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Notoungulata and Litopterna of the Early Miocene Chucal Fauna, Northern Chile

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Notoungulata and Litopterna of the Early Miocene Chucal Fauna, Northern Chile

Darin A. Croft   John J. Flynn   André R. Wyss

Abstract

This study describes the notoungulates and litopterns (endemic South American ungulates) from the Chucal Fauna of northern Chile. Eight species are known to date, including seven notoungulates and one litoptern. The bulk of the toxodontid notoungulate material, including a well-preserved partial skull, is referred to *Nesodon imbricatus.* A few postcranial elements and a single partial tooth are referred to *Adinotherium* sp. indet. Poorly preserved dental material may represent a third (indeterminate) toxodontid. Fragmentary dental and postcranial remains are referred to *Hegetotherium* cf. *H. mirabile* (Hegetotheriidae). *Theosodon* sp. indet. (Litopterna: Macraucheniidae) is recorded on the basis of a variety of diagnostic limb bones, but dental remains of this taxon are not yet recorded at Chucal. Three new species of mesotheriid notoungulates are described: *Altitypotherium paucidens, Altitypotherium chucalensis,* and *Eotypotherium chico.* The largest, *Altitypotherium paucidens,* differs from all previously described mesotheriids in the loss of an upper premolar (P3). *Altitypotherium chucalensis* is represented by an associated skull and mandibles plus postcranial remains. *Eotypotherium chico,* based on gnathic remains, is the smallest mesotheriid known. Bracketing radioisotopic dates and biostratigraphic correlation argue for referral of the Chucal Fauna to the Santacrucian South American Land Mammal "Age" (late early Miocene). The forms from Chucal are the only mesotheriids known for this temporal interval and also mark the earliest known occurrence of mesotheriines. A phylogenetic analysis places the three taxa from Chucal as early diverging members of the Mesotheriinae, with *Eotypotherium chico* representing the outgroup to all remaining members of the clade. In the presence and abundance of mesotheriines and in the absence of interatheriids, the Chucal Fauna more closely resembles geographically proximate (but younger) faunas in Bolivia and the Precordillera of northernmost Chile than temporally correlative faunas from southern South America. This pattern indicates significant faunal provinciality in South America during the late early Miocene and suggests that the intermediate latitudes might have been a center of diversification for mesotheriines and potentially other groups of mammals.

Introduction

Study of South American fossil mammals has traditionally focused on faunas from the high latitudes, especially Patagonian Argentina (Patterson & Pascual, 1972; Simpson, 1980). The discovery of faunas elsewhere in South America (e.g., Bolivia, Brazil, Chile, Colombia) has contributed to more complete understanding of the evolution of South American mammals but has also revealed unanticipated complexities (see Flynn & Wyss, 1998; Flynn, 2002). These extra-Patagonian faunas demonstrate, for one, that latitudinal provinciality characterized South American mammal faunas for much of the Cenozoic, necessitating sampling of a wide geographic range for any given time slice to gain a fuller understanding of mammal evolution on the continent (Pascual et al., 1985; Wyss et al., 1994; Madden et al., 1997).

Our research team has been working to uncover and develop fossil mammal faunas of var-

ious ages throughout the length of Chile. The Chucal Fauna represents the northeasternmost of these fossiliferous localities. The first fossil vertebrate specimen from this fauna, discovered in 1992 during the course of geologic mapping northeast of Salar de Surire (Fig. 1), pertains to *Nesodon,* an early Miocene toxodontid notoungulate (Charrier, Muñoz, Wyss, et al., 1994). To determine whether the Chucal Formation would produce other identifiable fossil mammal remains, a return trip to the area was undertaken in July 1998. This expedition yielded a variety of well-preserved specimens, including a diversity of endemic ungulates, as well as the oldest chinchilline rodent (Flynn, Croft, et al., 2002). A second expedition to the area in 2001 produced many additional specimens and at least five species not recorded previously (Charrier et al., 2002). The present study provides descriptions and taxonomic analyses of the most diverse and abundant component of the Chucal Fauna, of its notoungulates, as well as of its single litoptern.

Prior to discovery of the Chucal Fauna, only isolated Cenozoic mammal specimens had been reported from northern Chile. The first, a mesotheriid mandible (MLP 86-VIII-10-1), was collected by D. Pacci in 1969 in the area of Caragua (approx. 18° 25'S, 69°35'E) west of the town of Belén. The second, a nearly complete mesotheriid skull and mandibles with associated postcrania (SGOPV 4004), was discovered in 1989 (Salinas et al., 1991), probably from the same locality as Pacci's specimen. Both specimens were collected from the Huaylas Formation, a unit demonstrably younger (middle late Miocene, definitely <16 Ma and most likely ~10.8–11.7 Ma; Flynn et al., in press) than the Santacrucian-aged horizons described here. The two mesotheriid specimens from Caragua (and a third discovered in the same area by our team in 2001) have been referred to a new mesotheriine taxon (Flynn et al., in press).

Geographic and Geologic Setting

Material described herein is derived from the <600-m-thick Chucal Formation near Cerro Chucal, located on the Chilean Altiplano northwest of the Salar de Surire (18°43'S, 69°10'W). Several earlier studies have detailed the geology of this region (e.g., Muñoz, 1991; Charrier, Muñoz, & Palma-Heldt, 1994; Charrier, Muñoz, Wyss, et al., 1994; Riquelme & Hérail, 1997; Riquelme, 1998;

Charrier et al., 2000, 2002; Wörner et al., 2000; Chávez, 2001; Bond & García, 2002; Flynn, Croft, et al., 2002), including initial paleontological reports, geochronologic analysis, and studies of the syntectonic deposition of the fluviolacustrine sediments of the Chucal Formation (Fig. 1). Fossiliferous strata of the Chucal Formation are well exposed on both limbs of a major N–S-oriented growth anticline (the Chucal Anticline), which documents marked thickness and facies variation on either flank and at least four progressive erosional unconformities (U1–U4 in Charrier et al., 2002; Fig. 1; see also Riquelme & Hérail, 1997, and Riquelme, 1998). As detailed in Charrier et al. (2002), the Chucal Formation at Cerro Chucal is thickest (~600 m) on its west-dipping (35–40°) western flank (informal Members W1–W4) and is thinner on its steeply east-dipping (generally >50°) eastern flank (informal Members E1–E3), where the syntectonic erosional unconformities are most pronounced. Mammal fossils are most common in the floodplain facies (and some lacustrine-influenced intervals) in the lower parts of Members W3 and W4 and the fluviatile facies of Members E1 and E3 (Charrier et al., 2002).

Unconformities separate the Chucal Formation from the underlying Lupica Formation (early Miocene, dated at 21.7 ± 0.8 Ma at Chucal and at ≥18.5 Ma elsewhere in the region) and the overlying Quebrada Macusa Formation (the base of which is dated at 17.5 ± 0.4 Ma at Cerro Chucal; Muñoz, 1991; Riquelme, 1998; Bond & García, 2002; Charrier et al., 2002). The Chucal Formation, therefore, was deposited and deformed very rapidly (possibly over considerably less than 4–5 million years); it is no older than 22.5 Ma (possibly 18.5 Ma) and no younger than about 17 Ma. Thus, based on both the biostratigraphic occurrences and radioisotopic constraints, we consider the mammalian fossils from the Chucal Formation in this region to represent a single short-duration assemblage, the Chucal Fauna (Charrier et al., 2002; Flynn et al., 2002).

Materials and Methods

Upper tooth loci are indicated by uppercase letters (e.g., I1, P2, M1) and lower tooth loci by lowercase letters (e.g., i1, p2, m1); deciduous teeth are indicated by a "D/d" preceding the tooth position. Terminology for toxodontid molar morphology follows Madden (1990). All measure-
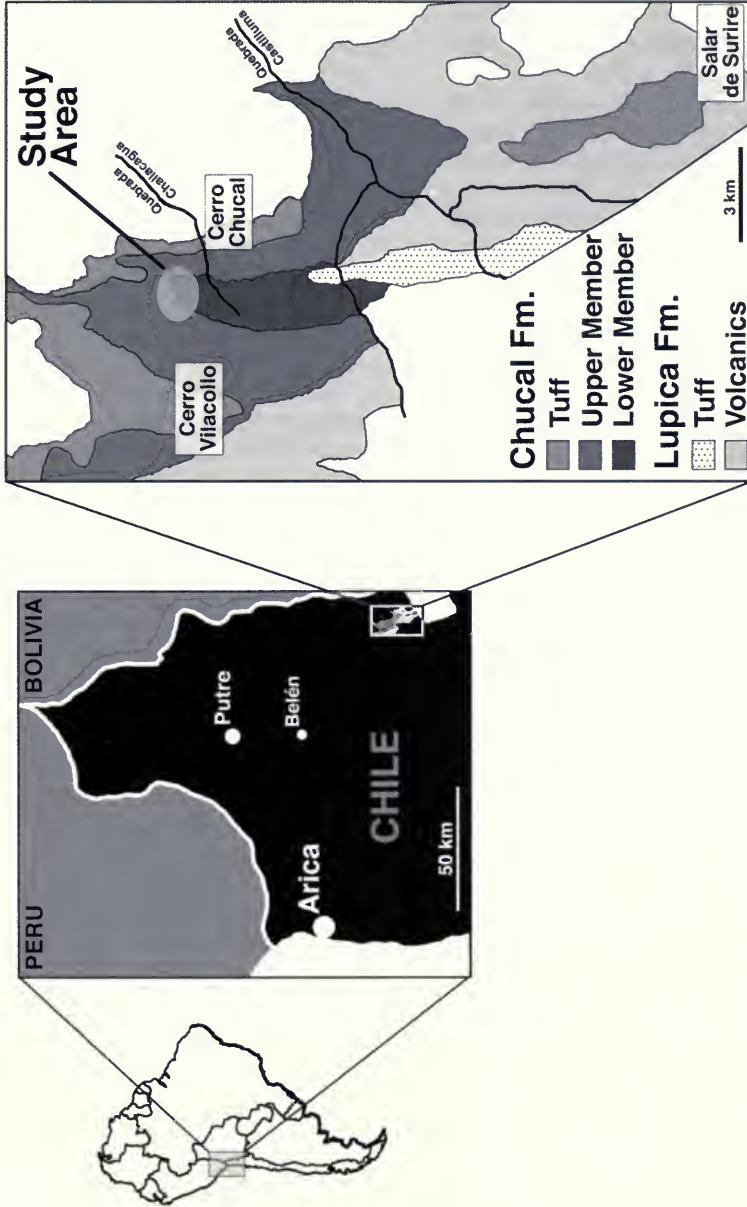
FIG. 1. Geography and geology of the Chucal Formation. The series of maps depicts the location of the study area within South America (left), northern Chile (middle), and a small region northwest of Salar de Surire (right). The map on the right also includes a schematic geologic map of the Chucal Formation in this region. Figure is modified from Flynn, Croft, et al. (2002).

ments were taken to the nearest 0.1 mm using digital calipers.

We recognize that many groups (e.g., Nesodontinae, Hegetotheriinae), as currently conceived, are likely paraphyletic. Because these names are familiar to South American paleomammalogists, we continue to employ them in their traditional sense until phylogenetic definitions and/or alternate names are proposed.

Taxonomic names that are potentially invalid because of synonymy (e.g., *Mesotherium* "*angustirostrum*") are indicated through the use of quotation marks.

To our knowledge, no comprehensive analysis of the stratigraphic and geographic occurrences of the taxa considered in the present study has been published previously. The distribution cited for each taxon therefore represents a preliminary effort to detail the geologic formations in which that taxon is known to occur based on firsthand observations and summary compilations of Bondesio et al. (1980), Marshall et al. (1983), Savage and Russell (1983), Mones (1986), Madden (1990), and Marshall and Sempere (1991).

The Friasian SALMA remains controversial (Flynn & Swisher, 1995; Madden et al., 1997; Flynn, Croft, et al., 2002). We distinguish between Friasian in its traditional sense (Friasian sensu lato; subsuming the Mayoan, Colloncuran, and Friasian sensu stricto SALMAs) and the term's more restrictive definition (Friasian sensu stricto; including only the temporal interval characterized by the type assemblage in southern Chile, and correlative faunas), following Flynn, Croft, et al. (2002).

Abbreviations

AMNH, American Museum of Natural History, New York; FMNH, Field Museum of Natural History, Chicago; GB, Servicio Geológico de Bolivia (housed at the Museo Nacional de Historia Natural, La Paz); MACN, Museo Argentino de Ciencias Naturales, "Bernardino Rivadavia," Buenos Aires; MLP, Museo de La Plata, Argentina; MNHN, Muséum National d'Histoire Naturelle, Paris; PU, Princeton University Collection (now housed at Yale University, New Haven, Connecticut); SGOPV, vertebrate paleontology collections, Museo Nacional de Historia Natural, Santiago; Ma, megannum; mm, millimeter; cm, centimeter; s.l., sensu lato; s.s., sensu stricto; SAL-

MA, South American Land Mammal "Age"; CI, consistency index; RI, retention index; RC, rescaled consistency index. Metacarpals and metatarsals are abbreviated MC and MT, respectively.

Systematic Paleontology

Mammalia Linnaeus, 1758
Notoungulata Roth, 1903
Toxodontia Owen, 1853
Toxodontidae Gervais 1847
Nesodontinae Murray, 1866

DIAGNOSIS—The Nesodontinae, as traditionally conceived (e.g., *Nesodon, Adinotherium, Proadinotherium,* etc.), is likely a paraphyletic group of toxodontids lacking derived character states present in other toxodontid subclades (Madden, 1990; Nasif et al., 2000). Specimens from Chucal are referred to the Toxodontidae based on large size; presence of very hypsodont cheek teeth; cheek teeth with protocone and hypocone united early in wear; upper molars with distinct and persistent first crista; lingual origin of the crochet in upper molars; triangular cross section of i1; hypselodont, procumbent, and tusklike i3; and reduced enamel along the lingual portions of the lower molars (Madden, 1990; Cifelli, 1993; Nasif et al., 2000). Nesodontines differ from other toxodontids in absence of derived mandibular symphysis morphology (Madden, 1990); unreduced sagittal crest (Nasif et al., 2000); lack of hypselodont molars (although M3 roots form only in old individuals; Madden, 1990); absence of simplified, straight ectoloph (i.e., lacking distinct parastyle, paracone, and metacone) on P2–4; presence of lingual folds on upper molars that become completely isolated as fossettes; and presence of two lingual folds plus an accessory fossettid in the lower molars.

Nesodon Owen, 1846

TYPE SPECIES—*Nesodon imbricatus.*
INCLUDED SPECIES—The type, *Nesodon conspurcatus,* and *Nesodon cornutus.*
DIAGNOSIS—A nesodontine differing from *Proadinotherium* in larger size; greater degree of hypsodonty; presence of I1 with trapezoidal cross section (triangular in *Proadinotherium*); absence of cingulae in I1; presence of simple and rounded

F3 fossette on upper molars; reduction of lingual enamel band on m1; presence of flattened and sharply angled posterior external face of m1 talonid; and presence of deep, wide lingual groove on molars (groove is shallow in *Proadinotherium*). Differs from *Adinotherium* in larger size (approximately twice as large in linear dimensions), absence of angled posteroventral border of mandible, presence of I1 with trapezoidal cross section (kidney shaped in *Adinotherium*), presence of P2–4 lingual precingulae, presence of relatively larger lower premolar row (p2–p4 length ≥50% m1–m3 length in *Nesodon*, <50% in *Adinotherium*), absence of anterior and entohypoconulid folds on p3, relatively lower-crowned p4, reduction of lingual enamel band on m1, presence of flattened and sharply angled posterior external face of m1 talonid, and distinct calcaneal morphology (see Scott, 1912). Differs from nearly contemporaneous *Palyeidodon* (likely a basal toxodontine and not a nesodontine, fide Madden, 1990; Cifelli, 1993; Nasif et al., 2000) in unreduced sagittal crest, presence of more developed upper premolar parastyles, presence of upper premolar lingual precingulum, presence of parastyle sulcus on M1, presence of accessory fossette on upper premolars, presence of F3 accessory fossette in upper molars, isolation of primary lingual fold as fossette in later wear stages in M2 and M3, presence of more persistent F3 fold/fossette in upper molars, and presence of accessory fossettid in lower molars (Madden, 1990; Cifelli, 1993; Nasif et al., 2000).

DISTRIBUTION—Santa Cruz Formation, Patagonia, Argentina, late early Miocene age, Santacrucian SALMA (Scott, 1912; Madden, 1990); Chucal Formation, northern Chile, late early Miocene age, Santacrucian SALMA; Cura-Mallín Formation, south-central Chile, late early Miocene age, Santacrucian SALMA (Croft, Radic, et al., 2003); unnamed formation (possibly equivalent to Río Zeballos Formation), southern Chile, late early Miocene age, Santacrucian SALMA (Flynn, Novacek, et al., 2002).

COMMENTS—*Nesodon* is best known from the rich late early Miocene Santa Cruz deposits along the Atlantic coast of Patagonia (Scott, 1912). Recent studies suggest that *Nesodon* may serve as a useful index taxon for the Santacrucian SALMA (Croft, Radic, et al., 2003). Reports of *Nesodon* from other time periods and from areas outside of Chile and Patagonia are poorly substantiated and are therefore not included in the above list (Flynn, Croft, et al., 2002; Croft, Radic, et al., 2003).

Bond and García (2002) questionably referred three poorly preserved and fragmentary toxodontid teeth from the upper part of the Chucal Formation to *Palyeidodon,* a taxon resembling *Nesodon* that occurs in slightly younger deposits (early middle Miocene Friasian s.s. and Colloncuran SALMAs; Madden, 1990). They further noted that these teeth (all pertaining to a single individual) possess a mix of features normally found in those two taxa as well as some distinct features (autapomorphies) that indicate it might represent a new taxon. The dental similarities of *Nesodon* and *Palyeidodon* make them difficult to distinguish without sufficiently complete and well-preserved specimens. Moreover, some of the characters used by Bond and García (2002) to differentiate the two are of ambiguous utility: the absence of a posteroexternal fossette in M1 (characteristic of *Palyeidodon*) also occurs in some specimens of *Nesodon* (e.g., FMNH P10379), the M1 lingual fold becomes isolated with wear in both *Nesodon* and *Palyeidodon* (although this is not the case for M2 and M3; Madden, 1990), and it is unknown whether the isolated M1 they described would eventually have formed roots (as in *Nesodon*) or would have maintained open roots (as in *Palyeidodon*) later in life. Additionally, the specimens described by Bond and García (2002) differ in several respects from both *Nesodon* and *Palyeidodon*: the parastylar region is much more pronounced and is deflected lingually instead of labially (as noted by Bond and García), the ectoloph is strongly convex instead of straight or slightly concave (also noted by Bond and García), and the teeth (especially M1) are significantly larger than those of both *Nesodon* (Scott, 1912) and *Palyeidodon* (Madden, 1990). It may therefore represent a new toxodontid, but one that currently is too poorly represented to be named. Pending description of more diagnostic material, we consider these teeth to pertain to an indeterminate toxodontid.

Nesodon imbricatus Owen, 1846
(Figures 2, 4, Table 1)

REFERRED SPECIMENS FROM THE CHUCAL FORMATION—SGOPV 5073, partial skull with broken right ?I2, right P2–M3, isolated left M2; SGOPV 4043, fragmentary and poorly preserved skull and right mandible; SGOPV 4027, left postorbital process; SGOPV 4054, incisor/canine and other tooth fragments (unprepared); SGOPV 4066, left M3;

TABLE 1. Measurements for Chucal specimens of *Nesodon imbricatus*.

Upper dentition	P2		P3		P4		M1		M2		M3	
	L	W	L	W	L	W	L	W	L	W	L	W
SGOPV 5073 (R)	—	—	19.8	25.2	21.6	28.3	31.4	27.6	45.1	34.5	58.6	31.3
SGOPV 5073 (L)									44.0	34.4		
SGOPV 4066 (L)											46.4	(26.6)

Lower dentition	m2		m3	
	L	W	L	W
SGOPV 4105 (R)	39.8	17.2		
SGOPV 4099 (L)			(75)	(22)

SGOPV 5036, right mandibular fragment with portions of ?p3–4; SGOPV 4105, right m2; SGOPV 4099, left mandibular fragment with m3; SGOPV 5118, right ?dp; SGOPV 4018 partial left glenoid; SGOPV 5225, left humerus (see Charrier, Muñoz, Wyss, et al., 1994); SGOPV 4044, proximal left ulna fragment; SGOPV 4040, fragmentary large postcranial bones, right metacarpal II, and right magnum; SGOPV 4015, fragmentary postcranial bones (associated with SGOPV 5036).

AGE AND DISTRIBUTION—Santa Cruz Formation, Patagonia, Argentina, late early Miocene age, Santacrucian SALMA; Chucal Formation, northern Chile, late early Miocene age, Santacrucian SALMA.

DIAGNOSIS—Differs from *Nesodon conspurcatus* in larger size. Differs from *N. cornutus* in lower occiput and absence of dermal horn.

DESCRIPTION—The most complete specimen of *Nesodon imbricatus* in the Chucal collections is SGOPV 5073, a partial skull with much of the right toothrow preserved. Although the bone is not especially well preserved, most of the teeth are in excellent condition. The skull is partially prepared, and the occlusal surfaces of right P2–M3 have been exposed, as has the entire length of an associated left M2 (almost certainly from the same individual but displaced from its alveolus). Other teeth are present as "float" in the block containing the skull but remain unprepared. Dental measurements for this and other specimens referred to *N. imbricatus* are presented in Table 1.

The premolars of SGOPV 5073 are all roughly quadrangular in outline. The anterior half of P2 is not preserved, portions of the anterior and lingual faces of P3 are missing, but P4 is essentially complete. The ectoloph of each tooth includes a parastyle and parastyle sulcus. These structures are most pronounced in P2 and less so in more posterior premolars. All three premolars show moderate wear, and the only occlusal feature remaining is the central fossa. The fossa is a very small oval in P2 and is larger and more elongate anteroposteriorly in P3 and P4.

A noteworthy feature of the premolar series is the variation in the level of the occlusal surfaces of the teeth. The occlusal surface of P4 is at the same level as the molars, while that of P2 is more dorsally situated, approximately 1.75 cm nearer the base of the tooth. The third premolar bridges this gap in occlusal surfaces; most of P3 is at the same level as P2, but the posterior quarter has been worn such that it forms an extremely steep dentine slope (ranging from 45° to 85° at the lingual and labial margins, respectively) that blends into the anterior face of M1. As in many other notoungulates, enamel is absent along the labial portions of both the posterior face of P4 and the anterior face of M1 in this area, resulting in the confluence of the two dentine surfaces.

The first and second upper molars are both trapezoidal. The ectolophs are straight with little evidence of a parastyle or parastyle sulcus. Only the central fossa is present on the occlusal surface of M1. In M2, the bifurcate primary lingual enamel fold has become isolated as a large, bifurcate, central fossa. The F3 fold is present as a small fossette located almost directly posterior to the point of bifurcation of the central fossa. The third upper molar is nearly triangular in shape and displays less wear than the two anterior molars. Both the primary lingual enamel fold and the F3 fold are present; the former has not yet become isolated by wear, while the latter recently has.

