal to assess some degree of metric homogeneity (often interpreted as taxon homogeneity); this was necessary since the visible morphology did not provide obvious differentiation for the Cerdas sample. Simpson et al. (1960) suggested that a CV exceeding 10.0 is evidence for the presence of multiple species in a fossil sample. Since then, some authors have noted that this criterion is meaningless considering the sample sizes afforded by the fossil record and other sources of error that can affect variation statistics (e.g., measurement error, element size, sample mean; Cope and Lacey 1992, 1995; Polly 1998; Plavcan and Cope 2001). One method of using the CV with fossil samples is to evaluate phylogenetically related and geographically restricted extant samples as references for single-species variation to address whether a fossil sample is a single-species or pooled-species sample (Cope and Lacey 1992, 1995). In the case of the mesotheriines (and notoungulates in general), this is not possible due to the lack of extant representatives. It is now evident that dental wear is a powerful gen-

erator of interpopulation metric variation in mesotheriines; combined with what has been reported for archaeohyracids and trachytheriines, it is clear that a high CV does not necessarily indicate a multi-taxon population.

Once again, notoungulates have provided insights into evolutionary questions that have previously been addressed with African, Eurasian, or North American fossil mammals: that is, whether or not a high degree of metric variation in a sample of fossils can be too great to be accommodated within a single species (Simpson et al. 1960; Gingerich 1974; Plavcan and Cope 2001). The mesotheriines of Cerdas have highlighted that conventional methods of identifying morphological species (i.e., identifying a holotype and a hypodigm) are problematic for some taxa. Working with these typotheres notoungulates suggests that we should look beyond the traditional morphological criteria and add an ecological component, such as wear state, to taxon diagnoses and definitions. This, in turn, may contribute toward developing a multi-dimensional understanding of these ancient species that we might not have thought possible or practical (Hutchinson 1958).

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