New Mesotheriidae (Mammalia, Notoungulata, Typotheria), geochronology and tectonics of the Caragua area, northernmost Chile

John J. Flynn[a,*], Darin A. Croft[b,a], Reynaldo Charrier[c], André R. Wyss[d,a], Gérard Hérail[e], Marcelo García[f]

[a]*Department of Geology, The Field Museum, 1400 S. Lake Shore Drive, Chicago, IL 60605, USA*
[b]*Department of Anatomy, Case Western Reserve University School of Medicine, 10900 Euclid Av., Cleveland, Ohio 44106-4930, USA*
[c]*Departamento de Geología, Universidad de Chile, Casilla 13518, Correo 21, Santiago, Chile*
[d]*Department of Geological Sciences, University of California-Santa Barbara, Santa Barbara, California 93106, USA*
[e]*IRD, LMTG, Université Paul Sabatier, 38 rue des 36 Ponts, 31400 Toulouse, France*
[f]*SERNAGEOMIN, Av. Santa Maria 0104, Providencia, Santiago, Chile*

Abstract

Few mammal fossils were known from the Altiplano or adjoining parts of northern Chile until recently. We report a partial mesotheriid palate from the vicinity of Caragua (Huaylas Formation) in northernmost Chile. The new material helps resolve contradictory taxonomic assignments (and age implications) of the two mesotheriid specimens previously reported from the area. Herein we refer all three mesotheriid specimens to a new taxon, *Caraguatypotherium munozi*, which is closely related to *Plesiotypotherium*, *Typotheriopsis*, *Pseudotypotherium*, and *Mesotherium*. This phylogenetic placement permits a revised biochronologic estimate of a post-Friasian/pre-Huayquerian ($\sim$15–9 Ma) age for the Huaylas Formation, consistent with new radioisotopic dates from the upper Huaylas Formation and its bracketing stratigraphic units. Improved geochronologic control for the Huaylas Formation has important implications for the timing of tectonic events in the Precordillera/Altiplano of northern Chile. Structural, stratigraphic, and temporal data suggest the onset of rapid, progressive deformation shortly after the deposition of the older Zapahuira Formation, continuing at least partly through deposition of the Huaylas Formation. Deposition of the Huaylas Formation was short lived (between $\sim$10–12 Ma), possibly stemming from activity on the Copaquilla-Tignámar Fault in the eastern Precordillera. This deformation is associated with the development of the Oxaya Anticline and activity of the Ausipar Fault west of the study region on the frontal limb of the anticline in the westernmost Precordillera. Faulting and folding occurred rapidly, beginning at $\sim$11.4 Ma (shortly after deposition of the youngest extrusives of the Zapahuira Formation) and before $\sim$10.7 Ma (the age of the gently dipping horizons within the upper Huaylas Formation that overlie the mammal fossils and an intraformational unconformity). Mesotheriids are the only Tertiary fossil mammals known from the Precordillera of northernmost Chile thus far; the group is common and diverse in faunas from the Altiplano of Bolivia (and a fauna recently recovered from the Chilean Altiplano), in contrast to most higher-latitude and tropical assemblages. This distinctiveness indicates that intermediate latitudes may have been biogeographically distinct and served as a center of diversification for mesotheriids and other groups of indigenous South American mammals.

Keywords: Chile; Fossil mammals; Geochronology; Miocene; Paleontology; Tectonics

Resumen

Damos a conocer el hallazgo de un resto parcial de un paladar de mesotérido en la Formación Huaylas en la cercanía de Caragua, en la Precordillera del norte de Chile, el cual complementa el escaso conocimiento que se disponía hasta hace poco sobre restos fósiles de

* Corresponding author. Division of Paleontology, American Museum of Natural History, New York, NY 10024, USA. Tel.: +1 212 769 5806; fax: +1 212 769 5842.
E-mail addresses: jflynn@amnh.org (J.J. Flynn), dcroft@case.edu (D.A. Croft), rcharrie@cec.uchile.cl (R. Charrier), wyss@geol.ucsb.edu (A.R. Wyss), gherail@paris.ird.fr (G. Hérail), mgarcia@sernageomin.cl (M. García).