Specimen SGOPV 5118 is apparently an unerupted deciduous right lower premolar. Its lack of wear, small size, and lack of roots suggest it was from a very young individual. The anterior
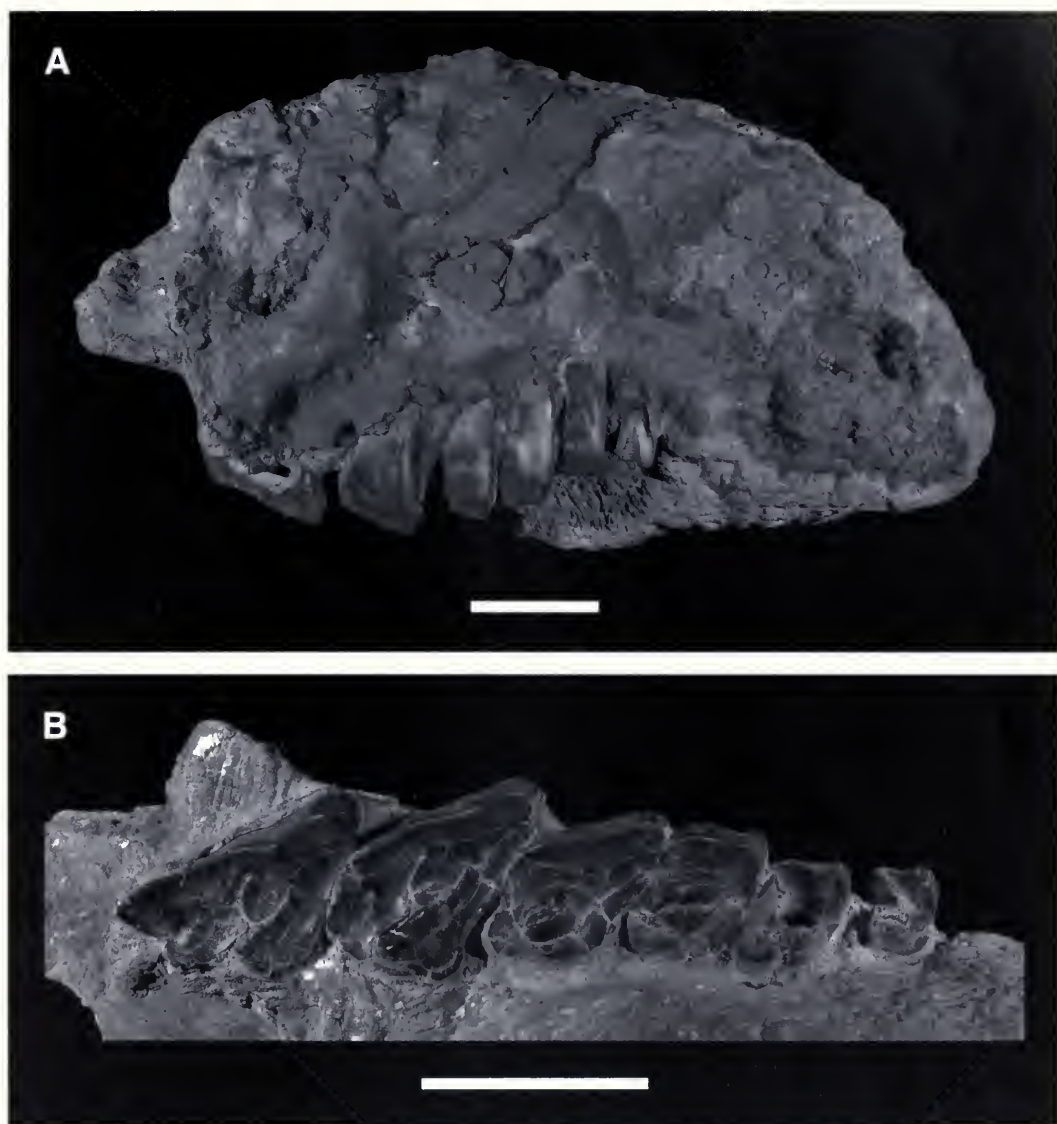
Fig. 2. Partial skull of *Nesodon imbricatus*, SGOPV 4053, including right ?I2 and P2–M3. **A.** Right lateral view. **B.** Occlusal view. Scale bars equal 5 cm.

and posterior faces converge slightly toward the base (in lingual view), indicating that the tooth would not have increased in size with further development. It is similar in overall form to the anterior tooth of MLP 12–245, a partial right mandible with ?dp4–m1 from Santa Cruz referred to *Nesodon imbricatus* (pers. observ.).

Relatively few postcranial bones from Chucal are referable to *Nesodon*; these include the left humerus found in 1992 (SGOPV 5225), a partial left glenoid (SGOPV 4018), a proximal left ulnar fragment (SGOPV 4044), and some fragmentary large long bones associated with a right MC II and right magnum.

COMMENTS—The size difference between *Nesodon imbricatus* and *N. conspurcatus* is pronounced, implying that the validity of the two species is well founded (Croft, Radic, et al., 2003); in this regard, specimens from Chucal compare well with *N. imbricatus* (Fig. 3). The status of *N. cornutus* is less certain; the species is represented only by the holotype (a nearly complete skull with heavily damaged teeth) and is distinguished from other species by skull proportions
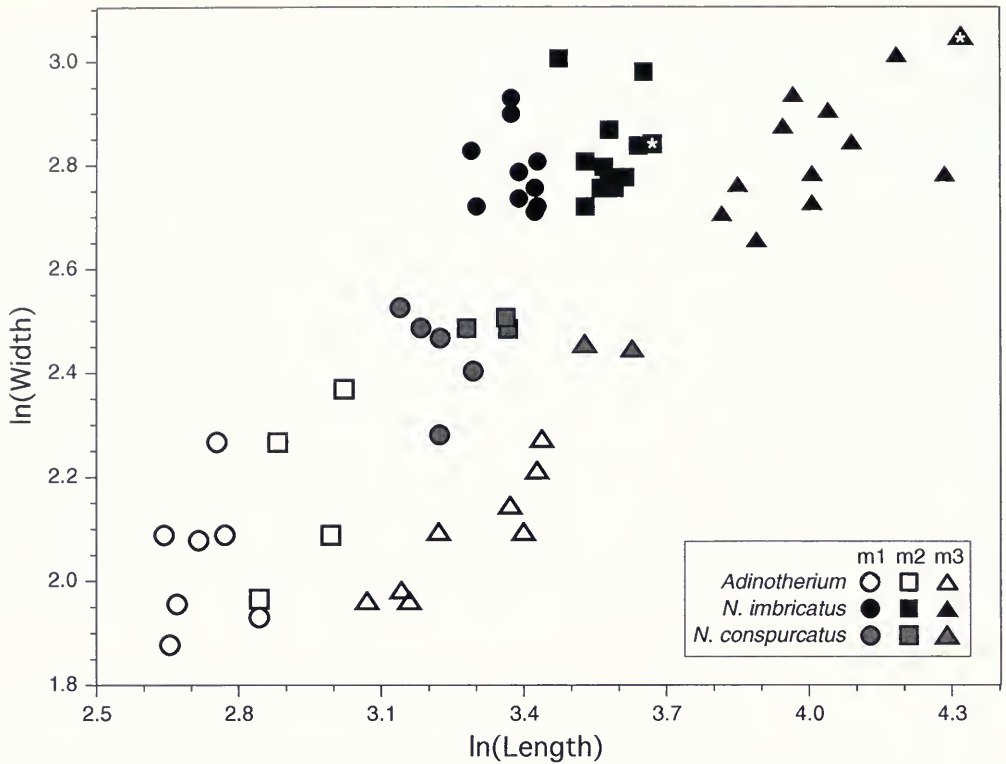
FIG. 3. Bivariate plot of log-transformed lower molar dimensions for various specimens of *Adinotherium, Nesodon imbricatus,* and *Nesodon conspurcatus.* Chucal specimens SGOPV 4105 (m2) and SGOPV 4099 (m3) are denoted by an asterisk (*).

and the possible presence of a dermal horn. It is similar in size to smaller specimens of *N. imbricatus* (Scott, 1912). Given the rarity of this taxon, the lack of diagnostic dental characters, the lack of appropriate cranial material for comparison, and the overall large size of the species of *Nesodon* from Chucal, there is no basis for referring it to *N. cornutus* (if indeed this species is valid).

Adinotherium Ameghino, 1887

TYPE SPECIES—*Adinotherium ovinum.*

INCLUDED SPECIES—The type, *Adinotherium karaikense, Adinotherium robustum, Adinotherium splendidum,* and *Adinotherium nitidum.*

DIAGNOSIS—A nesodontine differing from *Proadinotherium* in greater degree of hypsodonty; presence of I1 with kidney-shaped cross section and lingual groove (triangular cross section in *Proadinotherium*); absence of cingulae on I1; and presence of deep, wide lingual groove on molars (groove is shallow in *Proadinotherium*). Differs

from *Nesodon* in smaller size (40–50% smaller in tooth dimensions), presence of I1 with kidney-shaped cross section and lingual groove (trapezoidal cross section in *Nesodon*), presence of angled posteroventral border of mandible (rounded in *Nesodon*), absence of P2–4 lingual precingulae, presence of relatively shorter lower premolar row (p2–p4 length <50% m1–m3 length in *Adinotherium,* ≥50% in *Nesodon*), presence of anterior and entohypoconulid folds on p3, presence of relatively higher-crowned p4, larger lingual enamel band on m1, absence of flattened and sharply angled posterior external face of m1 talonid, and distinctive calcaneal morphology (see Scott, 1912).

DISTRIBUTION—Santa Cruz Formation, Patagonia, Argentina, late early Miocene age, Santacrucian SALMA (Scott, 1912; Madden, 1990); Chucal Formation, northern Chile, late early Miocene age, Santacrucian SALMA; unnamed formation (possibly equivalent to Río Zeballos Formation), southern Chile, late early Miocene age, Santacrucian SALMA (Flynn, Novacek, et al., 2002).
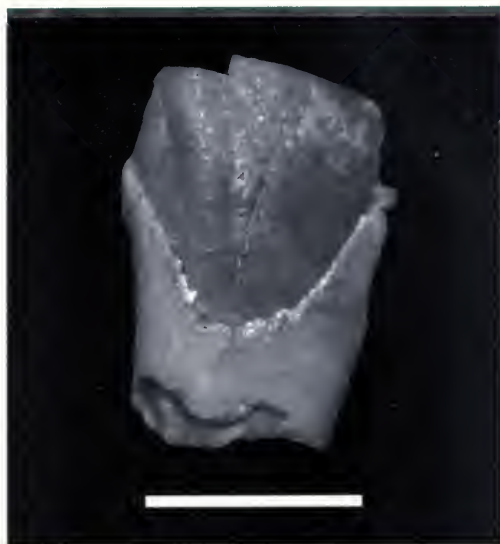
FIG. 4. Partial left ?i2 of *Adinotherium*, SGOPV 4064, in labial view. Scale bar = 5 mm.

COMMENTS—Although Scott (1912) noted differences in the vertebral column, scapula, and ankle of *Adinotherium* and *Nesodon*, morphological characters currently used to distinguish the two taxa are all craniodental (Madden, 1990; Nasif et al., 2000). The limb bones of toxodontids are fairly easy to distinguish from those of other endemic South American ungulate clades (e.g., litopterns, astrapotheres, pyrotheres) and other contemporaneous notoungulates (e.g., mesotheriids, hegetotheriids). Given the significant metric differences between *Adinotherium* and *Nesodon*, postcranial specimens of the two Santacrucian toxodontids can be discriminated on the basis of size alone (Scott, 1912; Croft, Radic, et al., 2003). Since only a single tooth of *Adinotherium* (a partial incisor, Fig. 4) has been collected at Chucal, reference of postcranial elements to this taxon is based on their similar morphology—but much smaller size—compared to *Nesodon* (Fig. 5).

Adinotherium sp. indet.
(Figures 4–6)

REFERRED SPECIMENS FROM CHUCAL—SGOPV 4064, partial ?left i2, partial right articular condyle, various ?mandibular fragments (Fig. 4); SGOPV 4012, left unciform, proximal left MC IV, left MC V, dorsal half of right magnum, many other partial hand/foot bones and bone fragments;

SGOPV 5035, phalanx, many small bone fragments; SGOPV 4065, partial femoral head, proximal ?MT II, many limb bone fragments; SGOPV 4084, proximal portions of left ulna and radius, ?elbow sesamoid (Figs. 5, 6).

DESCRIPTION—Only a single dental specimen clearly attributable to *Adinotherium* has been collected from Chucal: SGOPV 4064, a partial tooth, probably left i2 (Fig. 4). The tooth preserves only the base of its crown and part of the root; none of the occlusal surface is present. The root measures 5.6 × 6.5 mm. Enamel is restricted primarily to the front of the tooth but extends slightly onto the mesial surface toward the crown. The labial enamel is much thicker than the mesial. The labial enamel forms an inverted triangle in anterior view, with a rounded apex and a base formed by the broken surface of the tooth. In size and morphology, the specimen closely resembles the base of left i2 of FMNH P13097, a specimen of *Adinotherium* from Santa Cruz, Argentina; it is much smaller than FMNH UC1330, a specimen of *Nesodon* from Santa Cruz. The tooth is associated with various mandibular fragments, including a partial right articular condyle that compares well with *Adinotherium*.

A second craniodental specimen, SGOPV 4011, may pertain to *Adinotherium*. It appears to be a partial maxilla preserving the bases of two teeth, a fragment of a third, and part of the alveolus of a fourth. Based on the portions of teeth that are present and the size of the alveolus, the most notable aspect of SGOPV 4011 is the dramatic mesial-to-distal increase in tooth size; this resembles the condition seen in the premolar series of *Adinotherium* and does not closely resemble the condition present in any other specimens from Chucal. The fragmentary nature of the specimen precludes a precise identification, however.

Despite the paucity of dental remains, several well-preserved postcranial specimens (primarily forelimb elements) increase confidence in the recognition of *Adinotherium* at Chucal. Specimen SGOPV 4084 includes proximal fragments of the left ulna and radius (Figs. 5, 6). The radius is much more robust than that of the larger mesotheriids at Chucal (e.g., *A. chucalensis*, SGOPV 4042) and differs most conspicuously in having a very pronounced interosseous crest (Fig. 6). Similarly, the fragmentary ulna, while preserving only the distal portion of the sigmoid notch, differs from the corresponding bone of mesotheriids in lacking a well-demarcated fossa distal to the coronoid process (Fig 5.). Except for its much small-
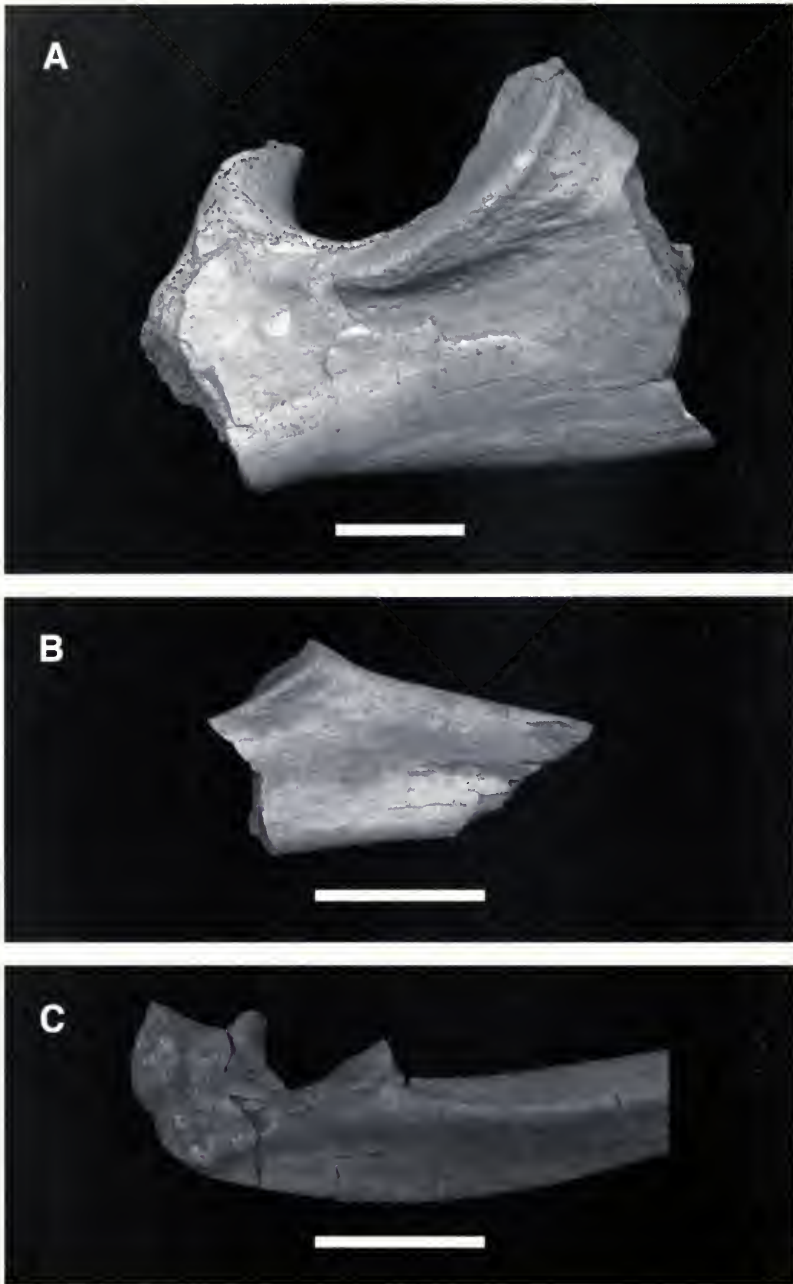
FIG. 5. Relative sizes of mesotheriines and toxodontids from Chucal, as illustrated by the size of the ulna. **A.** SGOPV 4044, proximal left ulna fragment of *Nesodon imbricatus*. **B.** SGOPV 4084, proximal portion of left ulna of *Adinotherium*. **C.** SGOPV 4042, left ulna of *A. chucalensis* (Mesotheriinae, described in text). All specimens are in medial view. Scale bars = 2 cm.

er size, it resembles a partial ulna from Chucal referred to *Nesodon* (SGOPV 4044). A small, rounded bone with two closely appressed facets found near the proximal ulna and radius may rep-

resent an elbow sesamoid bone of *Adinotherium* (as noted for specimens of similar morphology by Scott, 1912). The other specimens attributed to *Adinotherium* also resemble the corresponding el-
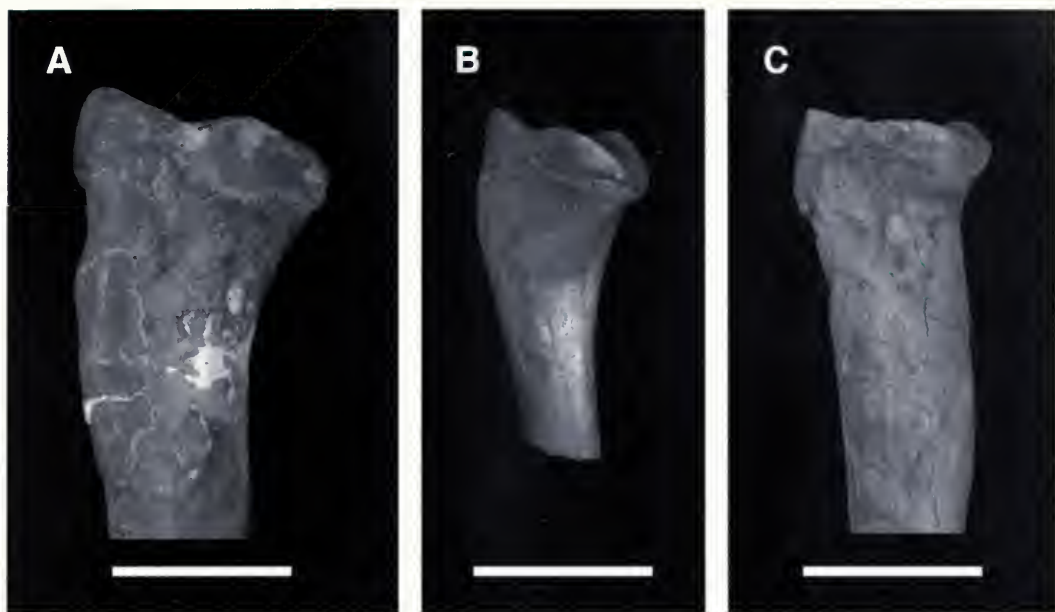
FIG. 6. Morphology of the proximal radius in mesotheriines and *Adinotherium*. **A.** FMNH P14482, proximal left radius of "*Typotheriopsis* sp." from the late Miocene Araucano Fm. of Catamarca, Argentina. **B.** SGOPV 4042, proximal right radius (pictured as left) of *A. chucalensis* (Mesotheriinae, described in text). **C.** SGOPV 4084, proximal left radius of *Adinotherium*. All specimens are in medial view. Scale bars = 2 cm.

ements of *Nesodon* while differing in morphology from those of mesotheriids (and other notoungulates).

COMMENTS—As discussed below (Litopterna) appendicular bones of the major South American ungulate clades are easily distinguished (Cifelli, 1983, 1985, 1993). Those from Chucal here referred to the Toxodontidae (viz., *Nesodon* and *Adinotherium*) are similar in morphology but differ markedly in size. This difference is well illustrated by SGOPV 4044, a partial left proximal ulna of *Nesodon*, versus SGOPV 4084, a partial left proximal ulna of *Adinotherium* (Fig. 5); the depth of the ulna just distal to the trochlear notch of the former is approximately 8 cm, while the corresponding measurement of the latter is less than 3 cm. The specimens attributed to *Adinotherium* above are all fully ossified and therefore do not pertain to immature individuals of *Nesodon*.

Typotheria Zittel, 1892
Mesotheriidae Alston, 1876
Mesotheriinae Simpson, 1945

Mesotheriids are traditionally divided into two subgroups: the Trachytheriinae (comprising Deseadan and earlier forms, most assigned to *Trach-*

ytherus) and the Mesotheriinae (including Friasian s.l. and later forms) characterized by the loss of I2–P2/i3–p3 and the presence of persistently trilobed upper molars, among other features (Francis, 1965; Villarroel, 1974a; Cerdeño & Montalvo, 2001; Reguero & Castro, 2002; Croft, Flynn, & Wyss, 2003; Flynn et al., in press). Mesotheriids are absent from faunas of Colhuehuapian age and had not been recorded in faunas of Santacrucian age prior to their discovery at Chucal (Flynn, Croft, et al., 2002).

Mesotheriines are in great need of systematic revision (Pascual & Bondesio, 1985; Cerdeño & Montalvo, 2001; Flynn, Croft, et al., 2002; Croft, Flynn, & Wyss, 2003; Flynn et al., in press), making taxonomic assignments of newly discovered forms challenging. Based on Francis's (1965) revision of Argentine taxa and the subsequent description of additional forms from Bolivia (Villarroel, 1974a,b), Flynn et al. (in press) recognized seven potentially valid mesotheriine "genera" and described a new taxon from the middle Miocene Huaylas Formation of northern Chile.

A character that has traditionally been important in mesotheriine taxonomy is imbrication: the degree to which the anteroexternal corner of an upper cheek tooth overlaps the posteroexternal

Upper dentition	I1		?P4		M1		M2		M3	
	L	W	L	W	L	W	L	W	L	W
SGOPV 4038 (R)			6.9	7.7	(12.3)	8.5				
SGOPV 4038 (L)	(14.4)	(6.7)	(6.9)	(7.6)	12.5	8.6	12.8	8.8	13.9	8.4
SGOPV 4024 (L)	14.0	6.8								
SGOPV 5041 (L)			7.0	8.3						
SGOPV 5072 (L)									14.1	8.3
SGOPV 5102 (R)									(12.5)	(8.6)

Lower dentition	i1		i2		p4		m1		m2		m3	
	L	W	L	W	L	W	L	W	L	W	L	W
SGOPV 4024 (R)					8.1	5.1	(10.5)	6.4	—	(6.4)	16.6	5.6
SGOPV 4024 (L)	—	—	—	—	8.3	5.6	10.7	6.5	13.0	6.6	16.2	5.8
SGOPV 5046 (R)							—	—	(11.3)	6.6	16.1	6.4
SGOPV 5046 (L)					7.3	5.0	(10.1)	(6.7)	—	—	16.1	6.3
SGOPV 4101 (R)	7.0	4.9	5.7	3.8	8.4	4.9	10.5	6.3	12.0	6.5	15.5	5.9
SGOPV 4101 (L)	7.1	4.9	5.0	3.8								
SGOPV 5142 (R)	7.1	4.7										
SGOPV 5088 (R)			5.5	4.0								
SGOPV 5045 (L)			6.0	4.0								
SGOPV 5125 (L)					7.5	5.3						
SGOPV 5091 (R)							10.8	6.3				
SGOPV 5051 (L)									(11.6)	(7.0)	(15.9)	(5.9)

corner of the tooth preceding it (Francis, 1965). In his review of mesotheriine evolution, Villarroel (1974a) noted that imbrication includes two components: "chevauchement," the degree of mesiodistal overlap between teeth, and "débordement," the amount of labiolingual overlap. He stated that the former shows little variation through the SALMA sequence and that the latter is more useful for distinguishing among mesotheriine species. Following Villarroel's observation, we measure imbrication ("débordement") as the width from M2 parastyle to M1 hypocone divided by the width of M1 posterior face (see also Flynn et al., in press).

Mesotheriine remains are among the most common fossils in the Chucal Formation; approximately one-third of identified specimens are referable to this group. Mesotheriids are also abundant in most Tertiary mammal faunas from Bolivia (e.g., Salla, Achiri, Nazareno), suggesting that intermediate latitudes (and possibly higher elevations) may have been a center of diversification for the group (Croft, Flynn, & Wyss, 2003). The mesotheriines from Chucal clearly pertain to at least three distinct species. A phylogenetic analysis of currently recognized mesotheriines and the Chucal taxa (discussed below) suggests that all three species from Chucal represent new, early diverging mesotheriines. Two of these appear to be mutual nearest relatives, and thus share a common anterior half of the binomial to reflect this provisional hypothesis of relationship.

Altitypotherium paucidens, species novum
(Figures 7, 8, Table 2)

HOLOTYPE—SGOPV 4038, partial rostrum with left I1, left P4–M3 and right P4–M1 (Fig. 7).

HYPODIGM—SGOPV 5041, left ?P4; SGOPV 5072, left M3; SGOPV 5102, partial right M3; SGOPV 4024, partial left and right mandibles and isolated left I1 (left mandible has partial i1–2 and complete p4–m3, right mandible has partial i1–2, m1–2, and complete p4, m3; Fig. 8A); SGOPV 5046, partial left and right mandibles and fragmentary incisors (left mandible bears complete p4–m1, m3, and partial m2, right has base of m1, complete m2–3); SGOPV 4101, partial right mandible and symphysis with full dentition plus left i1–2 (Fig. 8B); SGOPV 5142 right i1; SGOPV 5045, left i2; SGOPV 5088, right i1; SGOPV 5125, left p4; SGOPV 5091, right m1; SGOPV 5051, partial left mandible with m2–3.

TYPE LOCALITY—Loc. C-ALT-98-12B; Chucal Formation (Member W4 of Charrier et al., 2002); west flank of Chucal Anticline.

AGE AND DISTRIBUTION—Chucal Formation,
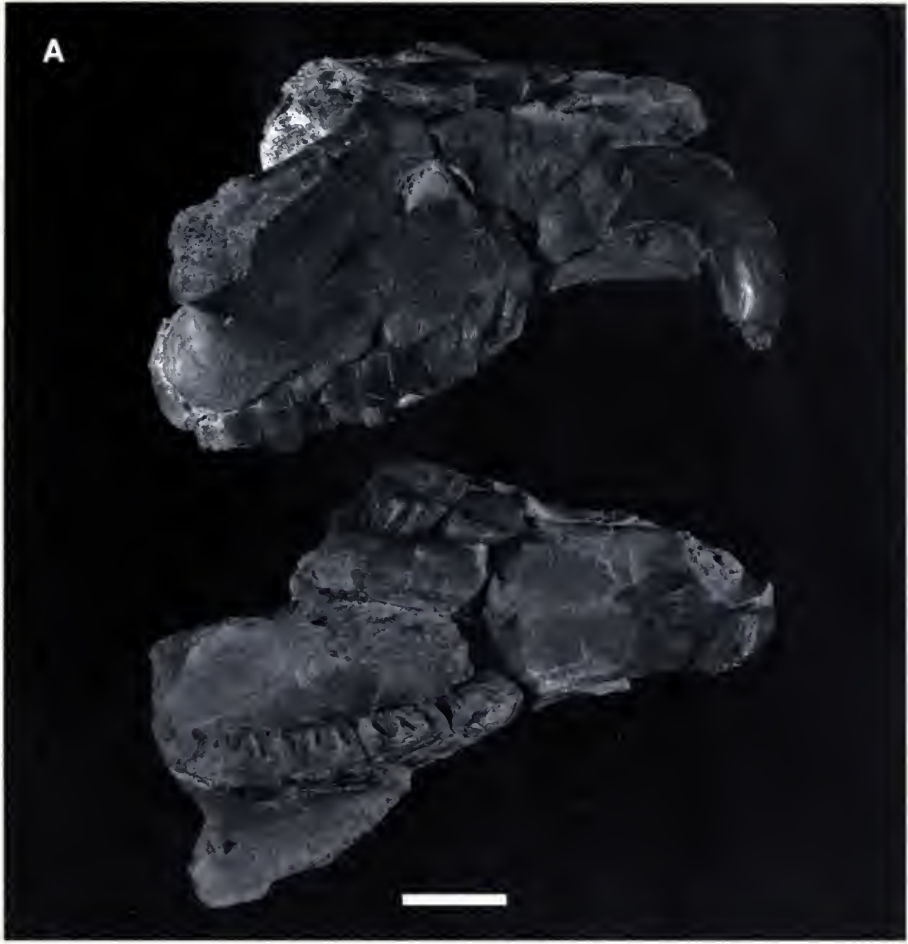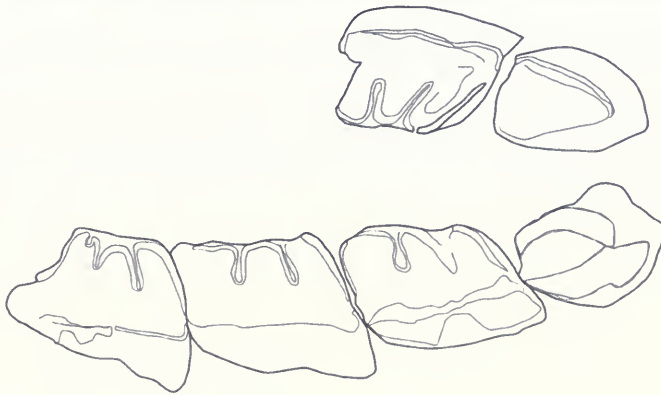
Fig. 7. Holotype of *Altitypotherium paucidens*, SGOPV 4038, a partial rostrum with left I1, left P4–M3 and right P4–M1. **A.** Left lateral (above, pictured as right) and occlusal (below) views. **B.** Line drawings of occlusal morphology (toothrows not in natural position). Scale bars = 1 cm.
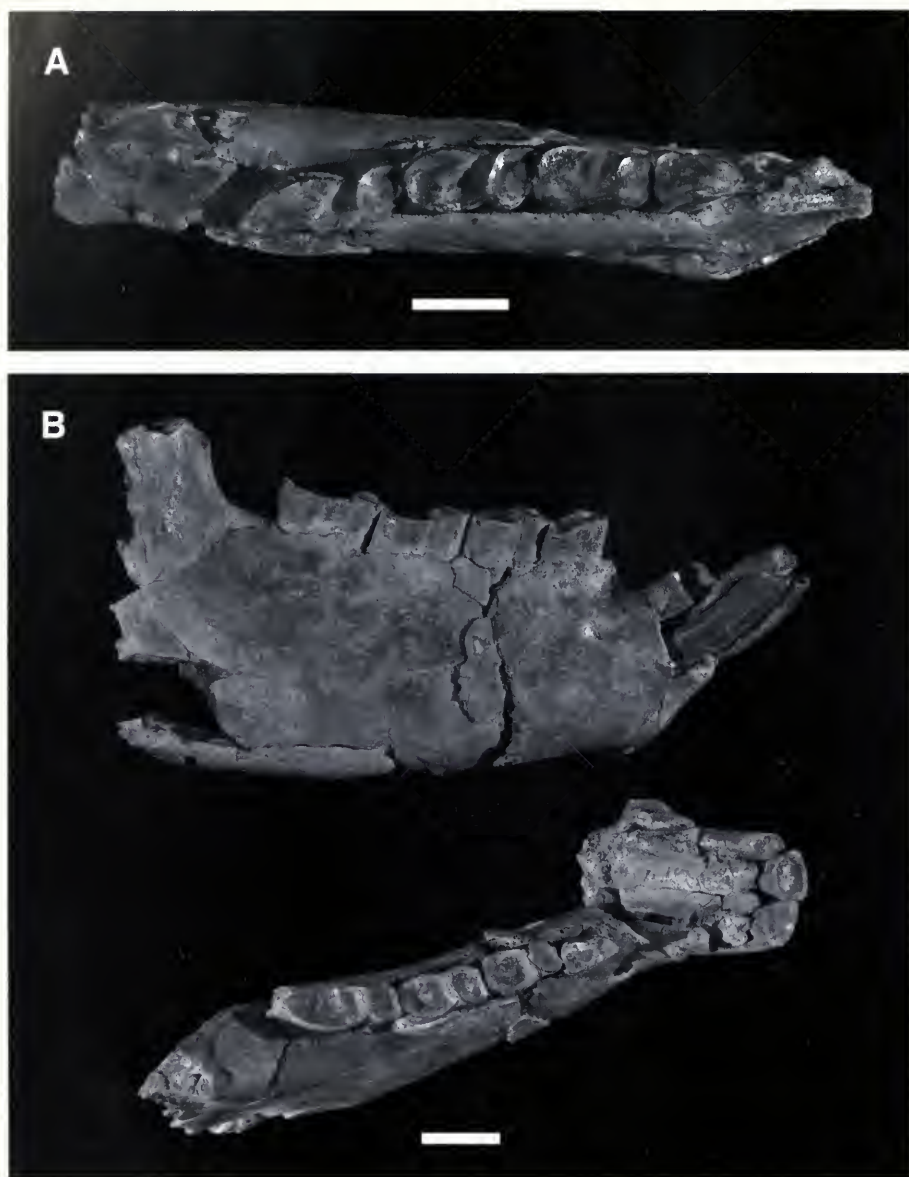
Fig. 8. Lower dentitions referred to *Altitypotherium paucidens*. **A.** SGOPV 4024, partial left mandible with fragmentary i1–2 and complete p4–m3 in occlusal view. **B.** SGOPV 4101, partial right mandible and symphysis with full dentition plus left i1–2 in lateral (above) and occlusal (below) views. Scale bars = 1 cm.

northern Chile, late early Miocene age, Santacrucian SALMA.

ETYMOLOGY—*Alti*, in reference to the Altiplano, the high plateau of northern Chile and neighboring Bolivia and Peru, where the referred specimens were collected, and *typotherium*, in reference to the familiar root commonly used in mesotheriine taxon names; *pauci*, Latin for "few,"

and *dens*, Latin for "tooth," in reference to the lack of P3, a characteristic feature of this species.

DIAGNOSIS—A mesotheriine that differs from all other mesotheriines in the absence of P3.

Differs from *Microtypotherium* in presence of deep, narrow postpalatal notch that extends to the level of M3 (does not reach M3 in *Microtypotherium*); presence of subtriangular I1 that is

pointed distally, with two lingual sulci (a single mesial sulcus is present in *Microtypotherium*); presence of enlarged M3 middle lobe (not surrounded by other two lobes); presence of one labial sulcus on premolar ectolophs (two sulci present in *Microtypotherium*); and absence of shortened m2 (length/width between 1.60 and 2.30 in *Altitypotherium*, <1.6 in *Microtypotherium*).

Differs from *Eutypotherium* in the root of zygomatic arch being directed perpendicular to M1 (posteriorly directed from the level of M1 or M2 in *Eutypotherium*); presence of deep, narrow postpalatal notch that extends to the level of M3 (wide and shallow in *Eutypotherium*); presence of subtriangular I1 that is pointed distally, with two lingual sulci (wide and rounded with lingual sulcus in *Eutypotherium*); presence of rounded i1 with little or no lingual sulcus (subtriangular with smooth sulcus in *Eutypotherium*); presence of one labial sulcus on premolar ectolophs (two sulci present in *Eutypotherium*); absence of extensive lingual exposure of M1 middle lobe; and smaller size (based on dental measurements, approximately 20% smaller than *Eutypotherium lehmannnitschei*).

Differs from *Plesiotypotherium* in posteriorly diverging upper and lower diastemata (parallel in *Plesiotypotherium*); absence of well-developed suborbital fossa; presence of deep, narrow postpalatal notch that extends to the level of M3 (wide and shallow in *Plesiotypotherium*); subtriangular I1 that is pointed distally, with two lingual sulci (wide and rounded with lingual sulcus in *Plesiotypotherium*); presence of rounded i1 with little or no lingual sulcus (subtriangular with smooth sulcus in *Plesiotypotherium*); presence of one labial sulcus on premolar ectolophs (two sulci present in *Plesiotypotherium*); presence of M1 middle lobe with lingually convergent anterior and posterior sides (subparallel in *Plesiotypotherium*); absence of extensive lingual exposure of M1 middle lobe; and smaller size (based on dental measurements, approximately 30% smaller than *Plesiotypotherium achirense*).

Differs from Caragua New Taxon (Flynn et al., in press) in presence of posteriorly divergent upper and lower diastemata (parallel in Caragua New Taxon); lesser degree of molar imbrication (<1.25 in *Altitypotherium*, between 1.25 and 1.50 in Caragua New Taxon); presence of subtriangular I1 that is pointed distally, with two lingual sulci (wide and rounded with lingual sulcus in Caragua New Taxon); presence of short, subtriangular P4 without central fossette (P4 bilobed with short and

poorly defined lingual plication in Caragua New Taxon); presence of enlarged M3 middle lobe (not surrounded by other two lobes); relatively smaller i1 (i1/i2 <1.50 in *Altitypotherium*, between 1.50 and 2.00 in Caragua New Taxon); presence of rounded i1 with little or no lingual sulcus (subtriangular with smooth sulcus in Caragua New Taxon); presence of one labial sulcus on premolar ectolophs (two sulci present in Caragua New Taxon); presence of M1 middle lobe with lingually convergent anterior and posterior sides (subparallel in Caragua New Taxon); absence of extensive lingual exposure of M1 middle lobe; and smaller size (based on dental measurements, approximately 20% smaller than Caragua New Taxon).

Differs from *Typotheriopsis* in presence of posterolaterally divergent upper and lower diastemata (parallel in *Typotheriopsis*); absence of well-developed suborbital fossa; presence of deep, narrow postpalatal notch that extends to the level of M3 (does not reach M3 in *Typotheriopsis*); presence of subtriangular I1 that is pointed distally, with two lingual sulci (wide and rounded with lingual sulcus in *Typotheriopsis*); presence of enlarged M3 middle lobe (not surrounded by other two lobes); relatively smaller i1 (i1/i2 <1.50 in *Altitypotherium*, between 1.50 and 3.00 in *Typotheriopsis*); presence of rounded i1 with little or no lingual sulcus (subtriangular with smooth sulcus in *Typotheriopsis*); presence of M1 middle lobe with lingually convergent anterior and posterior sides (subparallel in *Typotheriopsis*); absence of extensive lingual exposure of M1 middle lobe; and smaller size (based on dental measurements, approximately 30% smaller than *Typotheriopsis chasicoensis*).

Differs from *Pseudotypotherium* in presence of posterolaterally divergent upper and lower diastemata (parallel in *Pseudotypotherium*); absence of well-developed suborbital fossa; presence of deep, narrow postpalatal notch that extends to the level of M3 (does not reach M3 in *Pseudotypotherium*); lesser degree of molar imbrication (<1.25 in *Altitypotherium*, >1.50 in *Pseudotypotherium*); presence of short, subtriangular P4 without central fossette (P4 is bilobed in *Pseudotypotherium*); relatively smaller i1 (i1/i2 <1.50 in *Altitypotherium*, between 2.00 and 3.00 in *Pseudotypotherium*); presence of rounded i1 with little or no lingual sulcus (trapezoidal with well-demarcated lingual sulcus in *Pseudotypotherium*); presence of one labial sulcus on premolar ectolophs (two sulci present in *Pseudotypotherium*); absence of elongate

P4 (length/width <1.50 in *Altitypotherium,* ≥1.50 in *Pseudotypotherium*); absence of elongate M1 (length/width <1.75 in *Altitypotherium,* ≥1.75 in *Pseudotypotherium*); presence of M1 middle lobe with lingually convergent anterior and posterior sides (subparallel in *Pseudotypotherium*); absence of extensive lingual exposure of M1 middle lobe; absence of elongate m2 (length/width between 1.60 and 2.30 in *Altitypotherium,* >2.30 in *Pseudotypotherium*); and smaller size (based on dental measurements, approximately is 25% smaller than *Pseudotypotherium exiguum*).

Differs from *Mesotherium* in posterolaterally divergent upper and lower diastemata (parallel to strongly convergent in *Mesotherium*); presence of poorly defined suborbital fossa (absent in *Mesotherium*); lesser degree of molar imbrication (<1.25 in *Altitypotherium,* >1.50 in *Mesotherium*); presence of subtriangular I1 that is pointed distally, with two lingual sulci (wide and rounded with lingual sulcus or wide and compressed labiolingually with two lingual sulci in *Mesotherium*); presence of short, subtriangular P4 without central fossette (P4 is persistently bilobed in *Mesotherium*); relatively smaller i1 (i1/i2 <1.50 in *Altitypotherium,* >3.00 in *Mesotherium*); presence of rounded i1 with little or no lingual sulcus (trapezoidal with well-demarcated lingual sulcus or elliptical with smooth sulcus in *Mesotherium*); presence of one labial sulcus on premolar ectolophs (two sulci present in *Mesotherium*); absence of elongate P4 (length/width <1.50 in *Altitypotherium,* ≥1.50 in *Mesotherium*); absence of elongate M1 (length/width <1.75 in *Altitypotherium,* ≥1.75 in *Mesotherium*); presence of M1 middle lobe with lingually convergent anterior and posterior sides (lingually divergent in *Mesotherium*); absence of extensive lingual exposure of M1 middle lobe; absence of elongate m2 (length/width between 1.60 and 2.30 in *Altitypotherium,* >2.30 in *Mesotherium*); and smaller size (based on dental measurements, approximately 20% smaller than *Mesotherium maendrum* and half the size of *Mesotherium pachygnathum*).

Differs from *A. chucalensis* (described below) in absence of P3; presence of elongate M1 (length/width >1.3 in *A. paucidens,* ≤1.3 in *A. chucalensis*); middle lobe of M3 unreduced, not surrounded by anterior and posterior lobes; presence of narrower lower molars (widths ≤6.7 mm in *A. paucidens,* ≥7.3 mm in *A. chucalensis*); presence of elongate m3 (15–20% longer than m2 in *A. paucidens,* similar in length to m2 in *A. chucalensis*); and slightly larger size (based on dental

measurements, *A. paucidens* is approximately 10% larger than *A. chucalensis*).

DESCRIPTION—The holotype of *A. paucidens* consists of a moderately well-preserved rostrum (Fig. 7). The nasals have been crushed, and much of the premaxilla is missing, but the left side preserves the zygomatic arch, palate, and all the upper teeth.

The inferior surface of the zygomatic arch is slightly damaged but preserves a well-developed surface for the origin of the masseter. A shallow suborbital fossa is present on the dorsal surface of the arch. This fossa is similar in its degree of development to that of the holotype of *Eutypotherium superans* (MACN 11079), though it is oriented differently; in *A. paucidens,* the primary axis of the fossa is anteroposterior, whereas in *E. superans* it is transverse. In mesotheriines in which the suborbital fossa is developed to an even greater degree, it is also oriented transversely (e.g., *Typotheriopsis silveyrai,* MLP 36-XI-10-2). The suborbital fossa is demarcated posteriorly by a thick strut of bone oriented perpendicular to the toothrow. A large, elliptical infraorbital foramen is present, its major axis oriented dorsoventrally; it measures 10.5 × 5.5 mm.

Very little of right I1 is preserved in SGOPV 4038, but left I1 is well preserved except for its occlusal surface; in cross section, the major axis of the tooth is set at an angle of approximately 45° to the sagittal plane. Much of the premaxilla is missing from the left side of the specimen, revealing nearly the entire dorsoventral extent of I1. It is a strongly curved tooth (approximating a 90° arc) and lacks any evidence of a root. The entire surface of the tooth is covered by enamel, with the exception of the damaged occlusal surface. An isolated I1 referred to this species (SGOPV 4024) better demonstrates the occlusal morphology of the upper incisor; it is roughly subtriangular in cross section and pointed distally, with two smooth sulci present on the lingual face. The occlusal surface is worn such that it is strongly concave.

A large incisive foramen is present on the anterior surface of the palate just posterior to the pair of incisors. It measures approximately 9.5 × 7.3 mm and is divided longitudinally by a septum that is recessed relative to the surface of the palate. Large (nearly 25 mm long), posteriorly divergent diastemata separate the pair of incisors from the cheek teeth. The palate is relatively flat anterior to the cheek teeth but is highly arched between them.

The lone upper premolar (P4) is subtriangular in outline and has a single sulcus located near the anterior edge of its labial surface. The occlusal surface is featureless, and there is no evidence of a lingual groove or plication, as occurs in many mesotheriines. The shallower implantation angle of this tooth is reflected in the anteroposteriorly elongate wear on the occlusal surface. The three upper molars are of typical mesotheriine form. Each is rectangular with a pronounced parastyle and three lobes extending lingually from the ectoloph (formed by two labially directed invaginations of enamel from the lingual margins of the teeth). The first upper molar in *A. paucidens* is proportionately more elongate than the corresponding tooth in *A. chucalensis,* and the three lobes increase in size posteriorly. The anterior lobe is directed posterolingually, while the posterior lobe is roughly perpendicular to the ectoloph; the middle lobe therefore approximates a right triangle, with the hypotenuse forming its anterior face. The presence of a strongly triangular M1 middle lobe is unique among described mesotheriines, with the exception of *Microtypotherium choquecotense* (Villarroel, 1974b) and the other taxa from Chucal. However, one of the specimens from Nazareno, Bolivia (GB Naz-014) figured by Oiso (1991, p. 658, plate 2) and assigned to "*Plesiotypotherium* sp." also appears to possess this feature. Other mesotheriine specimens (e.g. GB Naz-001, GB Naz-013, GB Naz-047) from that site figured by Oiso (1991) lack a triangular M1 middle lobe. It is unknown whether this represents individual or interspecific variation among the specimens from Nazareno. Based on a phylogenetic analysis of mesotheriines (below), the presence of a triangular M1 middle lobe is judged ancestral for the group.

The posterior lobe of M1 bears a slight lingual plication in the posterior end of its lingual face. This plication is increasingly prominent on M2 and M3. A similar condition is present in the holotype of *Plesiotypotherium achirense* (although not noted in the original description; Villarroel 1974a, p. 267, fig. 9), in the holotype of *Pseudotypotherium carhuense* (MLP 37-III-7-1), and also in a juvenile specimen of *Trachytherus spegazzinianus* (MACN 3264) figured by Patterson (1934b, fig. 24). The increased prominence of this feature in more posterior cheek teeth, coupled with its absence in a more mature specimen of *Trachytherus* (e.g., FMNH P13281), suggests that this feature may be widespread among mesotheriids but is lost with wear.

The second upper molar of *A. paucidens* differs from M1 in having a slightly more rectangular middle lobe, although the anterior and posterior faces still converge lingually. The last upper molar has a smaller anterior lobe, similar to that seen in M1, and a small, anterolingually directed posterior lobe. The middle lobe therefore has subequal anterior and posterior faces. The enamel surface of this lobe does not reach the lingual face of the tooth but rather has a thick covering of cementum that fills the portion of the lingual face between the anterior and posterior lobes. The middle lobe of M3 is proportionately larger than that of *A. chucalensis,* and thus (unlike in *A. chucalensis*) this lobe remains unenclosed by the anterior and posterior lobes. A small but distinct invagination of enamel occurs on the lingual face of the posterior lobe; greater wear would presumably obliterate this structure. The posterior face of M3 bears a slight indentation near its center, isolating a posteriorly directed extension of the ectoloph known as the "fourth lobe" (Francis, 1965).

The degree of cheek tooth imbrication in *A. paucidens* is 1.16. The enamel is thinnest along the anterior and posterior faces of the cheek teeth, causing the occlusal surfaces of these teeth to join with wear. Almost no enamel is visible on the posterior face of M3. The cheek teeth are covered by moderate amounts of cementum. This cementum fills the lingual invaginations of enamel on the molars (that demarcate the three lobes) and is especially thick along the lingual face of M3 (much thicker than the enamel of the middle lobe). The hypselodont nature of the cheek teeth is visible in left M3 and right M1 of the holotype.

The dimensions of M1 of the holotype of *A. paucidens* are similar to those of *Microtypotherium choquecotense* (see below), the smallest mesotheriine known until now (Villarroel, 1974b). The second and third upper molars are significantly shorter in *A. paucidens* than in *Microtypotherium,* resulting in a shorter molar row overall. In size, *A. paucidens* closely matches most specimens assigned to "*Plesiotypotherium* sp." by Oiso (1991).

Several partial lower dentitions are referred to *A. paucidens* based on their relatively longer and narrower cheek teeth (as compared to the holotype of *A. chucalensis,* SGOPV 4100, an associated skull and mandibles). The best preserved of these is SGOPV 4101, a partial mandible and symphysis with complete right dentition plus left i1–2 (Fig. 8B). The symphysis, as in other me-

sotheriines, is solid and completely fused; there is no evidence of a suture. Its labial surface is smoothly rounded, joining the external surfaces of the mandibles. The lingual (dorsal) surface is strongly excavated, forming a long, concave spout flanked by the second lower incisors. This spout appears to be proportionately narrower and deeper than that of *E. lehmannnitschei*. The right dentary is approximately 27 mm high at the level of p4 and 35 mm high at the posterior end of m3. A wide, shallow, slightly roughened groove runs along the lingual surface of the right dentary. At the posterior margin of m3, this groove is positioned about midway between the superior and inferior surfaces of the ramus; its anterior end lies near the base of the horizontal ramus at the level of p4. No mandibular foramen is observed, likely because of incomplete preservation of the specimen. A mental foramen occurs on the external surface of the right dentary, just anterior to p4, at a level slightly higher than the dorsoventral midpoint of the horizontal ramus. It lies almost directly lateral to the base of i2.

The first lower incisor has a gently convex labial face and more strongly convex lingual face. Enamel covers the external surface of the tooth but is completely absent from the occlusal surface. The occlusal surface is gently concave, with the points of highest relief being the two labial corners of the tooth. In mesial view, the tooth is gently curved and procumbent, nearly aligned with the anterior surface of the mandibular symphysis. The second lower incisor is significantly smaller than the first, though not as proportionately reduced as in later-diverging mesotheriines. It is peglike in overall form. While the long axis of i1 runs nearly perpendicular to the sagittal plane, that of i2 is parasagittal. The most pronounced wear occurs on a surface approximately perpendicular to the tooth's vertical axis. Additional wear occurs on the posterior face of the tooth. The left i2 is visible in its entirety; it is approximately 25 mm long and has an open base. A small amount of cementum covers portions of all the incisors. The diastema separating i2 from p4 on the right side is incompletely preserved but was likely approximately 15 mm long.

The lower cheek teeth resemble those of other mesotheriines. The sole lower premolar has a small trigonid and a larger talonid. The dentine of the occlusal surface is fully confluent between the trigonid and talonid; no fossettes or sulci are present. The occlusal surface of the talonid is not worn completely perpendicular to the vertical axis

of the tooth but rather slopes to a low point at the posterior end of the labial side. The first and second lower molars are roughly the shape of a figure eight; the trigonid and the talonid are both rounded and are separated by a deep labial sulcus oriented slightly posterolingually. The second molar is slightly larger than the first. In both molars a very slight sulcus is present on the posterior end of the lingual face. The trigonid of m3 is similar in size and shape to that of m2, but the talonid is elongate with a pointed posterior end, typical of mesotheriines. A moderately pronounced sulcus is present on the lingual face of the talonid at approximately the midpoint, and a little-pronounced sulcus is present about halfway between the midpoint and the posterior edge of the tooth. The posterior end of m3 is visible in its entirety; the tooth is 31 mm high, and its "root" is completely open. Occlusal relief is highest on the molars where the deep labial sulcus divides the trigonid from the talonid (being formed of more resistant enamel) and the dentine surface of the talonid is the lowest. All cheek teeth are covered by a moderate amount of cementum.