mamíferos en el Altiplano y regiones adyacentes del norte de Chile. Este nuevo material permite resolver las asignaciones taxonómicas contradictorias (e implicaciones cronológicas) de los dos especímenes de mesotherido previamente informados para esta formación en el área. Referimos a los tres especímenes a un nuevo taxón, *Caraguatypotherium muñozi*, el cual está cercanamente relacionado con *Plesiotypotherium*, *Typotheriopsis*, *Pseudotypotherium* y *Mesotherium*. Esta asignación filogénica permite una estimación biocronológica revisada correspondiente a una edad post-Friasiano/pre-Huayqueriense (∼15–9 Ma) para la Formación Huaylas, la cual está acorde con las nuevas edades radioisotópicas obtenidas en esta formación y las unidades estratigráficas infra y suprayacentes. El mejor control geocronológico de la Formación Huaylas tiene importantes implicaciones para la cronología de los eventos tectónicos que afectaron a la Precordillera y el Altiplano del norte de Chile. Antecedentes estructurales, estratigráficos y cronológicos ponen en evidencia el inicio de una rápida deformación poco después de la depositación de la Formación Zapahuira, la cual habría continuado, por lo menos parcialmente, durante la depositación de la Formación Huaylas. La sedimentación de esta formación se realizó en corto tiempo, entre ∼10–12 Ma, y es probablemente consecuencia de la actividad de la Falla Copaquilla-Tignámar en la parte oriental de la Precordillera. Este episodio de rápida deformación, que se relaciona con la actividad de la Falla Auripar, en el borde occidental de la Precordillera, y que dio origen al Anticlinal Oxaya, se produjo entre ∼11,4 Ma, poco después de la depositación de la Formación Zapahuira y ∼10,7 Ma, edad de los depósitos horizontales de la Formación Huaylas. Estos últimos recubren con una discordancia intraformacional a los depósitos syntectónicos de esta formación, que contienen los niveles con restos fósiles. Los mesotéridos son el único tipo de mamífero terciario conocido hasta ahora en la Precordillera del norte de Chile. Este es un grupo común y diverso en las faunas fósiles del Altiplano de Bolivia y en una fauna recientemente descubierta en el Altiplano chileno, hecho que contrasta con la mayoría de las asociaciones faunísticas tropicales y de latitudes más altas. Este carácter de la fauna altiplánica sugiere que estas latitudes intermedias podrían haber sido distintas desde el punto de vista biográfico y actuado como centros de diversificación para los mesotheridos y otros grupos de mamíferos autóctonos sudamericanos.

1. Introduction

Only a single Tertiary mammal fauna (the Río Frías Fauna; Roth, 1908; 1925; Kraglievich, 1930) was known in Chile prior to the 1980s. Since 1986, our teams have uncovered numerous well-represented mammal faunas from the southern (Wyss et al., 1987; Flynn et al., 1988; 2002b) and central (see summary and references in Flynn and Wyss, 1998, 2004) Chilean Andes. Mammal fossils from the Altiplano and adjoining parts of northern Chile (Fig. 1) have