COMMENTS—The most unusual characteristic of *A. paucidens* is its single upper premolar (all other mesotheriines having two). Although large cracks are present in the rostrum immediately anterior of this tooth in the holotype, evidence for the lack of an alveolus for an additional premolar is persuasive; the specimen was recovered as three separate pieces (subsequently glued together), permitting a thorough examination of the region immediately anterior of the preserved cheek teeth. The absence of a second premolar is clearly not a preservational artifact. The single premolar in *A. paucidens* is assumed to be P4, but the possibility of another homology cannot be excluded. In lateral view, the premolar is not implanted parallel to the anterior face of M1, as P4 is in other mesotheriines, but rather approaches it at an angle of ~15°; a small portion of the maxilla (lacking an alveolus) is present between the bases of these teeth. This space suggests that the single large premolar may represent an enlarged P3 that presently fills all or most of the space formerly occupied by both P3 and P4 (no concomitant reduction in the number of lower cheek teeth seems to have occurred). While the loss of a cheek tooth in this position would be an unusual occurrence among mammals, mesotheriines are already peculiar in having three deciduous premolars that are replaced by only two permanent premolars. These permanent premolars are conventionally re-

TABLE 3. Development of suborbital fossa and size of infraorbital foramen in selected mesotheriines. Relative size = cross-sectional area of infraorbital foramen (estimated as an ellipse)/M1 occlusal area (estimated as a rectangle). Holotype specimens are denoted with an asterisk (*) next to the specimen number.

Taxon	Specimen	Suborbital fossa	Infraorbital foramen (mm)	M1 size (mm)	Relative size
Alitypotherium paucidens	SGOPV 4038*	shallow	10.5 × 5.5	12.5 × 8.6	0.42
Eutypotherium chico	SGOPV 5157*	shallow	4.0 × 3.5	9.5 × 6.4	0.18
Eutypotherium lehmannnitschei	MLP 12-1701*	shallow	7.5 × 5.4	14.6 × 10.0	0.22
Eutypotherium superans	MACN 11079*	shallow	5.5 × 4.1	14.1 × 10.0	0.13
Caragua New Taxon	SGOPV 4004*	shallow	6.5 × 4.9	16.5 × 10.0	0.15
Typotheriopsis silveyrai	MLP 36-XI-10-2*	deep	6.6 × 5.7	16.9 × 11.4	0.15
Typotheriopsis sp.	FMNH P14477	deep	7.5 × 6.2	22.5 × 14.5	0.11
?*Pseudotypotherium* sp.	MACN 8010	deep	14.2 × 12.4	23.8 × 11.0	0.53
?*Pseudotypotherium* sp.	MACN 1111	deep	12.2 × 7.7	19.2 × 10.5	0.37
Mesotherium cristatum	MACN 2036	absent	3.9 × 3.0	21.8 × 9.8	0.04
Mesotherium pachygnathum	MACN 1665	absent?	9.4 × 5.8	24.4 × 11.4	0.15
Mesotherium "*augustirostrum*"	MACN 6040*	absent	5.1 × 3.5	23.6 × 11.1	0.05

garded as P3–4, but in the absence of ontogenetic data with which to definitively establish homology, they could be P2–3 or even P2 and P4. Regardless of their identity, at some time during mesotheriine evolution, two permanent premolars came to fill the positions previously occupied by three permanent premolars (as suggested by the presence of three deciduous precursors). Perhaps the single premolar in *A. paucidens* represents the end stage of this process: a single, enlarged permanent premolar filling the position once occupied by three. No examples of the deciduous upper dentition of *A. paucidens* are currently known to establish the actual number of deciduous premolars in this taxon.

Previous workers have noted a close association between the development of the suborbital fossa and the size of the infraorbital foramen. Francis (1965:12) stated that "la presencia de foseta sub-orbitaria se asocia siempre a un agujero infra-orbitario grande; la ausencia a uno pequeño." He hypothesized that the presence of a gland (located in the suborbital fossa) that emptied its contents via the infraorbital foramen might explain the observed association between the two. In their analysis of mesotheriine relationships, Cerdeño and Montalvo (2001) included the suborbital fossa and infraorbital foramen as a single character (#6) with three states: fossa absent and foramen very small (0), fossa hinted at and foramen small (1), and fossa developed and foramen large (2). A more detailed examination of distributions of the fossa and foramen suggests that the relationship between the development of the suborbital fossa and the size of the infraorbital foramen might not be so straightforward (Table 3).

Relative to body size, the infraorbital foramen in *A. paucidens* is among the largest seen in mesotheriines, yet the suborbital fossa is only moderately developed. Conversely, *Typotheriopsis* has a relatively small infraorbital foramen, but it exhibits a well-developed suborbital fossa. A general pattern does seem to exist, however, in that the infraorbital foramen is relatively smallest in *Mesotherium* (which completely lacks a suborbital fossa), largest in *Pseudotypotherium* (which has a well-developed suborbital fossa), and intermediate in most other taxa. Since *Mesotherium* includes the largest mesotheriines, however, the relatively small size of its infraorbital foramen may result merely from allometric relationships. The lack of an obvious taxonomic pattern in these characters may be the result of intraspecific variability in one or both of these structures and/or subjective assessment of the degree of development of the suborbital fossa (which is difficult to quantify). Since the association between changes in the infraorbital foramen and the suborbital fossa (character #6) is unclear, only the development of the suborbital fossa has been included in the phylogenetic analysis below.

Two of the mesotheriines from Chucal, *Alitypotherium paucidens* and *Alitypotherium chucalensis* (below), form a clade diagnosed by the shared presence of a single labial sulcus on the premolar ectolophs (character #27, state #1) and the presence of upper first incisors that are subtriangular, pointed distally, with two lingual sulci (character #16, state #4; see phylogenetic analysis below). The two species differ slightly in size—by about 10% based on dental measurements—but both are among the smallest mesotheriines

Table 4. Measurements for specimens of *Altitypotherium chucalensis*.

Upper dentition	I1		P3		P4		M1		M2		M3	
	L	W	L	W	L	W	L	W	L	W	L	W
SGOPV 4100 (R)			(4.9)	(5.9)	6.3	7.3	10.4	8.6	12.9	8.5	13.1	7.6
SGOPV 4100 (L)			(4.5)	(6.0)	5.9	—	10.4	8.9	—	8.4	13.3	7.7
SGOPV 5148 (R)	12.4	6.6										
SGOPV 5172 (R)	(12.5)	6.8										
SGOPV 5148 (L)	11.9	6.5										
SGOPV 4033 (R)			5.5	5.8	6.8	7.6	—	—	—	(8.8)	—	(7.3)
SGOPV 4033 (L)			—	—	6.4	—						
SGOPV 5146 (R)			6.1	5.3								
SGOPV 5147 (L)			5.4	6.1								
SGOPV 5056 (R)			5.1	5.4	5.9	7.3						
SGOPV 5113 (L)					5.9	6.9						
SGOPV 5098 (R)									12.3	8.5		

Lower dentition	i1		i2		p4		m1		m2		m3	
	L	W	L	W	L	W	L	W	L	W	L	W
SGOPV 4042 (R)	6.9	4.6			7.0	4.7	10.3	6.2	—	6.1		
SGOPV 4042 (L)	(6.8)	(4.3)	5.5	3.7								
SGOPV 4110 (R)	6.7	4.3	5.0	3.4								
SGOPV 4110 (L)	6.8	4.4	5.0	3.4	7.2	4.3	10.0	5.8	—	(5.7)		
SGOPV 5179 (R)	6.8	—										
SGOPV 5109 (R)	6.2	4.0										
SGOPV 5110 (L)	6.0	4.0										
SGOPV 5178 (R)			5.2	3.4								
SGOPV 5084 (R)					(6.5)	(4.2)	10.0	5.9	10.7	5.7		
SGOPV 4100 (R)					6.9	4.5	9.7	6.1	10.9	6.1	13.8	5.7
SGOPV 4100 (L)					7.2	4.5	9.7	6.0	11.4	6.1		
SGOPV 4103 (R)					(6.1)	(4.0)	9.5	5.6	10.8	5.7		
SGOPV 5048 (R)							9.6	6.0				
SGOPV 5170 (L)							10.4	6.3				
SGOPV 5089 (R)									11.5	6.1		
SGOPV 5090 (R)									12.1	5.8		
SGOPV 5085 (L)									10.8	6.0		
SGOPV 5126 (R)									11.7	5.9		
SGOPV 5128 (R)									11.6	5.9		
SGOPV 5101 (L)									11.0	6.1		
SGOPV 5052 (L)									11.1	5.8		
SGOPV 5127 (L)									11.5	6.0		
SGOPV 4032 (R)											15.8	5.4
SGOPV 5083 (R)											(13.5)	(5.5)
SGOPV 5119 (L)											16.2	5.4
SGOPV 4107 (R)											(15.5)	5.5

known. Because the presence of these shared, derived characters suggests these two species share a unique common ancestry, we elect to provide them with the same first half of a bipartite species name (*praenomen,* sensu Griffiths, 1976).

Altitypotherium chucalensis, species novum
(Figures 9–11, Table 4)

Holotype—SGOPV 4100, partial skull and mandibles lacking upper incisors, portions of right P3 and left P3–4, and portions of lower incisors (Figs. 9, 10).

Hypodigm—SGOPV 5148, right I1; SGOPV 5172, right I1; SGOPV 5143 left I1; SGOPV 4033, fragmentary skull with portions of many teeth, right P3–4 well preserved, left M1–3 partially preserved; SGOPV 5146, right P3; SGOPV 5147, left P3; SGOPV 5056, partial right maxilla with P3–4; SGOPV 5113, partial left P4; SGOPV 5098, partial right M2; SGOPV 4042, partial skeleton including right mandible and symphysis (with left i2, portions of left and right i1, right p4–m1 and bases of m2–3) right femur, partial left
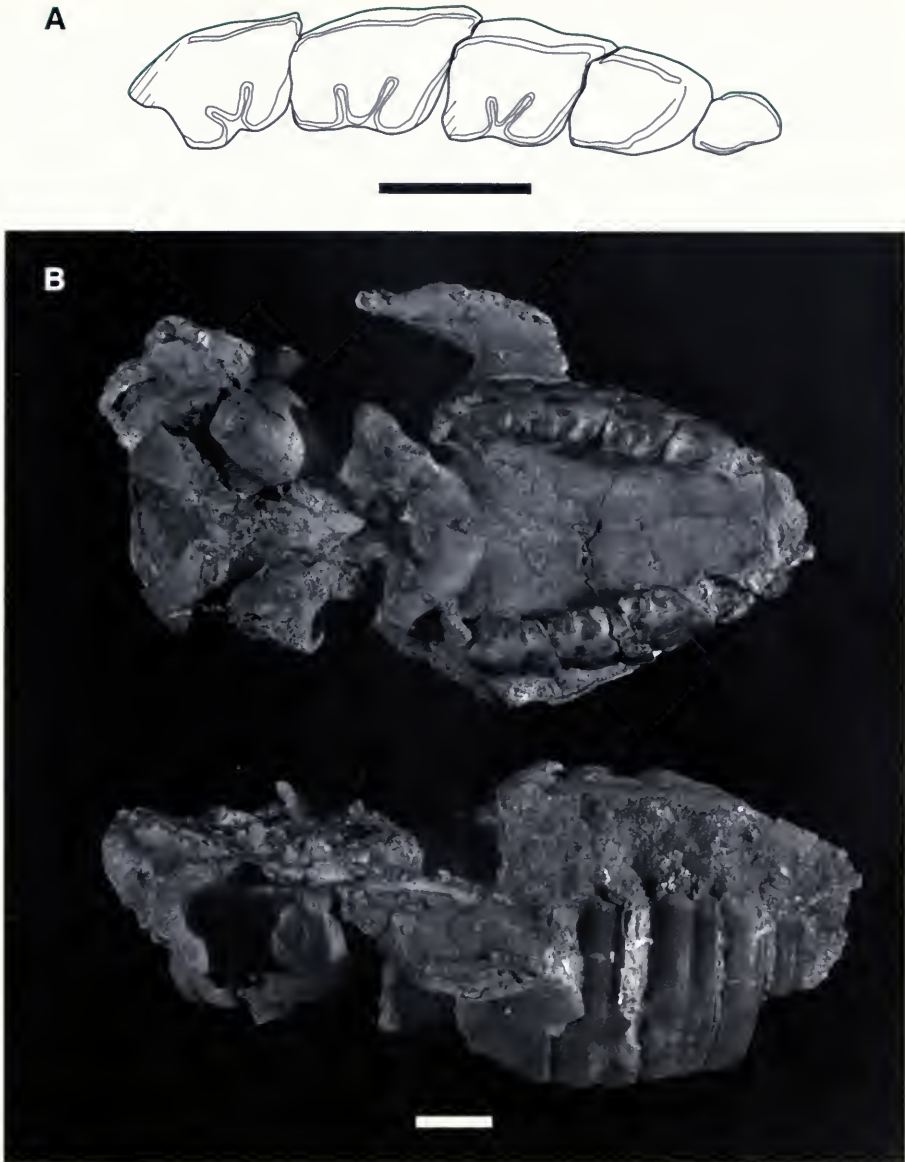
FIG. 9. Upper dentition of holotype of *Altitypotherium chucalensis,* SGOPV 4100, a partial skull with portions of all premolars and complete molars. **A.** Line drawing of occlusal morphology of right P3–M3. **B.** Skull in right lateral (above) and occlusal (below) views. Scale bars = 1 cm.

innominate including acetabulum, proximal and distal portions of left femur, distal half of left tibia, partial ?left fibula, left ulna and radius (lacking distal portion of each), proximal portion of right radius, atlas and axis (articulated) plus various other vertebrae; SGOPV 4110, partial left mandible and symphysis with i1–2 on both sides, left p4–m1, partial left m2, and partial left M1; SGOPV 5179, right i1; SGOPV 5109 right i1;

SGOPV 5110, left i1; SGOPV 5178, right i2; SGOPV 5084, partial right mandible with base of p4, m1–2; SGOPV 4103, partial right mandible with partial p4, m1–2; SGOPV 5048, partial right m1; SGOPV 5170, left m1; SGOPV 5089, right m2; SGOPV 5090, right m2; SGOPV 5085, partial left mandible with base of m2; SGOPV 5126, partial right m2; SGOPV 5128, partial right m2; SGOPV 5101, left m2; SGOPV 5052, left m2;

FIG. 10. Portions of lower dentition of *Altitypotherium chucalensis,* SGOPV 4100. **A.** Posterior left mandible and ascending ramus in lateral view (pictured as right). **B.** Partial right mandible with p4–m3 in occlusal view (pictured as left). Scale bars = 1 cm.
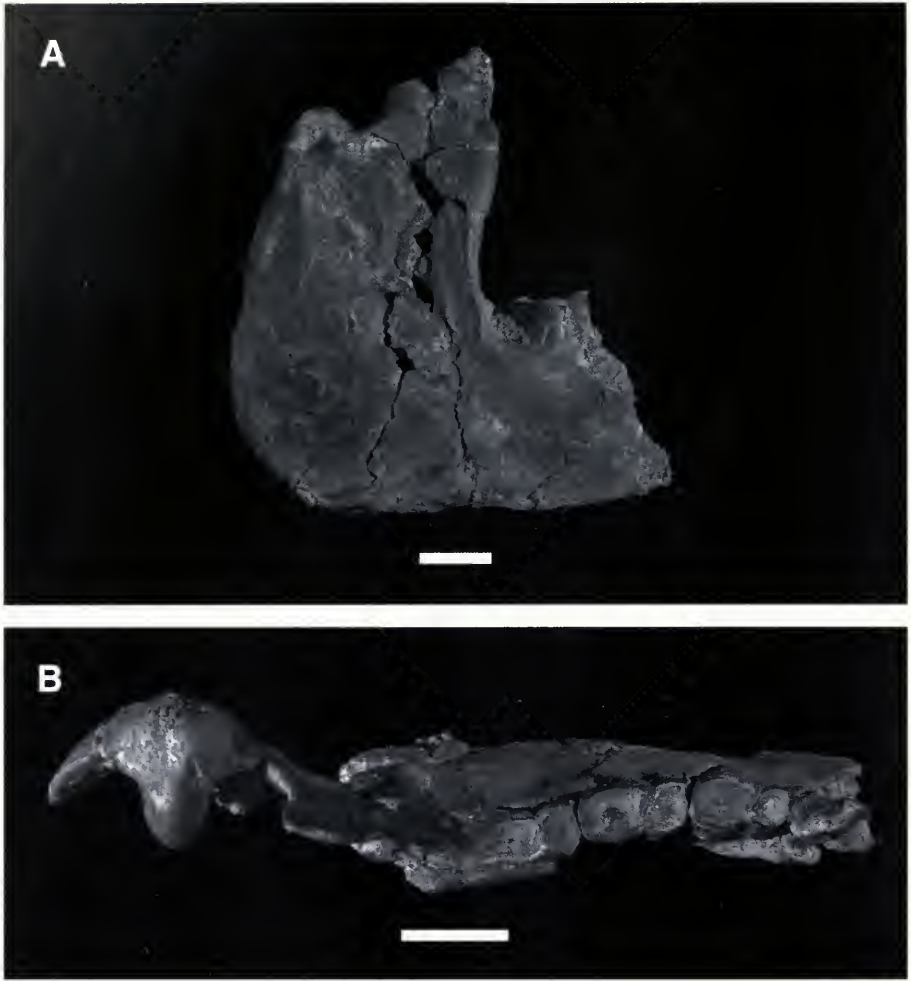
SGOPV 5127, partial left m2; SGOPV 4032, right m3; SGOPV 5083, partial right mandible with base of m3; SGOPV 5119, left m3; SGOPV 4107, partial right m3.

QUESTIONABLY REFERRED SPECIMENS—SGOPV 5138, partial right p4; SGOPV 5173, partial right p4.

TYPE LOCALITY—Loc. C-ALT-01-19; Chucal Formation (Member W4 of Charrier et al., 2002); west flank of Chucal Anticline.

AGE AND DISTRIBUTION—Chucal Formation, northern Chile, late early Miocene age, Santacrucian SALMA.

ETYMOLOGY—*Alti,* in reference to the Altiplano, the high plateau of northern Chile and neighboring Bolivia and Peru, where the referred spec-

imens were collected and *typotherium,* in reference to the familiar root commonly used in mesotheriine taxon names; *chucalensis,* in reference to Chucal, the area in which the holotype and all referred specimens were discovered.

DIAGNOSIS—A mesotheriine differing from all other described mesotheriines in having an unelongate M1 (length/width ≤1.30 in *A. chucalensis,* >1.30 in all other mesotheriines).

Differs from *Microtypotherium* in presence of deep, narrow postpalatal notch that extends to the level of M3 (does not reach M3 in *Microtypotherium*); presence of subtriangular I1 that is pointed distally, with two lingual sulci (a single mesial sulcus is present in *Microtypotherium*); presence of one labial sulcus on premolar ecto-

lophs (two sulci present in *Microtypotherium*); and absence of shortened m2 (length/width between 1.60 and 2.30 in *Altitypotherium*, <1.6 in *Microtypotherium*).

Differs from *Eutypotherium* in the root of zygomatic arch being directed perpendicular to M1 (posteriorly directed from the level of M1 or M2 in *Eutypotherium*); presence of deep, narrow postpalatal notch that extends to the level of M3 (wide and shallow in *Eutypotherium*); presence of subtriangular I1 that is pointed distally, with two lingual sulci (wide and rounded with lingual sulcus in *Eutypotherium*); presence of rounded i1 with little or no lingual sulcus (subtriangular with smooth sulcus in *Eutypotherium*); presence of one labial sulcus on premolar ectolophs (two sulci present in *Eutypotherium*); absence of extensive lingual exposure of M1 middle lobe; and smaller size (based on dental measurements, approximately 20% smaller than *Eutypotherium lehmannnitschei*).

Differs from *Plesiotypotherium* in posteriorly diverging upper and lower diastemata (parallel in *Plesiotypotherium*); absence of well-developed suborbital fossa; presence of deep, narrow postpalatal notch that extends to the level of M3 (wide and shallow in *Plesiotypotherium*); subtriangular I1 that is pointed distally, with two lingual sulci (wide and rounded with lingual sulcus in *Plesiotypotherium*); absence of enlarged middle lobe of M3 (surrounded by other lobes in *A. chucalensis*); presence of rounded i1 with little or no lingual sulcus (subtriangular with smooth sulcus in *Plesiotypotherium*); presence of one labial sulcus on premolar ectolophs (two sulci present in *Plesiotypotherium*); presence of M1 middle lobe with lingually convergent anterior and posterior sides (subparallel in *Plesiotypotherium*); absence of extensive lingual exposure of M1 middle lobe; and smaller size (based on dental measurements, 30% smaller than *Plesiotypotherium achirense*).

Differs from Caragua New Taxon (Flynn et al., in press) in presence of posteriorly divergent upper and lower diastemata (parallel in Caragua New Taxon); lesser degree of molar imbrication (<1.25 in *Altitypotherium*, between 1.25 and 1.50 in Caragua New Taxon); presence of subtriangular I1 that is pointed distally, with two lingual sulci (wide and rounded with lingual sulcus in Caragua New Taxon); presence of short, subtriangular P4 without central fossette (P4 bilobed with short and poorly defined lingual plication in Caragua New Taxon); relatively smaller i1 (i1/i2 <1.50 in *Altitypotherium*, between 1.50 and 2.00 in Caragua

New Taxon); presence of rounded i1 with little or no lingual sulcus (subtriangular with smooth sulcus in Caragua New Taxon); presence of one labial sulcus on premolar ectolophs (two sulci present in Caragua New Taxon); presence of M1 middle lobe with lingually convergent anterior and posterior sides (subparallel in Caragua New Taxon); absence of extensive lingual exposure of M1 middle lobe; and smaller size (based on dental measurements, approximately 20% smaller than Caragua New Taxon).

Differs from *Typotheriopsis* in posterolaterally divergent upper and lower diastemata (parallel in *Typotheriopsis*); absence of well-developed suborbital fossa; presence of deep, narrow postpalatal notch that extends to the level of M3 (does not reach M3 in *Typotheriopsis*); presence of subtriangular I1 that is pointed distally, with two lingual sulci (wide and rounded with lingual sulcus in *Typotheriopsis*); relatively smaller i1 (i1/i2 <1.50 in *Altitypotherium*, between 1.50 and 3.00 in *Typotheriopsis*); presence of rounded i1 with little or no lingual sulcus (subtriangular with smooth sulcus in *Typotheriopsis*); presence of M1 middle lobe with lingually convergent anterior and posterior sides (subparallel in *Typotheriopsis*); absence of extensive lingual exposure of M1 middle lobe; and smaller size (based on dental measurements, approximately 30% smaller than *Typotheriopsis chasicoensis*).

Differs from *Pseudotypotherium* in presence of posterolaterally divergent upper and lower diastemata (parallel in *Pseudotypotherium*); absence of well-developed suborbital fossa; presence of deep, narrow postpalatal notch that extends to the level of M3 (does not reach M3 in *Pseudotypotherium*); lesser degree of molar imbrication (<1.25 in *Altitypotherium*, >1.50 in *Pseudotypotherium*); presence of short, subtriangular P4 without central fossette (P4 is bilobed in *Pseudotypotherium*); relatively smaller i1 (i1/i2 <1.50 in *Altitypotherium*, between 2.00 and 3.00 in *Pseudotypotherium*); presence of rounded i1 with little or no lingual sulcus (trapezoidal with well demarcated lingual sulcus in *Pseudotypotherium*); presence of one labial sulcus on premolar ectolophs (two sulci present in *Pseudotypotherium*); absence of elongate P4 (length/width <1.50 in *Altitypotherium*, ≥1.50 in *Pseudotypotherium*); absence of elongate M1 (length/width <1.75 in *Altitypotherium*, ≥1.75 in *Pseudotypotherium*); presence of M1 middle lobe with lingually convergent anterior and posterior sides (subparallel in *Pseudotypotherium*); absence of extensive lingual exposure of M1 middle lobe;

absence of elongate m2 (length/width between 1.60 and 2.30 in *Altitypotherium*, >2.30 in *Pseudotypotherium*); and smaller size (based on dental measurements, approximately 25% smaller than *Pseudotypotherium exiguum*).

Differs from *Mesotherium* in posterolaterally divergent upper and lower diastemata (parallel to strongly convergent in *Mesotherium*); presence of poorly defined suborbital fossa (absent in *Mesotherium*); lesser degree of molar imbrication (<1.25 in *Altitypotherium*, >1.50 in *Mesotherium*); presence of subtriangular I1 that is pointed distally, with two lingual sulci (wide and rounded with lingual sulcus or wide and compressed labiolingually with two lingual sulci in *Mesotherium*); presence of short, subtriangular P4 without central fossette (P4 is persistently bilobed in *Mesotherium*); absence of enlarged middle lobe of M3 (surrounded by other lobes in *A. chucalensis*); relatively smaller i1 (i1/i2 <1.50 in *Altitypotherium*, >3.00 in *Mesotherium*); presence of rounded i1 with little or no lingual sulcus (trapezoidal with well-demarcated lingual sulcus or elliptical with smooth sulcus in *Mesotherium*); presence of one labial sulcus on premolar ectolophs (two sulci present in *Mesotherium*); absence of elongate P4 (length/width <1.50 in *Altitypotherium*, ≥1.50 in *Mesotherium*); absence of elongate M1 (length/width <1.75 in *Altitypotherium*, ≥1.75 in *Mesotherium*); presence of M1 middle lobe with lingually convergent anterior and posterior sides (lingually divergent in *Mesotherium*); absence of extensive lingual exposure of M1 middle lobe; absence of elongate m2 (length/width between 1.60 and 2.30 in *Altitypotherium*, >2.30 in *Mesotherium*); and smaller size (based on dental measurements, approximately 20% smaller than *Mesotherium maendrum* and about half the size of *Mesotherium pachygnathum*).

Differs from *A. paucidens* in presence of P3, absence of elongate M1 (length/width ≤1.3 in *A. chucalensis*, >1.3 in *A. paucidens*), presence of M3 with middle lobe surrounded by other two lobes, presence of wider lower molars (widths ≥7.3 mm in *A. chucalensis*; ≤6.7 mm in *A. paucidens*), absence of elongate m3 (similar in length to m2 in *A. chucalensis*, 15–20% longer than m2 in *A. paucidens*), and slightly smaller size (based on dental measurements, *A. chucalensis* is approximately 10% smaller than *A. paucidens*).

DESCRIPTION—*A. chucalensis* is the only mesotheriine species from Chucal for which the holotype includes associated upper and lower dentitions (SGOPV 4100, Figs. 9, 10). Additionally,

much of the palatal and basicranial anatomy of this taxon is preserved. The palate is arched, but not to the degree exhibited by *A. paucidens*. The postpalatal notches are narrow and deep, extending to the posterior edge of M3. The notch is fully prepared on the right side, demonstrating a rounded morphology more resembling a foramen than a notch. The general structure of the ear region of mesotheriines has been described elsewhere (Patterson, 1934a, 1936) and will not be repeated here, although this specimen should prove useful for future comparative studies within the Mesotheriidae and other typotheres.

The most obvious difference in the dentition between this taxon and *A. paucidens* is the presence of two premolars in *A. chucalensis* (interpreted as P3 and P4, but see discussion above). This is a primitive character state that *A. chucalensis* shares with all previously described mesotheriines. The possibility that these teeth represent deciduous premolars instead of permanent ones can be ruled out; the labial faces of the two teeth on the holotype are exposed to their bases (approximately 25 mm in P4), confirming their hypselodont condition and the lack of overlying replacement teeth above. They also do not demonstrate the occlusal morphology typical of mesotheriine deciduous premolars teeth (see Francis, 1965), instead exhibiting the typically adult morphology of featureless occlusal surfaces that are subtriangular in shape.

In the holotype and one of the referred specimens (SGOPV 4033, a fragmentary palate), P3 and P4 are closely appressed to each other and to M1. In another specimen (SGOPV 5056, a partial right maxilla with P3–4), there is a small (~2 mm) diastema between them, although both are implanted at approximately the same angle. A single sulcus is present near the posterior end of the labial face of P3, whereas P4 exhibits a sulcus situated near the anterior end of the labial face as in *A. paucidens* (and *Typotheriopsis*). The P3 is smaller than P4, and neither exhibits any sign of a fossette or lingual plication. In SGOPV 5056, the entire posterior face of P4 is visible, demonstrating the near total lack of enamel on this surface. On the anterior face of this tooth, enamel is absent only from a small strip along the labial edge. The same is true for P3.

A. chucalensis is further distinguished from *A. paucidens* by the absence of an elongate M1, an ancestral character state shared only with *Trachytherus* among mesotheriids. Unlike *Trachytherus*, however, the middle lobe of M1 in *A. chuca-*

lensis appears to persist throughout the tooth's wear and does not become isolated as a fossette (based on examinations of lingual faces and bases of isolated teeth). Like *Microtypotherium* and the other Chucal mesotheriines, the anterior and posterior sides of the middle lobe of M1 in *A. chucalensis* are lingually convergent, making the lobe triangular. This middle lobe is relatively smaller than in any of these other taxa, completely surrounded by the subequal anterior and posterior lobes. The second upper molar resembles M1, except that the parastyle is more pronounced and the middle lobe slightly larger. Imbrication of the upper molars is slight, as in all the other mesotheriines from Chucal and a few additional taxa (see Table 7). The third upper molar most closely resembles that of *Microtypotherium*, with a small middle lobe surrounded by the other two. No lingual sulcus is evident on the posterior lobe. A fourth lobe is present in M3 but is slightly shorter and broader than that of *A. paucidens*. Enamel is absent from the posterior face. All upper cheek teeth are covered by a moderate amount of cementum, which is thickest lingually as in *A. paucidens*. The degree of cheek tooth imbrication in *A. chucalensis* is 1.22.

The anterior lower dentition of *A. chucalensis* is best exhibited by SGOPV 4110, a partial left mandible with left and right i1–2, left p4–m1, partial left m2, and partial left M1. These teeth are very similar to the corresponding teeth of *A. paucidens*. The symphyseal region is unknown.

The cheek teeth and the posterior portion of the mandible are preserved in the holotype (Fig. 10). The horizontal ramus is less robust than that of *A. paucidens*; it measures approximately 18.5 mm deep between p4 and m1 and 30 mm deep at the posterior face of m3. On the left side, it appears that a mental foramen is present but incompletely preserved; its position is similar to that of *A. paucidens*. The anterior edge of the ascending ramus creates an angle of slightly less than 90° with the horizontal ramus and ends in a broad coronoid process. At its vertical midpoint, the ascending ramus measures approximately 35 mm from its anterior to its posterior edge. The coronoid process rises approximately 13.5 mm above the level of the articular condyle and is nearly 20 mm long. The articular condyle is broad, smooth, and ~14 mm wide. The angle of the mandible is large, but the bone comprising much of it is quite thin. A mandibular foramen is present along the lingual side of the dentary, where the horizontal ramus joins the ascending ramus. It measures approxi-

mately 7 × 4 mm. The posterior part of the inferior edge of the angle is inflected medially. Slightly anterior to this, a pronounced shelf is present on the lateral surface. The mandible's lateral surface is fairly smooth, but the medial surface of the angle and ascending ramus exhibits a series of well-pronounced ridges, suggesting that a well-developed medial pterygoid muscle inserted in this area.

The lower cheek teeth are similar to those of *A. paucidens*, except for their relatively smaller size. Additionally, the talonid of m3 is proportionately shorter and narrower.

A partial skeleton and other postcranial specimens are referred to *A. chucalensis* (SGOPV 4042). These will be described in detail and compared to other mesotheriid postcrania elsewhere.

COMMENTS—Although roughly similar in size to *A. paucidens, A. chucalensis* is clearly distinguished from the former species by the suite of character states presented in the diagnosis.

Eotypotherium chico, species novum
(Figures 11–13, Table 5)

HOLOTYPE—SGOPV 5157, partial right maxilla and zygomatic arch with P3–M3 (Fig. 11).

HYPODIGM—SGOPV 5108, partial right I1; SGOPV 5074, partial left maxilla with P3–M1 and partial M2 (Fig. 12A); SGOPV 5156, partial palate with right P3–M3 (M2 damaged labially; Fig. 12B); SGOPV 5124, little-worn left maxillary fragment with M1 and partial P4, M2; SGOPV 5132, left M1/2; SGOPV 5175 right M1/2; SGOPV 5095, partial left M1/2; SGOPV 5134, partial left M1/2; SGOPV 5133, left M3; SGOPV 4071, symphysis with portions of left and right i1–2; SGOPV 5050, right m1; SGOPV 5129, right mandibular fragment with partial m1; SGOPV 5159, partial right m1/2; SGOPV 5160, partial right m1/2; SGOPV 5158, partial left mandible with m2–3 (Fig. 13); SGOPV 5086, partial right mandible with bases of m2–3; SGOPV 5093, right m3.

TYPE LOCALITY—Loc. C-ALT-01-12; Chucal Formation (Member E3 of Charrier et al., 2002); east flank of Chucal Anticline.

AGE AND DISTRIBUTION—Chucal Formation, northern Chile, late early Miocene age, Santacrucian SALMA.

ETYMOLOGY—*Eo*, Greek for "dawn," in reference to the relative antiquity of this species with respect to previously known mesotheriines, and

TABLE 5. Measurements for specimens of *Eotypotherium chico*.

Upper dentition	I1		P3		P4		M1		M2		M3		M1/2	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W
SGOPV 5157 (R)			4.4	4.0	5.2	5.3	9.5	6.4	9.6	6.5	9.8	5.8		
SGOPV 5108 (R)	(6.7)	4.0												
SGOPV 5074 (L)			4.2	4.8	5.8	5.6	8.2	5.9	—	(6.6)				
SGOPV 5156 (R)			3.1	3.7	4.9	5.3	8.0	(6.2)	(9.5)	—	9.6	5.4		
SGOPV 5124 (L)					—	—	8.3	3.9	—	—				
SGOPV 5132 (L)													(8.5)	6.2
SGOPV 5175 (R)													9.4	5.5
SGOPV 5095 (L)													(9.6)	(6.7)
SGOPV 5134 (L)													(7.5)	(5.3)
SGOPV 5133 (L)											11.5	6.4		

Lower dentition	i1		i2		m1		m2		m3		m1/2	
	L	W	L	W	L	W	L	W	L	W	L	W
SGOPV 4071 (R)	4.3	3.0	3.5	(1.5)								
SGOPV 4071 (L)	4.4	2.7	3.2	1.8								
SGOPV 5050 (R)					9.6	6.0						
SGOPV 5129 (R)					8.7	4.9						
SGOPV 5159 (R)											8.9	4.6
SGOPV 5160 (R)											8.5	4.7
SGOPV 5158 (L)							8.9	4.7	11.0	3.8		
SGOPV 5086 (R)							(9.0)	4.7	7.3	3.4		
SGOPV 5093 (R)									8.0	3.6		

typotherium, a common suffix for mesotheriines; *chico,* Spanish for "little," referring to the small size of the species.

DIAGNOSIS—A mesotheriine differing from *Altitypotherium paucidens* (above) in absence of well-developed zygomatic plate; presence of wide postpalatal notch not reaching the level of M3 (narrow and reaching the level of M3 in *A. paucidens*); presence of subtriangular I1 that is pointed distally, with mesial sulcus (with two lingual sulci in *A. paucidens*); presence of short, subtriangular P4 with central fossette (fossette absent in *A. paucidens*); absence of enlarged middle lobe of M3 (surrounded by other lobes in *E. chico*); presence of subquadrangular P3 (P3 absent in *A. paucidens*); absence of single labial sulcus on premolar ectolophs; and smaller size (based on dental measurements, approximately 25% smaller).

Differs from *Altitypotherium chucalensis* (above) in absence of well-developed zygomatic plate; presence of wide postpalatal notch not reaching the level of M3 (narrow and reaching the level of M3 in *A. chucalensis*); presence of subtriangular I1 that is pointed distally, with mesial sulcus (with two lingual sulci in *A. chucalensis*); presence of short, subtriangular P4 with central fossette (fossette absent in *A. chucalensis*); presence of subquadrangular P3 (subtriangular in *A.*

chucalensis); absence of single labial sulcus on premolar ectolophs; presence of elongate M1 ($\leq$1.30 in *A. chucalensis,* >1.30 in *Eotypotherium*); and smaller size (based on dental measurements, approximately 20% smaller).

Differs from *Microtypotherium* in absence of well-developed zygomatic plate; presence of wide postpalatal notch not reaching the level of M3 (narrow in *Microtypotherium*); presence of short, subtriangular P4 with central fossette (fossette absent in *Microtypotherium*); presence of subquadrangular P3 (subtriangular in *Microtypotherium*); absence of elongate M1 (length/width $\leq$1.30 in *Eotypotherium,* between 1.30 and 1.75 in *Microtypotherium*); absence of shortened m2 (length/width between 1.60 and 2.30 in *Eotypotherium,* <1.60 in *Microtypotherium*); and smaller size (based on dental measurements, approximately 30% smaller than *Microtypotherium choquecotense*).

Differs from *Eutypotherium* in root of zygomatic arch perpendicular to M1 (posteriorly directed from the level of M1 or M2 in *Eutypotherium*); absence of well-developed zygomatic plate; presence of subtriangular I1 that is pointed distally, with mesial sulcus (wide, rounded, with lingual sulcus in *Eutypotherium*); presence of short, subtriangular P4 with central fossette (fos-
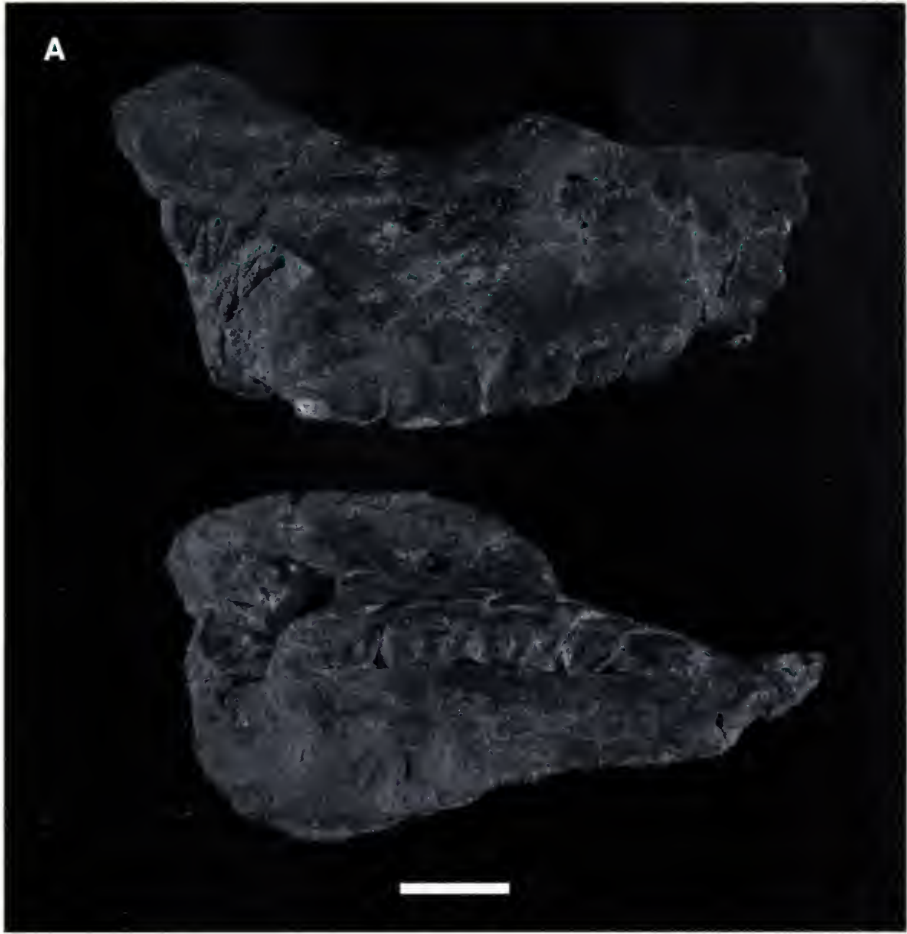
FIG. 11. Holotype of *Eotypotherium chico*, SGOPV 5157, a partial right maxilla and zygomatic arch with P3-M3. **A.** Labial (above) and occlusal (below) views. **B.** Line drawing of occlusal morphology. Scale bars = 1 cm.

sette absent in *Eutypotherium*, lingual plication sometimes present); presence of i1 that is rounded in cross section with little or no lingual sulcus (subtriangular with smooth sulcus in *Eutypotherium*); presence of subquadrangular P3 (subtriangular in *Eutypotherium*); absence of elongate M1 (length/width ≤1.30 in *Eotypotherium,* between 1.30 and 1.75 in *Eutypotherium*); absence of extensive lingual exposure of M1 middle lobe; and much smaller size (based on dental measure-

ments, approximately 40% smaller than *Eutypotherium lehmannnitschei*).

Differs from *Plesiotypotherium* in absence of well-developed suborbital fossa and large infraorbital foramen; absence of well-developed zygomatic plate; presence of subtriangular I1 that is pointed distally, with mesial sulcus (wide, rounded, with lingual sulcus in *Plesiotypotherium*); presence of short, subtriangular P4 with central fossette (fossette absent in *Plesiotypotherium,* lin-
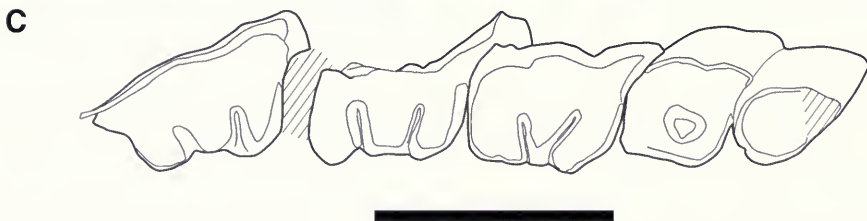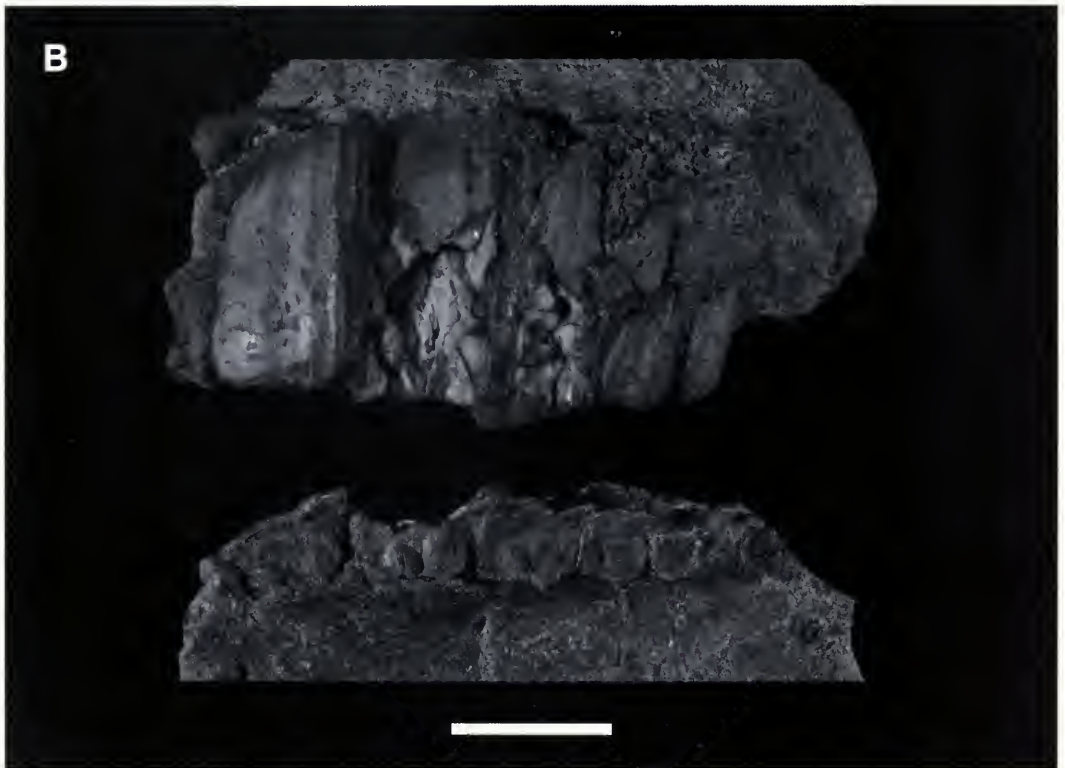
Fig. 12. Upper dentitions referred to *Eotypotherium chico*. **A.** SGOPV 5074, partial left maxilla (pictured as right) with P3–M1 and partial M2 in occlusal view. **B.** SGOPV 5156, a partial palate with right P3–M3 in labial (above) and occlusal (below) views. **C.** Line drawing of occlusal morphology. Scale bars = 1 cm.

FIG. 13. Partial left mandible with m2–3 in occlusal view, SGOPV 5158, referred to *Eotypotherium chico*. Scale bar = 1 cm.

gual plication sometimes present); presence of i1 that is rounded in cross section with little or no lingual sulcus (subtriangular with smooth sulcus in *Plesiotypotherium*); presence of subquadrangular P3 (subtriangular in *Plesiotypotherium*); absence of elongate M1 (length/width ≤1.30 in *Eotypotherium*, between 1.30 and 1.75 in *Plesiotypotherium*); presence of M1 middle lobe with lingually convergent anterior and posterior sides (subparallel in *Plesiotypotherium*); absence of extensive lingual exposure of M1 middle lobe; and much smaller size (based on dental measurements, approximately half the size of *Plesiotypotherium achirense*).

Differs from *Typotheriopsis* in absence of well-developed suborbital fossa and large infraorbital foramen; absence of well-developed zygomatic plate; presence of wide postpalatal notch not reaching the level of M3 (narrow in *Typotheriopsis*); presence of subtriangular I1 that is pointed distally, with mesial sulcus (wide, rounded, with lingual sulcus in *Typotheriopsis*); presence of short, subtriangular P4 with central fossette (fossette absent in *Typotheriopsis*); relatively smaller i1 (i1/i2 <1.50 in *Eotypotherium*, between 1.50 and 3.00 in *Typotheriopsis*); presence of i1 that is rounded in cross section with little or no lingual sulcus (subtriangular with smooth sulcus in *Typotheriopsis*); presence of subquadrangular P3 (subtriangular in *Typotheriopsis*); absence of single labial sulcus on premolar ectolophs; absence of elongate M1 (length/width ≤1.30 in *Eotypotherium*, between 1.30 and 1.75 in *Typotheriopsis*); presence of M1 middle lobe with lingually convergent anterior and posterior sides (subparallel in *Typotheriopsis*); absence of extensive lingual exposure of M1 middle lobe; and much smaller size

(based on dental measurements, approximately half the size of *Typotheriopsis chasicoensis*).

Differs from Caragua New Taxon in presence of wide postpalatal notch not reaching the level of M3 (narrow and reaching the level of M3 in Caragua New Taxon); lesser degree of molar imbrication (<1.25 in *Eotypotherium*, between 1.25 and 1.50 in Caragua New Taxon); presence of subtriangular I1 that is pointed distally, with mesial sulcus (wide, rounded, with lingual sulcus in Caragua New Taxon); presence of short, subtriangular P4 with central fossette (fossette absent in Caragua New Taxon, lingual plication present); relatively smaller i1 (i1/i2 <1.50 in *Eotypotherium*, between 1.50 and 2.00 in Caragua New Taxon); presence of i1 that is rounded in cross section with little or no lingual sulcus (subtriangular with smooth sulcus in Caragua New Taxon); presence of subquadrangular P3 (subtriangular in Caragua New Taxon); absence of elongate M1 (length/width ≤1.30 in *Eotypotherium*, between 1.30 and 1.75 in Caragua New Taxon); presence of M1 middle lobe with lingually convergent anterior and posterior sides (subparallel in Caragua New Taxon); absence of extensive lingual exposure of M1 middle lobe; absence of two lingual sulci on m3 talonid; and much smaller size (based on dental measurements, approximately 40% smaller than Caragua New Taxon).

Differs from *Pseudotypotherium* in absence of well-developed suborbital fossa and large infraorbital foramen; absence of well-developed zygomatic plate; lesser degree of molar imbrication (<1.25 in *Eotypotherium*, >1.50 in *Pseudotypotherium*); presence of short, subtriangular P4 with central fossette (fossette absent and tooth bilobed in *Pseudotypotherium*); presence of M3 with mid-

dle lobe surrounded by the other two (not surrounded in *Pseudotypotherium*); relatively smaller i1 (i1/i2 <1.50 in *Eotypotherium*, between 2.00 and 3.00 in *Pseudotypotherium*); presence of i1 that is rounded in cross section with little or no lingual sulcus (trapezoidal with well-demarcated lingual sulcus in *Pseudotypotherium*); presence of subquadrangular P3 (subtriangular in *Pseudotypotherium*); absence of elongate P4 (length/width <1.50 in *Eotypotherium*, ≥1.50 in *Pseudotypotherium*); absence of elongate M1 (length/width ≤1.30 in *Eotypotherium*, ≥1.75 in *Pseudotypotherium*); presence of M1 middle lobe with lingually convergent anterior and posterior sides (subparallel in *Pseudotypotherium*); absence of extensive lingual exposure of M1 middle lobe; absence of elongate m2 (length/width between 1.60 and 2.30 in *Eotypotherium*, >2.30 in *Pseudotypotherium*); and much smaller size (based on dental measurements, approximately 40% smaller than *Pseudotypotherium exiguum*).