been particularly rare, known only in isolated fragments (Bargo and Reguero, 1989; Salinas et al., 1991; Charrier et al., 1994). The discovery of a toxodontid humerus (Charrier et al., 1994) prompted our 1998 paleontological survey of the region, which uncovered many fossiliferous sites from multiple stratigraphic horizons. This fossil assemblage, the Chucal Fauna (Flynn, 2002; Flynn et al., 2002a; Charrier et al., 2002; Croft et al., 2004; see also Charrier et al., 1999, 2000), represents the first Tertiary mammal fauna known from the Chilean Altiplano.
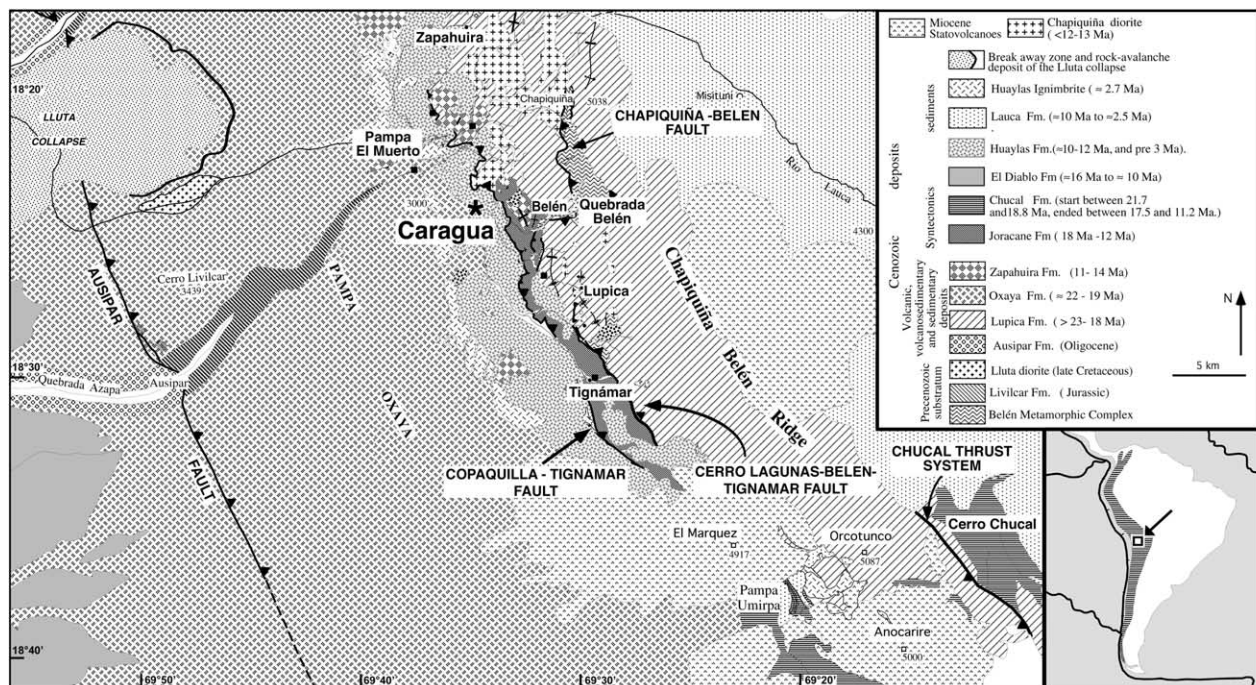

Fig. 1. Map indicating major geographic, morphostructural, and tectonic features, as well as stratigraphic units and their estimated age ranges, for the Caragua area of northernmost Chile and surrounding regions of the Precordillera and Altiplano.

We recovered hundreds of additional specimens during a follow-up expedition in 2001, doubling the number of mammalian taxa recorded in the Chucal Fauna. In conjunction with that work, we briefly prospected exposures of the Huaylas Formation near the confluence of Quebradas Belén and Lupica (Caragua area) to assess its paleontological potential (Figs. 1 and 2). We recovered craniodental remains of a mesotheriid from strata that previously yielded two such specimens (Bargo and Reguero, 1989; Salinas et al., 1991). Although Bargo and Reguero (1989) present only limited locality and stratigraphic information, both previous specimens were likely derived from the same locality (Salinas et al., 1991). It is notable therefore that the mesotheriid specimens described in previous reports were assigned to different taxa (aff. *Eutypotherium* sp., Bargo and Reguero, 1989; *Typotheriopsis* sp., Salinas et al., 1991) each having dissimilar implications for the age of the stratigraphic unit in which they occur (undifferentiated middle Miocene in the former, late Miocene [8–9 Ma] in the latter). Although units bracketing the fossiliferous horizons have

been radioisotopically dated, the Huaylas Formation was first dated only recently (Wörner et al., 2000; García et al., 2002). Prior to that dating, most geologic studies of the area accepted the age suggested by Salinas et al. (1991) for the Huaylas Formation (including the informal 'Estratos de Caragua' of Salinas et al., 1991), which had important implications for the timing of deposition and subsequent deformation of the unit (Naranjo and Paskoff, 1985; Muñoz and Charrier, 1996; García, 1996; García et al., 1997; Flynn et al., 2002a).