Differs from *Mesotherium* in presence of poorly defined suborbital fossa (absent in *Mesotherium*); absence of well-developed zygomatic plate; presence of wide postpalatal notch not reaching the level of M3 (narrow in *Mesotherium*, sometimes extending to the level of M3); lesser degree of molar imbrication (<1.25 in *Eotypotherium*, >1.50 in *Mesotherium*); presence of subtriangular I1 that is pointed distally, with mesial sulcus (wide, rounded, with lingual sulcus or wide and compressed labiolingually with two lingual sulci in *Mesotherium*); presence of short, subtriangular P4 with central fossette (fossette absent and tooth bilobed in *Mesotherium*); presence of M3 with middle lobe surrounded by the other two (not surrounded in *Mesotherium*); relatively smaller i1 (i1/i2 <1.50 in *Eotypotherium*, >3.00 in *Mesotherium*); presence of i1 that is rounded in cross section with little or no lingual sulcus (trapezoidal with well-demarcated lingual sulcus or elliptical with smooth sulcus in *Mesotherium*); presence of subquadrangular P3 (subtriangular in *Mesotherium*); absence of elongate P4 (length/width <1.50 in *Eotypotherium*, ≥1.50 in *Mesotherium*); absence of elongate M1 (length/width ≤1.30 in *Eotypotherium*, ≥1.75 in *Mesotherium*); presence of M1 middle lobe with lingually convergent anterior and posterior sides (lingually divergent in *Mesotherium*); absence of extensive lingual exposure of M1 middle lobe; absence of elongate m2 (length/width between 1.60 and 2.30 in *Eotypotherium*, >2.30 in *Mesotherium*); and much smaller size (based on dental measurements, approximately 40% smaller than *Mesotherium maendrum*, 60% smaller than *Mesotherium pachygnathum*).

DESCRIPTION—This mesotheriine is much smaller than the other two known from Chucal; indeed, it represents the smallest mesotheriid known. In addition to its small size, it is distinguished from all other mesotheriines by the retention of several primitive character states lost in other taxa (see phylogenetic analysis below).

The holotype (SGOPV 5157; Fig. 11) consists of a partial right maxilla and zygomatic arch bearing P3–M3. The superior surface of the zygomatic arch is well preserved, and the suborbital fossa is present but poorly developed, much less so than in *Eotypotherium*. A second specimen referred to *Eotypotherium* (SGOPV 5074; Fig. 12A) also preserves this region and confirms the lack of a well-developed fossa. The zygomatic plate is also poorly developed, more resembling the condition seen in *Trachytherus* than other mesotheriines. The infraorbital foramen, although small in absolute size (4.0 × 3.5 mm), is similar to that of most other mesotheriines when scaled to body size (Table 3).

No upper incisors are preserved in the holotype (only I1 would be predicted to be present), but their morphology can be discerned from an isolated partial I1 referred to this taxon based on its small size (SGOPV 5108). Like I1 of *Altitypotherium*, that of *Eotypotherium* is subtriangular and pointed distally in cross section. However, unlike *Altitypotherium*, a single mesial sulcus is present on I1 instead of two lingual ones. In this respect, the tooth resembles that of *Trachytherus* and *Microtypotherium*. Unlike that of *Trachytherus* (and like those in all other mesotheriines), I1 is completely surrounded by enamel, save for its occlusal surface.

As in *A. chucalensis, Eotypotherium* possesses two premolars, presumably P3 and P4. These are both subquadrangular (as opposed to subtriangular, as in most other mesotheriines), and each possesses a single labial sulcus. Although the occlusal surfaces of the premolars in the holotype are featureless, another specimen referred to *Eotypotherium* (SGOPV 5074, a partial left maxilla with P3–M1 and partial M2) demonstrates that these likely vary in occlusal morphology with wear in this species. In SGOPV 5074, a small enamel lake is present in the center of P3. Presumably, this is the remnant of a lingual sulcus that has been isolated with wear and that would probably have disappeared altogether with addi-

tional wear. The presence of such an internal sulcus (or an enamel lake) in P3 is unknown among mesotheriines, although it has been reported in DP3 (Francis, 1965). In P4 the sulcus has similarly been isolated by wear but differs from that of P3 in being "Y" shaped; the base of the "Y" is directed lingually and the two arms anterolabially and posterolabially, isolating a very small middle lobe adjacent to the ectoloph. The morphology of P3–4 in SGOPV 5156 (a third maxilla referred to *Eotypotherium;* Fig. 12B) is similar to that exhibited by SGOPV 5074, except that the fossettes are less pronounced, likely because of greater wear. A lingual P4 sulcus (or plication) is absent in *Typotheriopsis* and *Microtypotherium choquecotense,* variably present in *Eutypotherium* (potentially interspecific variation) and *Plesiotypotherium* (potentially intraspecific variation), and consistently present in Caragua New Taxon, *Pseudotypotherium,* and *Mesotherium* (Francis, 1965; Cerdeño and Montalvo, 2001; Flynn et al., in press). In none of these taxa, however, is the sulcus isolated with wear or shaped like a "Y." The presence of isolated fossettes in the premolars in *Eotypotherium* most closely resembles the condition seen in *Trachytherus,* suggesting that it is a retained primitive feature (see phylogenetic analysis below). The fourth upper premolar is implanted at ~10° relative to M1 in the holotype, while P3 is at an even greater angle, closer to 25°.

The first upper molar in the holotype has a triangular middle lobe, more reminiscent of that in *A. paucidens* than *A. chucalensis.* A triangular lobe is also present in M1 of SGOPV 5156, while SGOPV 5074 exhibits a more rectangular middle lobe, more typical of later mesotheriines. The morphology of the middle lobe of M1 therefore seems somewhat variable in this taxon. This tooth is also relatively elongate, unlike the condition seen in *A. chucalensis.* The remaining molars resemble those of *A. paucidens,* save for their much smaller size; the degree of imbrication (1.12) is similar to that exhibited by other mesotheriines from Chucal.

The lower anterior dentition is represented by SGOPV 4071, a symphysis bearing portions of left and right i1–2. As in other mesotheriines, the symphysis is completely fused and relatively thick; even in this diminutive taxon, the symphysis is approximately 8.5 mm thick at the midline. The dorsal surface of the symphysis is strongly concave and spoutlike, as in *A. paucidens.* The spout is approximately 5 mm wide. Both i1 and i2 are small and rounded; i1 lacks a lingual sulcus.

The lower incisors are procumbent and implanted at an angle, as in other mesotheriines. Little of the occlusal morphology is preserved, save for the anterior portion of left i1. No p4 referable to *Eotypotherium* is known. The lower molars referred to this taxon closely resemble those of the other mesotheriines from Chucal, except for their smaller size. Specimen SGOPV 5158 preserves a small portion of the dentary, which is approximately 28 mm deep at the posterior face of m3 (Fig. 13). The corresponding measure from SGOPV 5086, likely from a young individual, is approximately 20 mm.

COMMENTS—The most distinctive aspect of *Eotypotherium* is its small size; it is approximately two-thirds the size of *A. paucidens* and *Microtypotherium choquecotense,* making it the smallest, securely identified mesotheriine known. Villarroel (1978) described a specimen (GB 223) from near Quehua that he assigned to *Microtypotherium* cf. *M. choquecotense;* despite this assignment, he noted that it was smaller than *M. choquecotense* (presumably referring to the holotype) and therefore was the smallest mesotheriine known. The dental measurements provided by Villarroel (1978) indicate that this specimen is roughly similar in size to, or perhaps a bit larger than, *Eotypotherium;* the lengths for i1 and m1 are close to those measured for *Eotypotherium,* but the widths for these and other teeth are greater. Similarly, m2 is slightly longer and m3 significantly (50%) longer than that of *Eotypotherium.* It is therefore unlikely that GB 223 represents a taxon smaller than *Eotypotherium.* The only published specimen representing a mesotheriine possibly smaller than *Eotypotherium* was collected by Oiso (1991) in Nazareno, Bolivia, and included without comment under "*Plesiotypotherium* sp." (Oiso, 1991, table 2, GB Naz-060). If this isolated Nazareno specimen (about half the size of *Eotypotherium*) represents an adult individual (the deciduous premolars of mesotheriines resemble adult permanent molars and have historically caused confusion; Francis, 1965), it undoubtedly represents a species distinct from the remaining Nazareno specimens and would represent the smallest mesotheriine known.

Hegetotheria Simpson, 1945
Hegetotheriidae Ameghino, 1894
Hegetotheriinae Ameghino, 1894

DIAGNOSIS—Hegetotheriids are distinguished from other notoungulates by the unique combi-
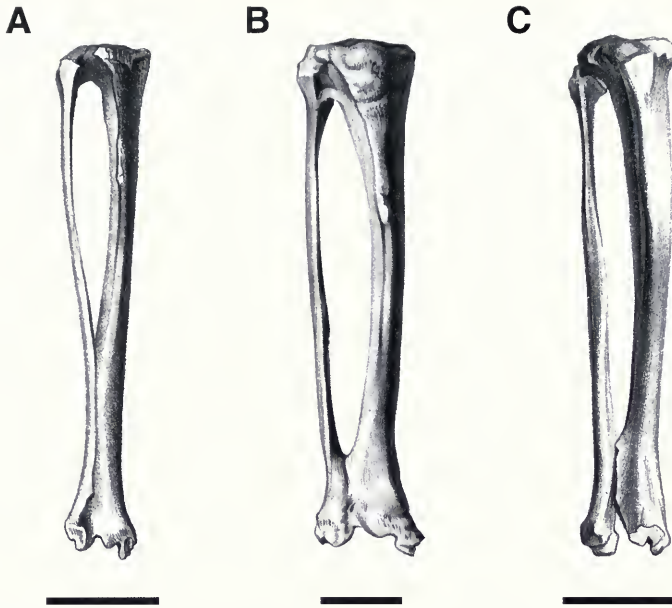
Fig. 14. Comparison of the degree of fusion of the tibia and fibula among selected Santacrucian typotheres. **A.** *Pachyrukhos moyani* (Hegetotheriidae: Pachyrukhinae), AMNH 9242, left tibiofibula, pictured as right. **B.** *Hegetotherium mirabile* (Hegetotheriidae: Hegetotheriinae), PU 15298, right tibiofibula. **C.** *Protypotherium attenuatum* (Interatheriidae: Interatheriinae), PU 15341, right tibia and fibula. All specimens in anterior view. Scale bars = 1 cm. Individual illustrations are modified from Sinclair (1909).

nation of the following derived character states: presence of hypselodont first incisors and cheek teeth; presence of flat wall on lingual faces of upper and lower molars; presence of deep, labial sulcus on m1 and m2; presence of cementum; absence of fossettes in upper and lower cheek teeth; and proximal and distal fusion of tibia and fibula (Cifelli, 1993; Croft, 2000). Among hegetotheriids, hegetotheriines share a uniquely configured distal fusion of the tibia and fibula (see below) and lack many derived character states typical of pachyrukhines. Derived character states of the dentition diagnostic of the Pachyrukhinae (and lacking in the Hegetotheriinae) include the presence of a sharply defined third lobe on m3 (Cerdeño and Bond, 1998), significant reduction or absence of I3-C/i3-c, and presence of i1 much larger than i2.

COMMENTS—The hegetotheriid material from the Chucal Formation includes isolated and/or potentially associated dental and postcranial specimens that fall within the size range typical of hegetotheriids. Currently, there are no size or morphological differences suggesting that more than one hegetotheriid taxon occurs in the Chucal Fauna. Assignment to the Pachyrukhinae is precluded by the morphology of m3: the Chucal taxon has

a bilobed or weakly trilobed m3, whereas in all known pachyrukhines this tooth is sharply trilobed. Moreover, the Chucal taxon is larger than any described pachyrukhine, and occlusal outlines of the upper molars are dissimilar.

In addition to dental morphology, recovered postcranial elements support referral of this material to the Hegetotheriinae. In most hegetotheriids for which postcrania are known, the tibia and fibula are fused at both the proximal and the distal ends. In typical pachyrukhines (e.g., *Pachyrukhos, Paedotherium, Tremacyllus*), the distal fusion is long, comprising approximately 40% the length of the two elements. The fibula bows medially at the proximal point of fusion but then bows laterally again at the distal articulation with the ankle (Fig. 14A). In overall structure, the condition resembles that seen in modern leporids (Sinclair, 1909). In hegetotheriines (and, potentially, the pachyrukhine *Propachyrucos*), the distal fusion is quite short, approximately 15% the length of the tibia and fibula. Additionally, the fibula parallels the tibia throughout its length, resulting in a much broader articulation distally—approximately equal in breadth to the fused proximal ends of the two bones (Fig. 14B). A similar configuration occurs in interatheriids, but it differs from that of hege-

totheriines in lacking complete distal fusion of the tibia and fibula (Fig. 14C). Two partial hegetotheriid tibiofibula specimens have been recovered from the Chucal Formation, both with the hegetotheriine configuration of a short, broad distal fusion.

Hegetotherium Ameghino, 1887

TYPE SPECIES—*Hegetotherium mirabile*.

INCLUDED SPECIES—The type, *H. convexum, H. minum, H. anceps,* and *H. novum.*

DIAGNOSIS—A hegetotheriine differing from *Ethegotherium* in absence of median labial sulcus/groove between paracone and metacone on upper molars, presence of imbrication in lower molars, presence of lower canine root labial to toothrow, and presence of labial groove on m3 talonid. Differs from *Prohegetotherium* in absence of median labial sulcus between paracone and metacone on upper molars, presence of P2/p2 notably smaller than P3/p3, presence of small diastemata between i2 and p3, and reduction or absence of lingual groove on m3 talonid. Differs from *Hemihegetotherium* (including *Pseudohegetotherium*; see below) in absence of thick cementum on lingual faces of upper and lower molars, absence of molars with convex lingual faces and posterior faces that are narrow in comparison to the rest of the occlusal surface, variable presence of small but well-demarcated parastyle and parastyle sulcus on M1–2, and presence of notch on posterior face of M3.

DISTRIBUTION—Sarmiento Formation, Patagonia, Argentina, early Miocene age, Colhuehuapian SALMA (Bordas, 1939); Santa Cruz Formation, Patagonia, Argentina, late early Miocene age, Santacrucian SALMA (Sinclair, 1909); Chucal Formation, northern Chile, late early Miocene age, Santacrucian SALMA (present study); unnamed formation (possibly equivalent to Río Zeballos Formation), southern Chile, late early Miocene age, Santacrucian SALMA (Flynn, Novacek, et al., 2002); Collón-Curá Formation, Patagonia, middle Miocene age, Colloncuran SALMA (Bondesio et al., 1980); Nazareno Formation, southern Bolivia, ?middle Miocene age, ?Colloncuran SALMA (Oiso, 1991).

COMMENTS—The hegetotheriid material collected from Chucal in 1998 was tentatively referred to cf. *Pseudohegetotherium torresi* (Flynn et al., 1999; Flynn, Croft, et al., 2002). Additional hegetotheriine specimens collected in 2001 have

clarified the morphology of the Chucal taxon (especially characters of the upper dentition), suggesting it more likely pertains to *Hegetotherium.*

Bond and López (1997) concluded that although *P. torresi* (the only species of *Pseudohegetotherium*) is a valid taxon, it should perhaps be included within *Hemihegetotherium.* In the above diagnosis and discussion below, *Hemihegetotherium* subsumes "*Pseudohegetotherium*" *torresi.*

The earlier members of the Hegetotheriinae (i.e., *Ethegotherium, Prohegetotherium,* and *Hegetotherium*) have upper molars that are roughly rectangular in outline; the lingual and labial faces are approximately straight and parallel (Croft, 2000). In contrast, the upper molars of later forms (*Hemihegetotherium*) have more convex lingual faces and posterior faces that are narrower than the rest of the occlusal surface. Additionally, the cementum is thicker in these later hegetotheriines, and molar paracones and metacones are less pronounced than in earlier members of the group (Bond and López, 1997). Although hegetotheriid upper molars from the Chucal Formation exhibit relatively thick cementum, this feature is not developed to the degree seen in later hegetotheriines. Moreover, the cheek teeth are roughly rectangular in outline, with a posterior face that is about as wide as the rest of the occlusal surface. The paracones and metacones are variably pronounced on specimens from Chucal, but most exhibit a small yet well-demarcated parastyle and parastyle sulcus. The latter features are absent in later hegetotheriines. The single hegetotheriine M3 known from Chucal also exhibits a prominent notch on the distal face.

A report of *Hegetotherium* from the middle Miocene Quebrada Honda Fauna of Bolivia (Marshall & Sempere, 1991) appears to be in error, based on the taxon's large size and sharply trilobed m3 (pers. observ.); this fauna is thus excluded from the cited distribution of *Hegetotherium.*

Hegetotherium sp. cf. *H. mirabile*
(Figures 15, 16, Table 6)

REFERRED SPECIMENS—SGOPV 5047, left I1; SGOPV 5039, left maxillary fragment with bases of P1–2; SGOPV 5120, right P3; SGOPV 5040, right P4 (Fig. 15A); SGOPV 5058, left ?M1 (Fig. 15B); SGOPV 5121, left ?M1 (Fig. 15C); SGOPV 5122, partial left ?M2 (lacking occlusal surface); SGOPV 5123, left M3 (Fig. 15D); SGOPV 4055,
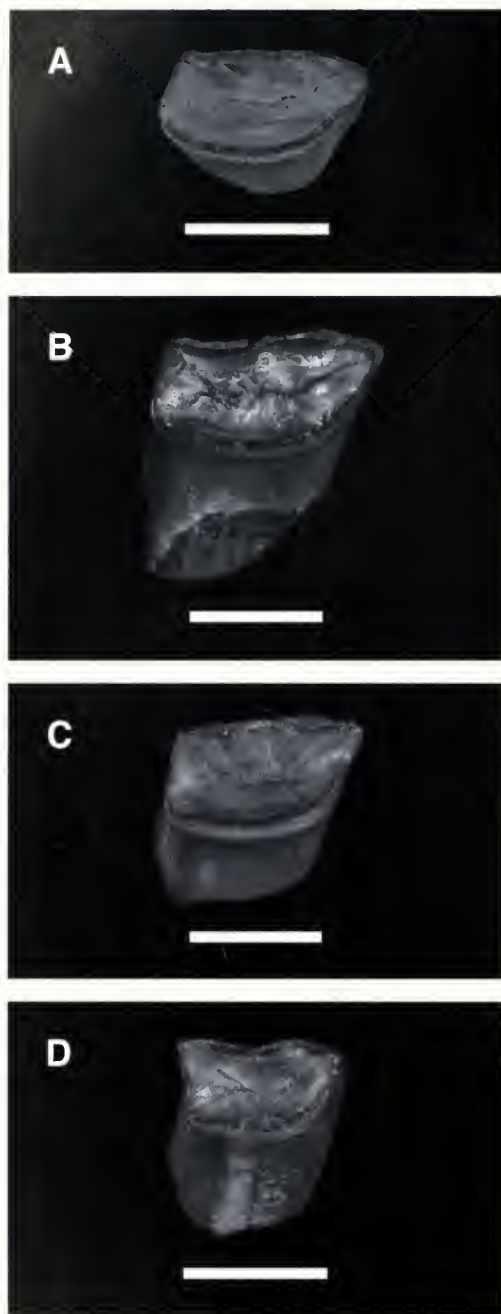
FIG. 15. Isolated upper cheek teeth referred to *Hegetotherium* cf. *H. mirabile,* in occlusal view. **A.** SGOPV 5040, right P4. **B.** SGOPV 5058, left ?M1 (pictured as right). **C.** SGOPV 5121, left ?M1 (pictured as right). **D.** SGOPV 5123g, left M3 (pictured as right). Scale bars = 5 mm.

partial left mandible with root of c, p1–2 (Fig. 16A); SGOPV 5096, partial right mandible with root of c, p1–2; SGOPV 4104, partial left mandible with p4-m3 (Fig. 16B); SGOPV 5042, left m1 with labial fragment of mandible; SGOPV 5049, partial right mandible with m1–2; SGOPV 5082, partial left mandible with bases of m1–2; SGOPV 5222, partial right mandible with m2; SGOPV 4023, partial right mandible with talonid of m1, complete m2–3 (Fig. 16C); SGOPV 5038, partial right mandible with base of m3; SGOPV 5059, left distal tibiofibula fragment lacking epiphysis; SGOPV 5070, partial right leg and pes including distal tibiofibula (lacking epiphyses), calcaneus (epiphysis reattached), cuboid, ?mesocuneiform, metatarsal IV, partial metatarsal ?III, proximal phalanx, distal phalanx; SGOPV 5224, left calcaneus.

DIAGNOSIS—Differs from *Hegetotherium convexum* in presence of M3 ≥ M2 in length, absence of highly convex lingual face of M3, and presence of pronounced posteroexternal angle of M3. Differs from *H. minum* in deeper mandibular ramus. Differs from *H. anceps* in presence of M3 ≥ M2 in length. Differs from *H. novum* in presence of convex internal face on P2, presence of relatively wider cheek teeth, and presence of M3 ≥ M2 in length.

AGE AND DISTRIBUTION—Santa Cruz Formation, Patagonia, Argentina, late early Miocene age, Santacrucian SALMA; Chucal Formation, northern Chile, late early Miocene age, Santacrucian SALMA.

DESCRIPTION—The hegetotheriine specimens from Chucal are fragmentary, the most complete specimen being SGOPV 4104, a partial right mandible with p4–m3 (Fig. 16B). A variety of other mandibular fragments with partial lower dentitions are known, but the upper dentition is known exclusively from isolated teeth.

Specimen SGOPV 5047 is a left upper first incisor with an occlusal surface measuring approximately 7.8 × 2.8 mm. It is rootless and was implanted obliquely, as in other hegetotheriids. At least as judged from the length of the occlusal surface, this specimen is small for *Hegetotherium mirabile*; the corresponding tooth in PU 15542 (Sinclair, 1909, Plate I) measures approximately 11.5 × 3.0 mm, and in FMNH P13194 it measures approximately 10.0 × 2.9 mm. Since the occlusal surface of the Chucal specimen is set at approximately the same angle to the rest of the tooth as in other specimens of *H. mirabile* examined, this difference in surface dimensions may
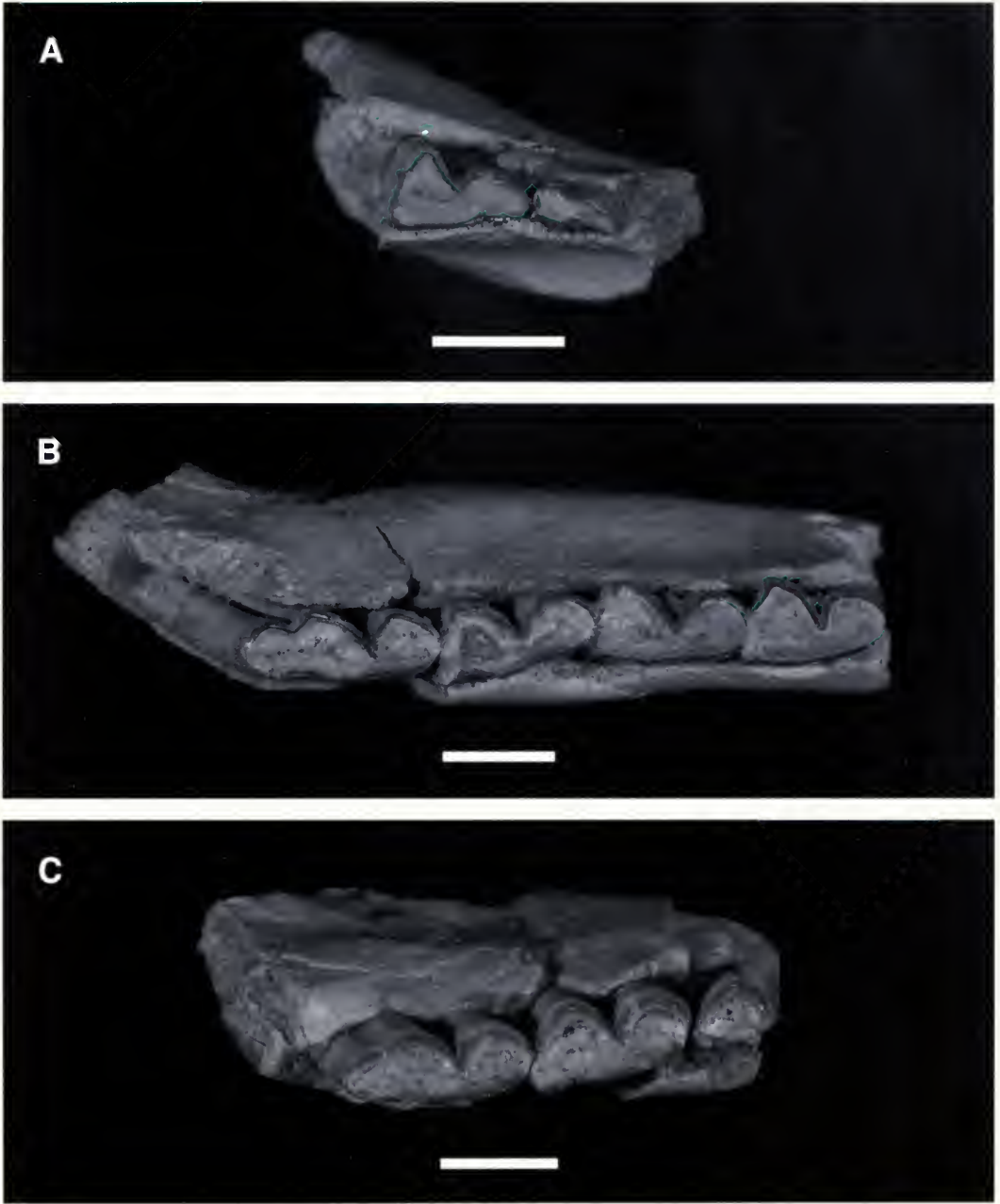
Fig. 16. Lower dentitions referred to *Hegetotherium* cf. *H. mirabile*, in occlusal view. **A.** SGOPV 4055, partial left mandible with root of c, p1–2. **B.** SGOPV 4104, partial left mandible with p4–m3. **C.** SGOPV 4023, partial right mandible with talonid of m1 and complete m2–3 (viewed as left). Scale bars equal 5 mm.

result from differences in wear. Alternatively, the Chucal specimen might be from a smaller than average individual (as in SGOPV 5123; Fig. 15D).

Most examples of the upper dentition from Chucal compare favorably with specimens of *H. mirabile* from Patagonia both in size and in morphology (Fig. 15). Although somewhat small, the upper third molar (SGOPV 5123) has a pronounced notch in the posterior face of the tooth,

characteristic of *Hegetotherium* (Fig. 15D). Of the two posterior projections created by this notch, the labial one is slightly longer. This feature is variable within *Hegetotherium* from Patagonia; the labial projection ranges from slightly longer to significantly longer than the lingual (Sinclair, 1909). Several Chucal specimens from the same locality (SGOPV 5121, left ?M1; SGOPV 5122, partial left ?M2; SGOPV 5123, left M3) may represent the left upper molar series from a single individual. However, since this locality has produced an abundance of isolated teeth from a variety of taxa, the basis for such an association is not compelling.

The lower dentition of the Chucal hegetotheriid is much better represented than the upper dentition; seven well-preserved partial mandibles have been collected, although none preserves the incisors or p3. The specimens resemble *H. mirabile* in morphology and are comparable in size. As in M3, the morphology of m3 is variable among *H. mirabile* specimens both from Patagonia and from Chucal. In some specimens, the labial talonid groove on m3 is very shallow; in others, it is pronounced, lending the tooth a nearly trilobed appearance. This feature is also variably expressed in the three specimens from Chucal; in SGOPV 4023 (Fig. 16C) and SGOPV 5038, the groove is very weakly present, whereas in SGOPV 4104 (Fig. 16B), the talonid groove is deep, and a third lobe is present (though it is not developed to the extent seen in pachyrukhines).

COMMENTS—In his description of the typotheres of the Santa Cruz Beds, Sinclair (1909) referred all hegetotheriines in the Princeton collections to *Hegetotherium mirabile*. He considered five other taxa to be junior synonyms of *H. mirabile* (*H. strigatum, H. cuneatum, H. costatum,* "*Selatherium*" *pachymorphum,* and "*Selatherium*" *remissum*) and listed three others as of questionable status (*H. convexum, H. minum,* and *H. anceps*). All three questionable taxa were named by Ameghino based on Santacrucian specimens. The holotype of *H. convexum* is a partial left maxilla with M2–3 figured by Ameghino (1891, fig. 30). If the figure and the description provided are accurate, the specimen would not appear to pertain to *H. mirabile* (see diagnosis above) and may be distinct. *H. minum* is said to be distinguished from *H. mirabile* primarily by its shallower mandibular ramus (Ameghino, 1894), but the variability of this character (especially with wear) is uncertain. *H. anceps* differs from *H. mirabile* in having an M3 that is shorter than M2 (as in *H. convexum*) but

is not described as differing from *H. mirabile* in M3 shape (Ameghino, 1891). *H. anceps* may represent a species distinct from both *H. mirabile* and *H. convexum,* or may be synonymous with the latter. *H. novum* was named by Bordas (1939) based on a partial skull recovered from Colhuehuapian strata in the Valle del Río Chubut and shares with both *H. convexum* and *H. anceps* the shortened M3 in relation to M2. The other distinguishing characters of *H. novum* described by Bordas (1939) suggest this taxon may be distinct from *H. mirabile* and other recognized species of *Hegetotherium.*

Owing to the incompleteness of *Hegetotherium* specimens from Chucal and the lack of a comprehensive revision of *Hegetotherium* taxonomy, a definitive identification of the material cannot now be made. Nevertheless, no compelling evidence argues against reference of these specimens to *H. mirabile.* Upper cheek teeth from Chucal (Table 6) are wider than those of *H. novum,* and SGOPV 5039 confirms that P2 of the Chucal form lacks the concave lingual face (characteristic of *H. novum*). Two mandibular fragments from Chucal (SGOPV 5104 and SGOPV 5049) illustrate that the horizontal ramus below m1 is deeper in the Chucal taxon than in *H. minum* (15.5 mm and 15.4 mm in the Chucal specimens versus 14.0 mm in *H. minum*). The single hegetotheriine M3 collected from Chucal (SGOPV 5123) is a small tooth, shorter than any of the other hegetotheriine molars known from the area (Table 6). Although this may imply that the Chucal *Hegetotherium* has an M3 shorter than M2 (as in *H. convexum* and *H. anceps*), the lack of an associated M2 clouds this interpretation; the possibility that this M3 merely pertains to a smaller individual (whose M2 is not preserved) cannot be excluded. Moreover, even though the Chucal M3 is smaller than the other upper molars from Chucal, it is larger than M3 in the holotypes of both *H. convexum* and *H. anceps.* The presence of a pronounced posteroexternal angle and the lack of a greatly concave lingual face in this M3 differs from the holotype of *H. convexum* and more closely resembles *H. mirabile.*

Litopterna Ameghino, 1889
Macraucheniidae Gervais, 1855
Cramaucheniinae Ameghino, 1902

DIAGNOSIS—The postcrania (especially the tarsals) of litopterns are highly diagnostic and read-

Upper dentition	Position	L	W
SGOPV 5120 (R)	P3	4.9	3.7
SGOPV 5040 (R)	P4	6.8	4.1
SGOPV 5058 (L)	?M1	8.1	(4.9)
SGOPV 5121 (L)	?M1	7.4	4.7
SGOPV 5122 (L)	?M2	(7.2)	(4.6)
SGOPV 5123 (L)	M3	6.0	3.8

	p1		p2		p3		p4		m1		m2		m3	
Lower dentition	L	W	L	W	L	W	L	W	L	W	L	W	L	W
SGOPV 4055 (L)	3.2	(1.7)	5.2	3.3										
SGOPV 5096 (R)	(2.8)	(1.7)	5	2.8										
SGOPV 4104 (L)							6.5	4.1	7.4	3.9	7.1	3.9	9	3.6
SGOPV 5042 (L)									7.3	3.9				
SGOPV 5049 (R)									(7.0)	4.4	7.3	4.3		
SGOPV 5082 (L)									(7.1)	(3.7)	—	—		
SGOPV 5222 (R)											7.5	4		
SGOPV 4023 (R)											7.0	4.2	8.5	3.5
SGOPV 5038 (R)													(7.7)	(3.1)

ily distinguishable from those of other South American ungulates by presence of cuneiform-magnum contact in the manus (and loss of lunate-unciform contact), presence of elongate neck of calcaneus with strongly oblique calcaneocuboid facet, sustentacular facet of calcaneus anteroposteriorly concave, presence of deeply grooved astragalar surface of the tibia; absence of medial malleolus of tibia, and a variety of astragalar features (see Cifelli, 1983, 1985). Macraucheniids are distinguished from adianthids postcranially by relatively large size; absence of fenestrate olecranon fossa; absence of pronounced tubercle on dorsolateral ischium, posterior to acetabulum; presence of well-developed third trochanter on femur; and absence of fusion between proximal tibia and fibula (Cifelli, 1991). Macraucheniids are distinguished from proterotheriids postcranially by relatively large size; absence of fenestrate olecranon fossa; presence of tridactyl pes with metatarsals II, III, and IV subequal in size (Shockey, 1999); absence of tall greater trochanter of femur (not extending far above level of femoral head); and presence of astragalus with broad body, foreshortened neck, and flattened head (Cifelli & Guerrero Diaz, 1989). Among macraucheniids, cramaucheniines are distinguished from macraucheniines by generally smaller size, lack of elongate rostrum, unreduced nasals, absence of dorsally positioned nasal aperture, absence of dorsally projecting maxillae, unshortened zygomatic arch, absence of closed orbit, absence of imbrication in i1–p1, absence of fossettes in p3–m3

trigonid basin, absence of cementum, lack of radioulnar fusion, and presence of elongate calcaneus (Soria, 1981).

COMMENTS—Although a variety of cranial and dental characters are diagnostic of Litopterna and various subgroups within that clade, no craniodental specimens definitely pertaining to the group have been collected from the Chucal Formation. In contrast, well-preserved diagnostic postcranial bones are known (see below). No metric or morphological evidence suggests that the litoptern postcrania from Chucal pertain to more than one species. The size and morphology of the two calcaneae and the humerus collected at Chucal closely resemble other members of the Macraucheniidae. Three associated litoptern metatarsals (MT II–IV) are subequal in size, supporting this identification.

Theosodon Ameghino, 1887

TYPE SPECIES—*Theosodon lydekkeri*.

INCLUDED SPECIES—The type, ?*T. frenguelli* (Colhuehuapian), *T. lallemanti, T. fontanae, T. garretorum, T. gracilis, T. patagonicus, T. karaikensis, T. pozzii* (Kraglievich & Parodi, 1931), and *T. hystatus* (Chasicoan).

POSTCRANIAL DIAGNOSIS—A cramaucheniine that differs from *Cramauchenia* in larger size (approximately 20–30% larger in linear dimensions); articular facets of astragalus and calcaneus relatively larger than in *Cramauchenia* (Soria, 1981).

Differs from *Coniopternium* (including *Caliphrium* and *Notodiaphorus* sensu Cifelli & Soria, 1983) in larger size (approximately 20–25% larger in linear dimensions) and in having broader calcaneus with larger peroneal facet, more robust calcaneal tuber, and tendon grooves (Cifelli & Soria, 1983). Differs from *Pternoconius* in larger size (approximately 20–25% larger in linear dimensions); postcranial elements of *Pternoconius* are unknown. Differs from *Polymorphis* in much larger size (approximately twice as large as *Polymorphis* in linear dimensions); we are unaware of any postcrania referable to *Polymorphis*.

DISTRIBUTION—Early Miocene of Chubut, Argentina, Colhuehuapian SALMA (Simpson, 1935; Soria, 1981); late early Miocene of Patagonia, Argentina, Santacrucian SALMA; ?early middle Miocene of Río Frías/Cisnes, Chile, Friasian s.s. SALMA (Kraglievich, 1930); middle Miocene of La Venta, Colombia, Laventan SALMA (Cifelli & Guerrero, 1997); ?early late Miocene of Buenos Aires Province, Argentina, Chasicoan SALMA (Cabrera & Kraglievich, 1931).

DISCUSSION—Cifelli and Guerrero (1997) suggested that Chasicoan "*Cullinia*" *laevis* (Cabrera & Kraglievich, 1931) and Mayoan "*Phoenixauchenia*" *tehuelche* (Kraglievich, 1930) may also pertain to *Theosodon*.

Theosodon sp. indet.
(Figure 17)

REFERRED SPECIMENS—SGOPV 4013, articulated proximal left ulna and radius (Fig. 17A); SGOPV 4019, partial distal radius; SGOPV 4037, associated limb bones including left and right tibiae (lacking epiphyses except for the right distal epiphysis), articulated right distal humerus and proximal ulna, right proximal humerus fragment, ?radius fragment, proximal left MT IV, proximal right MC II and III, partial shafts of two other large limb bones (Fig. 17B); SGOPV 4014, partial right calcaneus (Fig. 17C); SGOPV 5054, partial left calcaneus.

DESCRIPTION—The litoptern postcrania from Chucal are among the best preserved limb bones of the fauna, but no elements of the pectoral or pelvic girdle are preserved. Most of the Chucal litoptern postcranial elements pertain to a single partial skeleton, SGOPV 4037. The proximal humerus from this specimen preserves little morphology, save for most of the articular surface of the head. The distal humerus is complete and was found in articulation with a partial proximal ulna. It measures approximately 4.5 cm across the condyles, the lateral being broader than the medial. The lateral epicondyle is much larger than the medial, though a distinct process projects from the posterior surface of the medial condyle. The olecranon fossa is very deep and the supratrochlear fossa shallow; these two structures are not joined by a foramen.

Little of the ulna is preserved in SGOPV 4037, except for the articular surface and surrounding area. A pronounced intercondylar ridge bisects the sigmoid notch, separating the larger medial surface from the smaller lateral one. It lateral view, the notch approximates a semicircle. A large rugose area for attachment of the elbow flexors is present distal to the articular surface, and two small facets mark the proximal articulation of the radius. The olecranon process is incompletely preserved in SGOPV 4037 but measures more than 6.5 cm in length in SGOPV 4013. The latter specimen preserves most of the ulna except its distal end and measures approximately 33 cm in length; the corresponding bone in *T. garretorum* measures 37.5 cm (Scott, 1910). A similar portion of the radius is preserved in SGOPV 4013. The proximal facet is oblong and gently concave and is reflected for a short distance onto the medial surface. A prominent tuberosity is present just distal to the extension of the articular surface. The ulnar and radial shafts are subequal in length and diameter.

Of the manus, only the proximal portions of MC II and III are preserved. These bones are subequal in size; the shaft of MC II is approximately 18 mm in its greatest diameter. The second metacarpal has a roughly triangular proximal articular surface for the trapezoid, the latter of which is incompletely preserved in SGOPV 4037. A prominent facet is present on the lateral surface for contact with the magnum; it is oriented at an angle of approximately 45° to the long axis of the bone. The medial surface of MC II overlaps the proximal articular surface of MC III, creating one facet that is positioned distally and another that is positioned laterally. Very little of MC III is preserved, but part of the surface articulating with the distally oriented MC II facet is present.

Of the hind limb, the tibia and portions of the pes have been recovered. Specimen SGOPV 4037 includes both tibiae, mostly lacking epiphyses. The right tibia, which preserves the distal epiphyses, is approximately 24 cm long. Scott (1910) listed the length of the corresponding
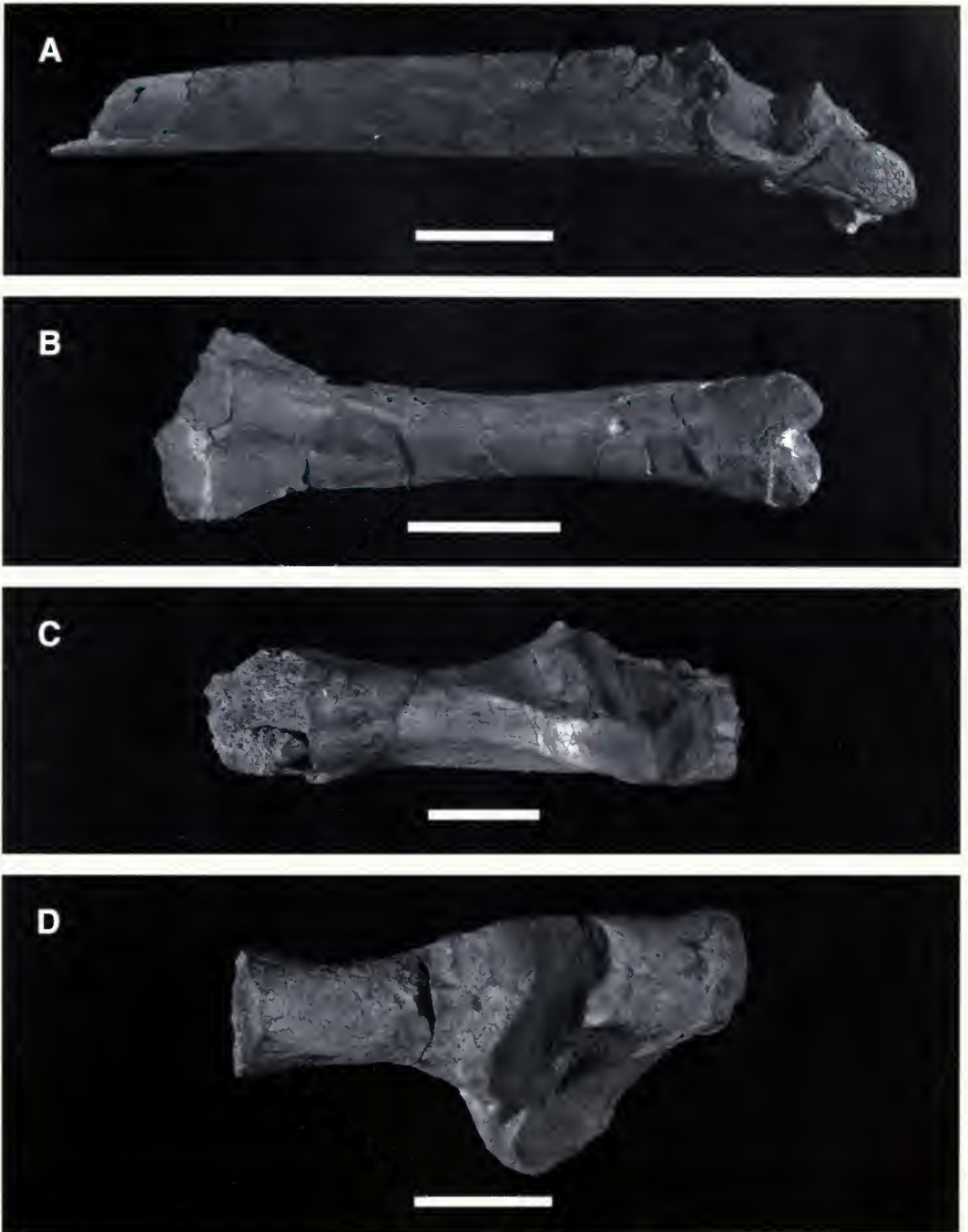
Fig. 17.   Selected postcranial specimens referred to *Theosodon* sp. indet. **A.** SGOPV 4013, proximal left ulna in anterolateral view. **B.** SGOPV 4037, left tibia, lacking epiphyses, in anterior view. **C.** SGOPV 4014, partial right calcaneus in superior view. **D.** SGOPV 5054, partial left calcaneus in superior view. Scale bars = 5 cm in **A** and **B**, 2 cm in **C** and **D**.

bone in *T. garretorum* as 27 cm. The astragalar surface of the tibia has two deep grooves for articulation with the astragalar trochlea and a small lateral facet for articulation with the fibula. The posterior portion of the intercondylar ridge extends much farther distally than the anterior portion.

Two partial calcanea are represented, SGOPV 4014 and SGOPV 5054; the former includes the poster two-thirds of the element, while the latter preserves the anterior half (Fig. 17C, D). The tuber is long, narrow, and dorsoventrally broad. A narrow, strongly convex facet is present for articulation with the fibula. Medial to this, a large, triangular facet is present for articulation with a portion of the ectal facet of the astragalus. This triangular facet is continuous distally with a smaller, oval facet that articulates with the remainder of the ectal facet. The astragalar facet on the sustentaculum is also oval, and a large nonarticular surface is interposed between this and the other astragalar facets of the calcaneus. The distal surface of the calcaneus is almost saddle shaped and evidently articulated only with the cuboid; no distal articulation with the astragalus is indicated.

The fourth metatarsal (SGOPV 4037) is similar in size to MC II described above. Its proximal articular surface, for articulation with the middle cuneiform, is gently convex and has a prominent plantar hook. A prominent, oblong facet is present on the dorsal side of the medial surface for articulation with MT III. A second facet for articulation with MT III is only partly present along the medial surface of the plantar hook. Two small facets are present on the lateral surface for articulation with MT V.

COMMENTS—As discussed by Cifelli and Guerrero (1997, p. 298), taxonomy within the Macraucheniidae is in a state of "general disrepair." *Theosodon* has been reported from the Colhuehuapian (Simpson, 1935; Soria, 1981) through the Chasicoan SALMA (Pascual, 1966)—a temporal range of some 10 million years (Flynn & Swisher, 1995)—but many of these reports are based on fragmentary remains of questionable taxonomic utility. The Santacrucian members of *Theosodon* likely form a clade, but the differences among some of the species are unclear (Cifelli & Guerrero, 1997).

In size and morphology, the Chucal litoptern resembles the various species of *Theosodon* from the Santa Cruz Formation of Patagonia described by Scott (1910). Owing to the relatively small number of specimens from the Chucal Formation and the lack of well-differentiated species within *Theosodon,* the taxonomic reliability of these features currently cannot be assessed. Accordingly, a more tightly circumscribed identification of the Chucal taxon cannot be made at this time.

Phylogeny of Mesotheriines

To assess the taxonomic affinities of the mesotheriids from Chucal, we performed a phylogenetic analysis of mesotheriines based primarily on an emended version of the data matrix of Flynn et al. (in press; see also Cerdeño & Montalvo, 2001). A single character was added to this matrix (#29: M1 proportions), and an additional character state was added to character #16 (state #4: I1 subtriangular, pointed distally, with two talonid sulci) and to character #26 (state #2: P3 absent). The list of characters used in this analysis is presented in Table 7, and the complete data matrix is given in Table 8. Two analyses were performed, both using Archaeohyracidae as the outgroup (following Cerdeño & Montalvo, 2001). In the first analysis, all characters were considered unordered. In the second, selected characters were ordered (indicated in Table 7) on the basis of developmental and metric criteria (e.g., it was assumed that a taxon could not proceed from "small" to "large" without passing through "medium"). For both analyses, trees were generated using the heuristic search option in PAUP 3.11 for the Macintosh computer. OTUs with multiple character states were considered polymorphic. The first analysis (using unordered characters) resulted in nine equally most parsimonious trees, each with a length of 93 steps. The second analysis (using the ordered characters) resulted in 81 equally most parsimonious trees, each with a length of 96 steps. The strict consensus trees for the two analyses have identical topologies at the base and near the crown of the tree, but the first analysis (with unordered character states) exhibits greater resolution in the middle (Fig. 18). We favor the first analysis, as it makes fewer assumptions regarding character evolution and is better resolved.

The relationships in the resulting consensus trees are nearly identical to those of Flynn et al. (in press). Aside from the greater resolution in the unordered analysis, the only other difference is that both analyses here suggest that *E. lehmann-*

TABLE 7. List of characters and character states used in phylogenetic analysis of mesotheriine relationships. Characters with multiple derived character states were ordered in analysis #2 unless denoted by an asterisk (*).

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); protohyposodont (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 implantaton 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)

TABLE 7. Continued.

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)

nitschei and *E. superans* share a common ancestor exclusive of other mesotheriines; in Flynn et al. (in press), these two taxa form a polytomy with a later diverging clade of mesotheriines (node 5 of Fig. 18). In the present analyses, this paring of *Eutypotherium* species is weakly supported by the loss of a single character state, having the root of the zygomatic arch perpendicular to M1 (character #7, state 1 >0; variable in *T. chasicoensis,* lost independently in *M. hystatum*).

The names Mesotheriinae and Mesotheriidae have never before been defined phylogenetically (sensu de Quieroz & Gauthier, 1990). The phylogeny established here facilitates this undertaking whereby names are explicitly tied to given clades. Consistent with previous usage, we define Mesotheriidae as all notoungulates more closely related to *Mesotherium* than to *Hegetotherium, Archaeohyrax,* or *Oldfieldthomasia* (essentially equivalent to node 1 of Fig. 18 plus its stem), and we define Mesotheriinae as all mesotheriids more closely related to *Mesotherium* than to *Trachytherus* (node 2 of Fig. 18 plus its stem).

Following this definition of the name Mesotheriinae, the phylogenetic analyses place the three Chucal mesotheriids at the base of the Mesotheriinae, with *Eotypotherium* as its earliest diverging member. *Eotypotherium* is a member of

Table 8. Character-taxon matrix for phylogenetic analysis of mesotheriine relationships.

| | | 1 | 11111 | 11112 | 22222 | 22223 | 333 |
	12345	67890	12345	67890	12345	67890	123
Archaeohyracidae	00000	00000 [a]	00000 [a]	00000	00000	0000?	?01
Trachytheriinae	10101	20111	01011	11101 [a]	10100 [a]	00000	000
Eutypotherium lehmannnitschei	21?1?	10211	?2001	22222	20211	10010	100
Eutypotherium superans	2121?	10211	?2001	22212	3???0	10010	1?0
Typotheriopsis chasicoensis	21?22	20201 [a]	12001 [a]	22212	21211 [b]	11011	100
Typotheriopsis silveyrai	21222	21201	120?1	?2212	2????	11011	1?0
Pseudotypotherium subinsigne	21?21	21201 [a]	12201 [c]	?2222 [c]	22311	10121	110
Pseudotypotherium exiguum	2???1	?121?	?22??	???32	32?11	10121	110
Mesotherium hystatum	21231	?0201	122?1	?2232	3??11	1012?	110
Mesotherium cristatum	22332	02221	12200	22232	33311	10122	110
Mesotherium pachygnathum	21?22	01221	12202	22232	33?11	10122	110
Mesotherium maendrum	22232	01221	12202	32232	33411	10122	110
Plesiotypotherium achirense	21122	21211	12001	22212 [b]	30211	10011	100
Microtypotherium choquecotense	2??1?	?1201	?2001	12212	2???1	10010	020
Caragua New Taxon	2112?	11221	12101	22222	21211	10011	101
Altitypotherium paucidens	2??1?	112??	?2001	42212	30111	21010	000
Altitypotherium chucalensis	???1?	????2?	?200?	42212	20111	11000	000
Eotypotherium chico	?????	1111?	?200?	12202	20111	00010	000

[a] polymorphic secondary state "1" noted below cell; [b] polymorphic secondary state "2" noted below cell; [c] polymorphic secondary state "3" noted below cell.

the Mesotheriinae based on its possession of numerous characters typifying the clade (node 2 of Fig. 18), including the presence of a poorly defined suborbital fossa and small infraorbital foramen (character #6, state 1; DELTRAN optimization only, lost in most *Mesotherium* species), root of zygomatic arch perpendicular to M1 (character #7, state 1; lost in *Eutypotherium* clade and *M. hystatum,* variably present in *T. chasicoensis*). hypselodont (euhypsodont) dentition (character #12, state 2), I2-I3-C-P1/i3-c-p1 always absent (character #17, state 2), P2 absent (character #18, state 2), M1–M2 with persistent middle lobe (character #21, state 2), M3 with short middle lobe surrounded by the other two lobes (character #21, state 2), p3 absent (character #24, state 1), lower molars without fossettes (character #25, state 1), and M1 proportions (length/width) >1.30 (character #29, state 1).