The abstract by Bargo and Reguero (1989), reporting on a specimen collected in 1969 by Chilean geologist David Pacci (MLP 86-VII-10-1), was the first account of a Tertiary mammal from northernmost Chile. On the basis of the configuration and position of the lobules, they referred this specimen, a right mandibular fragment with m1–3, to a mesotheriine 'aff. *Eutypotherium*,' noting that it was much closer in morphology to that middle Miocene Patagonian taxon than to mesotheriids recorded from the Bolivian Altiplano. This assignment led Bargo and Reguero (1989) to suggest a middle Miocene age for the Caragua locality strata, as well as a geographic range extension from Patagonia to more northerly tropical latitudes for the *Eutypotherium* lineage/clade ('estirpe').

The extended abstract of Salinas et al. (1991) presented a preliminary description and analysis of a second, much more complete mesotheriid specimen (SGO PV 4004) collected by Nelson Muñoz from the same area and general stratigraphic interval, low in the Huaylas Formation. The elements of this specimen were found in articulation (Salinas et al., 1991), including a virtually complete skull and mandibles (Figs. 3 and 4), eight vertebrae (atlas attached to the skull, axis and six subsequent vertebrae associated with another block; Fig. 5), an articulated left distal humerus and complete ulna and radius (Fig. 6A), distal portions of the right ulna and radius, and moderately complete hands (both sides, right manus in articulation with distal ulna and radius; Fig. 6B and C). Salinas et al. (1991) presented photos and preliminary descriptions of various anatomical details of the skull and jaws. The authors referred this material to *Typotheriopsis* sp., suggesting that it might pertain to a new species. They also indicated that the specimen possessed several features more advanced than those in *Typotheriopsis chasicoensis* and *T. silveyrai*, suggesting an early Huayquerian (rather than Chasicoan) age for this specimen (Salinas et al., 1991).

The morphology revealed by the specimen collected in 2001, the rough temporal correspondence between the Huaylas Formation and various mesotheriid-bearing faunas in the Altiplano of Chile (i.e., the recently described but older Chucal Fauna) and Bolivia, and the conflicting age implications of the two previously reported specimens highlight the need for a reanalysis of the Caragua mesotheriid material. We reassess the anatomical information for all three specimens to evaluate whether they represent a single species (the simplest, or null, hypothesis,
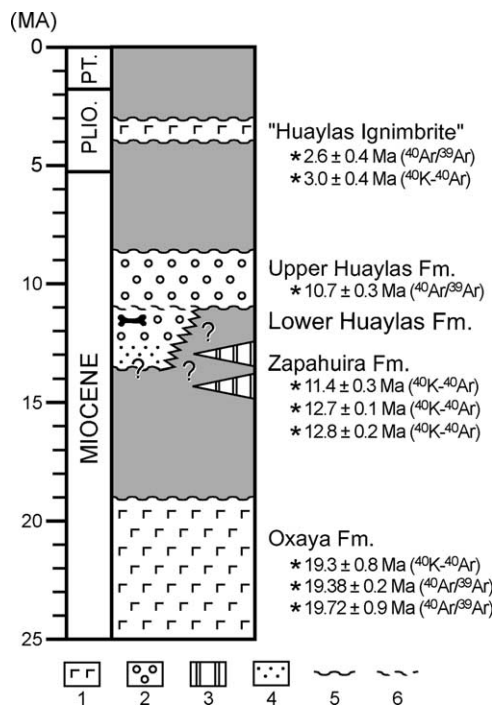