A. paucidens and *A. chucalensis* are united by the unique presence of a subtriangular I1 that is pointed distally, with two lingual sulci (character #16, state 4) and the presence of a single labial sulcus on premolar ectolophs (character #27, state 1). Within the Mesotheriinae, *Altitypotherium* forms a polytomy (node 3 of Fig. 18) with *Microtypotherium* and a clade including all other later diverging mesotheriines (node 4 of Fig. 18). Node 3 is diagnosed by the presence of a short,

rodentlike rostrum (character #1, state 2; unknown in *Eotypotherium* and *A. chucalensis*); presence of posterolaterally divergent diastemata (character #4, state 1; unknown in *Eotypotherium*); presence of a well-developed zygomatic plate (character #8, state 2); presence of short, subtriangular P4, without a central fossette (character #19, state 1); and presence of subtriangular P3 (character # 26, state 1; absent in *A. paucidens*).

Altitypotherium and *Microtypotherium* are excluded from membership in the clade stemming from node 4 (Fig. 18) by the lack of the following derived character states: wide, rounded I1 with a lingual sulcus (character #16, state 2; unknown in *T. silveyrai* and *Pseudotypotherium*); i1 with subtriangular section and smooth lingual sulcus (character #23, state 2; unknown in *Microtypotherium, P. exiguum, M. hystatum,* and *M. pachygnathum*); and extensive lingual exposure of M1 middle lobe (character #31, state 1).

Age and Faunal Comparisons

Although the preliminary report on the Chucal Fauna suggested that it might be as old as Santacrucian (late early Miocene) or as young as
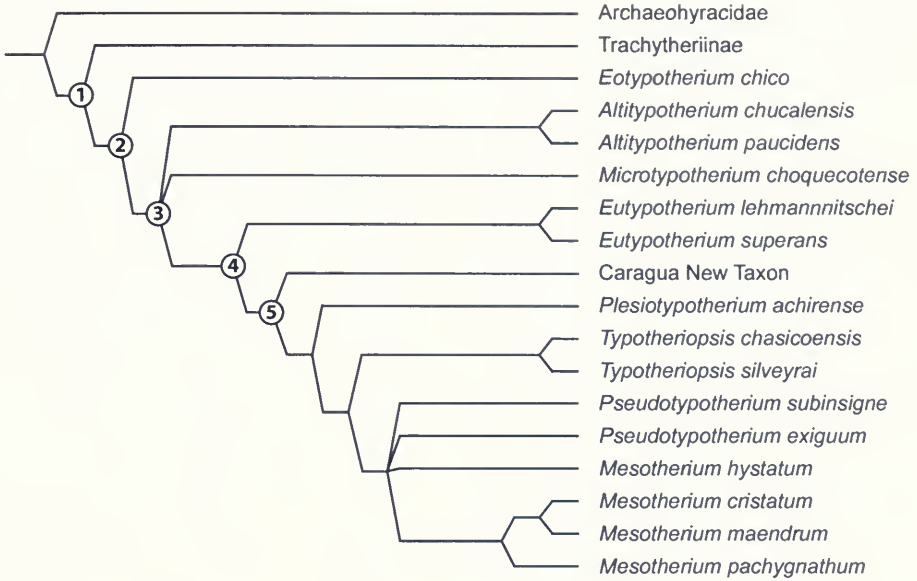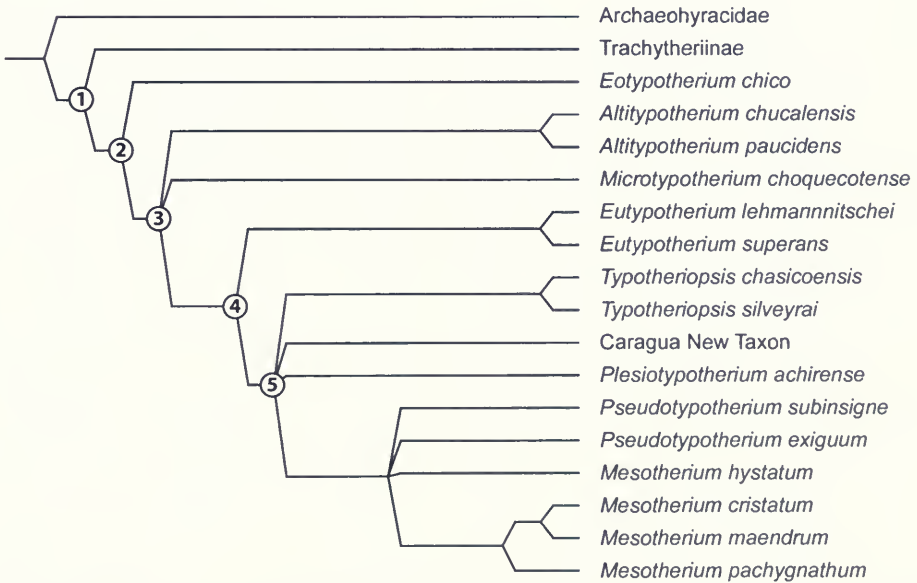
FIG. 18. Strict consensus trees of mesotheriine relationships based on the phylogenetic analyses in the present study. **A.** Strict consensus of nine trees resulting from the analysis with all characters unordered; length = 82, CI = 0.79, RI = 0.83, RC = 0.66. **B.** Strict consensus of 81 trees resulting from the analysis with some characters ordered (see Table 7); length = 88, CI = 0.74, RI = 0.81, RC = 0.60. In both trees, node 1 is Mesotheriidae, node 2 is Mesotheriinae, and nodes 3–5 are unnamed clades discussed in the text.

Chasicoan (late Miocene) (Flynn, Croft, et al., 2002), new dates from a subsequent report (Bond & García, 2002) have restricted the age the fauna to within a 4- to 5-million-year-long interval (Table 9; see also Charrier et al., 2002). The overlying Quebrada Macusa Formation has been dated at 17.4 ± 0.4 Ma (Bond & García, 2002), and the underlying Lupica Formation has been dated at 21.7 ± 0.8 Ma at Chucal (Riquelme, 1998) and at 18.79 ± 0.11 Ma in the surrounding area (Wörner et al., 2000). Based on the radioisotopic dates from the Chucal region and the most recent revision of SALMAs (Flynn & Swisher, 1995), this interval overlaps with or slightly pre-dates the Santacrucian SALMA (~16.3–17.5 Ma). There is a remote possibility, however, that it coincides with the Colhuehuapian SALMA (estimated to be ?19–21? Ma since the Colhuehuapian is unconstrained within the 24.5–17.5-Ma gap between the dated Deseadan and Santacrucian SALMAs), as no such faunas have been dated. Paleomagnetic correlations for Chucal are not yet available, but samples for a preliminary analysis are currently being analyzed.

These uncertainties notwithstanding, based on biochronologic evidence, the Chucal Fauna almost certainly pertains to the Santacrucian SALMA; *Nesodon* likely is an indicator taxon of the Santacrucian SALMA (Croft, Radic, et al., 2003), as is *Neoreomys* (A. Kramarz, pers. comm.; Table 12), and *Hegetotherium mirabile* is recorded only in Santacrucian deposits (see above). Taking into account the geochronologic constraints on the Chucal Fauna, the Santacrucian SALMA may extend slightly older than previously believed, at least in intermediate latitudes. This is not entirely unexpected, as most high-latitude strata bearing Santacrucian assemblages are underlain by either an unconformity and/or marine strata, thus precluding determination of the complete duration of this SALMA; the youngest dated assemblages that definitively pre-date the Santacrucian are ~25.5-Ma Deseadan sites near Salla, Bolivia (Kay et al., 1998) and the ~20.1-Ma? Colhuehuapian Río Las Leñas assemblage from central Chile (Flynn et al., 1995). The greater resemblance of the Chucal Fauna to lower Santacrucian levels compared to upper ones (Tables 10 and 11) lends additional support to the relative antiquity of the Chucal Fauna. Paleomagnetic analyses currently under way may further constrain the age of the Chucal Fauna and clarify the onset of the Santacrucian SALMA.

Despite several shared taxa, there are profound differences between the ungulate fauna of Chucal and those from typical Santacrucian localities in Argentina and southern Chile (Table 10). Simpson coefficients, comparing Chucal to these faunas, range only from 43–57 (Table 11). These differences arise primarily because mesotheriids—constituting one-third of the ungulate "genera" at Chucal—have never before been recorded in Santacrucian-aged strata. This lack of Santacrucian mesotheriids elsewhere represents but a small portion of an even larger middle Cenozoic gap in the fossil record of mesotheriids in higher latitudes: none has been recorded there between the Deseadan and Mayoan SALMAs (early to middle Miocene), a span of some 13 million years (Flynn & Swisher, 1995; Croft, Flynn, & Wyss, 2003). In contrast, mesotheriines are characteristic components of Bolivian Miocene faunas (Table 10) and a very large fraction of isolated Miocene vertebrate specimens collected in northern Chile and Bolivia are referable to mesotheriines (Marshall & Sempere, 1991; Flynn et al., in press).

Another conspicuous difference between the Chucal Fauna and typical Santacrucian faunas is the complete absence of interatheriid notoungulates in northern Chile. In this respect, Chucal resembles other middle-latitude Miocene faunas of Bolivia (i.e., Nazareno, Quebrada Honda, and Achiri), in which interatheriids also are rare and/or absent (Table 10). Although it is certainly possible that interatheriids were present at Chucal but remain unsampled, the lack of specimens referable to this clade from among more than 300 identified specimens at least speaks to the rarity of this group, if they existed in this region at that time; it is difficult to envision a taphonomic bias that would preserve other closely related and similarly sized typothere notoungulates (i.e., hegetotheriines and mesotheriines) to the exclusion of interatheriids. The absence of interatheriids is particularly striking given their abundance not only in the Santa Cruz Formation of Argentina (Sinclair, 1909) and the Santacrucian-aged Pampa Castillo Fauna of southern Chile (Flynn, Novacek, et al., 2002) but also in nearly all Oligocene through early Miocene faunas of South America. The close geographic proximity of the faunas in which interatheriids are rare or absent (Bolivian and Chilean Altiplano) suggests that some biogeographic and/or ecological factor served to limit or exclude interatheriids from at least the western portion of these intermediate latitudes (eastern, noncordilleran faunas of this age are unknown) during much of the Miocene. In

TABLE 9. Ungulates of middle-latitude early to middle Miocene faunas of northern Chile and Bolivia.

	Chucal	Nazareno	Quebrada Honda	Achiri
Fauna: SALMA *Correlation:*	?Santacrucian	?Colloncuran	?Laventan	?Chasicoan
Radioisotopic Constraints:	17.4 ± 0.4 Ma to 21.7 ± 0.8 Ma	9.58 ± 0.51 Ma to 20.9 ± 0.6 Ma	11.96 ± 0.11 Ma to 12.83 ± 0.11 Ma	7.6 Ma to 10.35 Ma
TAXA				
Notoungulata				
Toxodontidae	*Nesodon imbricatus* / *Adinotherium* sp. / Toxodontidae ?new taxon		Toxodontidae sp.	Toxodontinae sp. nov. / Toxodontinae sp. indet.
Mesotheriidae	*Altitypotherium paucidens* / *Altitypotherium chucalensis* / *Eotypotherium chico*	*Plesiotypotherium* sp.	Mesotheriinae sp. indet.	*Plesiotypotherium achirense* / *Plesiotypotherium majus*
Interatheriidae	—		?Interatheriinae	—
Hegetotheriidae	*Hegetotherium* cf. *H. mirabile*	*Hegetotherium* sp.	Hegetotheriinae sp. nov.	—
Litopterna				
Proterotheriidae	—	*Diadiaphorus* sp.	*Diadiaphorus* sp.	—
Macraucheniidae	*Theosodon* sp.		Macraucheniidae sp. indet.	—
Astrapotheria				
Astrapotheriidae	—		?*Xenastrapotherium* sp.	—
FAUNAL DATA	present study; Flynn, Croft, et al. (2002); Bond and García (2002)	Oiso (1991)	Marshall and Sempere (1991)	Marshall et al. (1992)
RADIOISOTOPIC DATA	Riquelme (1998); Bond and García (2002)	Hérail et al. (1996)	MacFadden et al. (1990)	Marshall et al. (1992)

TABLE 10. Ungulates of selected low-, middle-, and high-latitude Miocene faunas of South America.

Fauna: Age: Stratum: Location: Faunal data:	La Venta Middle Miocene Monkey Beds Colombia (3°N) Kay and Madden (1997)	Chucal Late early Miocene — N Chile (23°S) Present study; Flynn, Croft et al. (2002); Bond and García (2002)	Pampa Castillo Late early Miocene — S Chile (47°S) Flynn, Novacek, et al. (2002); pers. observ.	Lower Santa Cruz Late early Miocene Spaniomys riparius Biozone SE Patagonia (51°S) Tauber (1997a)	Upper Santa Cruz Late early Miocene Protypotherium australe Biozone SE Patagonia (51°S) Tauber (1997a)
TAXON **Notoungulata** Toxodontidae	Pericotoxodon platignathus	Nesodon imbricatus Adinotherium sp. Toxodontidae ?new taxon	Nesodon sp. Adinotherium sp.	Nesodon sp. Adinotherium robustum Adinotherium sp.	Nesodon imbricatus Nesodon sp. Adinotherium ovinum Adinotherium robustum
Leontiniidae	Huilatherium pluriplicatum	—	—	—	—
Homalodotheriidae	—	—	Homalodotherium	Homalodotherium cunninghami	Homalodotherium cunninghami
Mesotheriidae	—	Altitypotherium paucidens Altitypotherium chucalensis Eotypotherium chico	—	—	—
Interatheriidae	Miocochilius anamopodus	—	Interatherium sp. Protypotherium sp.	Interatherium robustum Interatherium sp. Protypotherium praerutilum Protypotherium attenuatum Cochilius sp. nov.	Interatherium sp. Protypotherium australe Protypotherium praerutilum
Hegetotheriidae	—	Hegetotherium cf. H. mirabile	Hegetotherium sp.	Hegetotherium mirabile	Hegetotherium mirabile
Litopterna Proterotheriidae	Prolicaphrium sanalfolensis Prothoatherium colombianus Megadolodus molariformis	—	Proterotherium sp.	Diadiaphorus robustus Diadiaphorus sp. Licaphrium floweri "Proterotherium" cavum Thoatherium minisculum	Licaphrium floweri "Proterotherium" internedium Thoatherium minisculum
Macraucheniidae	Theosodon sp. indet.	Theosodon sp.	Theosodon cf. T. gracilis	Theosodon lallemanti	—
Astrapotheria Astrapotheriidae	Xenastrapotherium kraglievichi Granastrapotherium snorki	—	Astrapotherium sp.	Astrapotherium magnum	Astrapotherium ?nanum Astrapotherium sp.
% HYPSODONT	33%	86%	56%	47%	54%

TABLE 11. Ungulate faunal resemblance indices (Simpson coefficients) among selected low-, intermediate-, and high-latitude Miocene faunas of South America. Simpson coefficients were calculated as (# of shared genera/# of genera in the smaller fauna)*100.

	La Venta	Chu-cal	Pampa Cas-tillo	Lower Santa Cruz
Chucal	14	—		
Pampa Castillo	11	57	—	
Lower Santa Cruz	8	57	100	—
Upper Santa Cruz	0	43	89	100

Patagonia, interatheriids declined dramatically in both diversity and abundance after the Santacrucian (M. Reguero, pers. comm.), although they evidently remained a dominant component of low-latitude faunas (i.e., La Venta, Colombia) through at least the middle Miocene (Stirton, 1953; Kay et al., 1997).

Many of the nonungulate elements of the Chucal Fauna are equally unusual in comparison to contemporaneous Patagonian faunas (e.g., very low rodent diversity, low abundance of nonchinchilline rodents, low glyptodontid abundance, absence, and/or low abundance of sloths; Table 12), further supporting the existence of a significant biogeographic and/or ecological barrier between the two regions during the middle Cenozoic.

Discussion and Conclusions

The revised faunal list for Chucal (Table 12) now includes 16 mammal species. The present list represents a two-thirds increase in the number of species relative to the preliminary faunal list (based on a single field season) presented in Flynn, Croft, et al. (2002); this is due to the addition of taxa recognized following a second field season (September 2001) and newly identified taxa represented only by postcrania. Also, an indeterminate, possibly new toxodontid was described by Bond and García (2002; see discussion above). Although the nonungulates from Chucal have yet to be described, preliminary analyses indicate that, for the most part, they pertain to taxa recorded in other Santacrucian faunas, consistent with the ungulate-based biochronologic age estimate and with the geochronologic constraints of bracketing high-precision radioisotopic dates. As is true for the ungulates, however, several species

TABLE 12. Revised taxonomic list of the Chucal fauna.

Mammalia
  Notoungulata
    Toxodontidae
      Toxodontidae ?new taxon (*Palyeidodon* [?] sp. of Bond and García, 2002)
      Nesodontinae
        Nesodon imbricatus
        Adinotherium sp. indet.
    Mesotheriidae
      Mesotheriinae
        Altitypotherium paucidens (Undescribed Taxon A, aff. *Microtypotherium* sp. of Flynn, Croft, et al., 2002)
        Altitypotherium chucalensis (Undescribed Taxon B, aff. *Microtypotherium* sp. of Flynn, Croft, et al., 2002)
        Eotypotherium chico (Undescribed Taxon C, aff. *Typotheriopsis* sp., *Plesiotypotherium* sp., or *Eutypotherium* sp. of Flynn, Croft, et al., 2002)
    Hegetotheriidae
      Hegetotheriinae
        Hegetotherium cf. *H. mirabile* (cf. *Pseudohegetotherium torresi* of Flynn, Croft, et al., 2002)
  Litopterna
    Macraucheniidae
      Cramaucheniinae
        Theosodon sp. indet.
  Rodentia
    Chinchillidae
      Chinchillinae
        Undescribed taxon
    Dasyproctidae
      Neoreomys sp. nov.
    Octodontoidea
      Undescribed taxon
  Xenarthra
    Cingulata
      Dasypodidae
        Euphractini sp. indet.
      Glyptodontidae sp. indet.
      Peltephilidae
        Peltephilus sp.
Mammalia incertae sedis
        Tiny Undescribed Taxon 1
        Tiny Undescribed Taxon 2

from Chucal are unique compared to other Santacrucian faunas, including the earliest known chinchilline chinchillid (Flynn, Croft, et al., 2002) and a new basal octodontoid rodent. The presence of these distinctive taxa (both ungulates and other mammals) at Chucal demonstrates that significant provinciality had begun to develop among South American faunas by at least early Miocene time, possibly attributable to Andean tectonics or other paleoenvironmental factors.

TABLE 13. Body masses of mesotheriines estimated by regression of M1 length on body mass for extant ungulates (based on the equation: ln[mass in g] = 3.09*ln[M1 length in mm] + 1.21 [Damuth, 1990]) and caviomorph rodents (based on the equation ln[mass in g] = 3.09*ln[M1 length in mm] + 3.08 [Croft, 2000]). Holotypes are indicated by an asterisk (*) following the specimen number.

Taxon	Specimen	Age	M1 length (mm)	Ungulate body mass estimate (kg)	Rodent body mass estimate (kg)
Eotypotherium chico	SGOPV 5157*	late early Miocene	9.5	3.52	22.85
Altitypotherium paucidens	SGOPV 4038*	late early Miocene	12.5	8.22	53.34
Altitypotherium chucalensis	SGOPV 4100*	late early Miocene	10.4	4.66	30.22
Microtypotherium choquecotense	GB 002*	middle Miocene	11.6	6.53	42.35
Plesiotypotherium achirense	MNHN ACH 26*	middle Miocene	17.0	21.26	137.95
Eutypotherium lehmannitschei	MLP 12-1701*	late middle Miocene	14.6	13.28	86.19
Eutypotherium superans	MACN 11079*	late middle Miocene	14.1	11.93	77.40
Caragua New Taxon	SGOPV 4004*	late middle Miocene	16.5	19.39	125.79
Typotheriopsis chasicoensis	MLP 12-1666*	early late Miocene	17.3	22.44	145.61
Typotheriopsis silveyrai	MLP 36-XI-10-2*	middle late Miocene	16.9	20.88	135.46
?Pseudotypotherium sp.	MACN 8010	late Miocene–early Pliocene	23.8	60.13	390.17
?Pseudotypotherium sp.	MACN 1111	late Miocene–early Pliocene	19.2	30.97	200.92
Mesotherium cristatum	MACN 2036	late Pliocene–early Pleistocene	21.8	45.85	297.48
Mesotherium pachygnathum	MACN 1665	late Pliocene–early Pleistocene	24.4	64.94	421.368
Mesotherium maendrum	MACN 2648*	late Pliocene–early Pleistocene	16.1	17.97	116.61

Of the eight species of ungulates present at Chucal, seven (all but *Theosodon*) have hypselodont (rootless, ever-growing) or very hypsodont (very high-crowned) cheek teeth. In modern mammals, hypsodonty is highly correlated with dietary preference and can be used to distinguish animals feeding on vegetation in open habitats (which have more hypsodont teeth) from those feeding in closed habitats (Janis, 1988, 1995; Williams & Kay, 2001; Janis et al., 2002). This high proportion of hypsodont taxa suggests that the mammals of the Chucal Fauna lived in a relatively dry, open environment, especially as compared to roughly contemporaneous faunas from elsewhere in South America (Table 11). Two of the three rodent species at Chucal for which cheek teeth are known are also very hypsodont or hypselodont, a proportion congruent with that of the ungulates. The single hypselodont rodent taxon (the chinchilline) dominates the rodent fauna numerically, with only a single specimen representing each of the other two taxa.

The phylogenetic analysis presented here suggests that the smallest mesotheriines (*Eotypotherium, Altitypotherium,* and *Microtypotherium*; Table 13) represent early diverging members of

the clade. Although the size of the most recent common ancestor (MRCA) of mesotheriines and trachytheriines cannot be reliably estimated without a more detailed knowledge of the topology within Trachytheriinae, the presence of four small species near the base of Mesotheriinae (the smallest being the nearest outgroup to all the remaining mesotheriines) suggests that the initial diversification of mesotheriines took place at diminutive body size. The latest-occurring mesotheriines (*Mesotherium* spp.) are also the largest, but there does not appear to be a progressive or stepwise increase in body size throughout the group's evolution (Table 13); most mesotheriines are similar in size from the late middle Miocene (approx. 12 Ma) until the beginning of the Pliocene (approx. 5 Ma). Of the two regression equations used to estimate mesotheriine body masses, the ungulate regression appears to be more appropriate for these notoungulates, even though mesotheriines more closely resemble extant caviomorph rodents than artiodactyls or perissodactyls; mass estimates based on rodents seem unreasonably high.

Perhaps the most striking aspect of the Chucal Fauna, especially given its age, is the abundance and diversity of mesotheriine notoungulates. In

terms of abundance, Chucal is similar to other early to middle Miocene faunas of Bolivia, where mesotheriines constitute a significant proportion of identified specimens (e.g., Cerdas; MacFadden et al., 1995). This is in stark contrast to both high latitudes (Argentina) and the lower latitudes (e.g., La Venta, Colombia; Kay et al., 1997) of South America, where early to middle Miocene mesotheriines are uncommon or absent. In terms of mesotheriine diversity, the Chucal Fauna is unique, even compared to Bolivian faunas also containing mesotheriines; no other South American locality records three contemporaneous species of this clade. Bracketing dates indicate the age of the Chucal mesotheriines is at least 17.5 Ma (or ~17–18 Ma taking into account the uncertainty of the date from levels overlying the fauna), pre-dating the earliest Patagonian mesotheriines (*Eutypotherium* of the Mayoan SALMA) by more than 5 million years. Although slightly younger than the Chucal specimens, other Bolivian taxa also significantly pre-date *Eutypotherium*; both *Microtypotherium* cf. *M. choquecotense* and *Plesiotypotherium minor* have been collected from the Quehua Formation near Cerdas, Bolivia, (16.5–15.5 Ma; MacFadden et al., 1995). Consistent with the conclusion reached by Reguero and Castro (2001) based on trachytheriine relationships, the presence of the earliest members of the Mesotheriinae in northern Chile and Bolivia, including early diverging species, suggests that the intermediate latitudes of South America served as a center of diversification for this clade of notoungulates (Croft, Flynn, & Wyss, 2003). Only later did this clade disperse to higher latitudes, not becoming common there until some 10 million years after the group's origin. Although the earliest taxa occur in the modern high-altitude Altiplano or Puna, the potential role of elevation in this diversification is uncertain; paleoelevations at these latitudes certainly were lower than modern elevations, and definitively low-elevation faunas of this age are unknown from the midlatitudes.

Acknowledgments

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