Fig. 2. Schematic stratigraphic column illustrating the late Cenozoic formations present in the Caragua area and their approximate temporal durations (see text for details). Question marks (?) indicate uncertainty in the superpositional relationship(s) between the lower Huaylas Formation and the various Zapahuira Formation extrusives; the bone symbol indicates the approximate location of the mesotheriid-bearing localities in the lower Huaylas Formation; asterisks (*) indicate associated radioisotopic dates. The Lupica (∼23–18 Ma) and Joracane (∼18–12 or 11 Ma) Formations may roughly correlate to the Oxaya and Zapahuira Formations, respectively, but the former do not occur at Caragua and therefore are of limited utility in constraining the age of the fossil-bearing portions of the lower Huaylas Formation. Key to lithologic symbols: (1) ignimbrite, (2) conglomerate, (3) basaltic lava, (4) sandstone, (5) unconformity, and (6) intraformational unconformity.
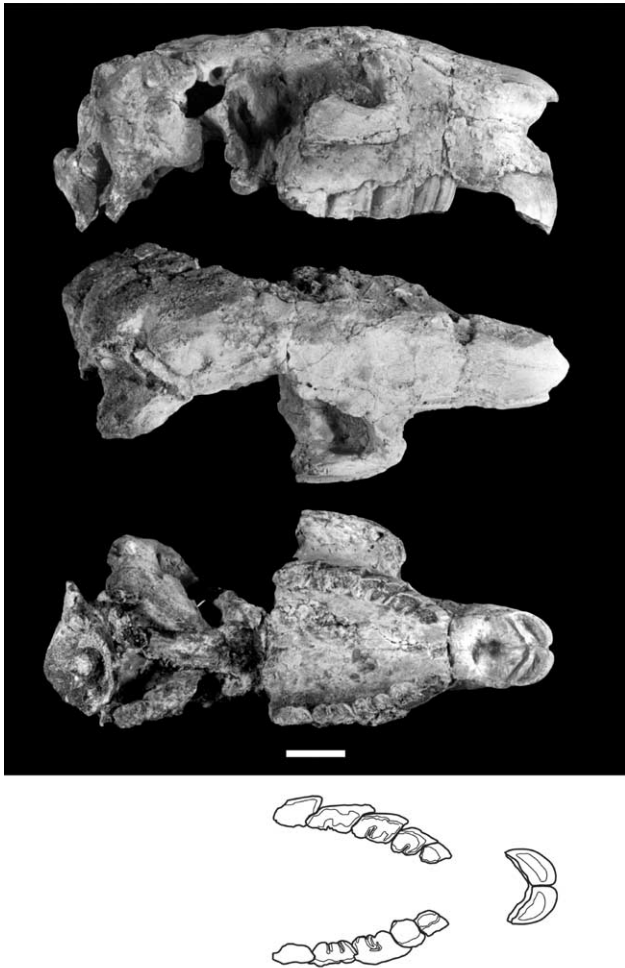
Fig. 3. Skull of SGO PV 4004, holotype of *Caraguatypotherium munozi*, in left lateral (top, pictured as right), dorsal (middle, flipped to match lateral), and palatal (bottom, inverted to match lateral) views, with line drawing of dentition below. Scale bar equals 2 cm.

Fig. 4. Mandibles and vertebrae of SGO PV 4004, holotype of *Caraguatypotherium munozi*. Mandibles in left lateral (top, pictured as right) and occlusal (bottom, inverted to match lateral, with line drawing of dentition below) views. Scale bars equal 2 cm.

in that all the mammal specimens recovered from this area are mesotheriids, which are otherwise low in diversity in most South American faunas) or multiple species (faunas containing more than a single species are known from some parts of the Altiplano; e.g., Achiri, Villarroel, 1974a; Cerdas, Villarroel, 1978; Chucal Fauna, Flynn et al., 2002a) and undertake a preliminary phylogenetic analysis.

Mesotheriids are in much need of systematic revision, complicating taxonomic assignments of newly discovered forms (Pascual and Bondesio, 1985; Cerdeño and Montalvo, 2001; Flynn et al., 2002a; Croft et al., 2004). The most recent revision of the mesotheriine subclade (Francis, 1965) recognized four valid 'genera'. However, that work included only Argentine forms because it predated publication of the first reports of taxa from Bolivia (beginning with Villarroel, 1974a, b). Forms recognized by Francis (1965; South American Land Mammal 'Age' [SALMA] sequence following Flynn and Swisher, 1995) include the following: *Eutypotherium* (middle Miocene Mayoan SALMA), *Typotheriopsis* (late Miocene Chasicoan

and Huayquerian SALMAs), *Pseudotypotherium* (late Miocene–early Pliocene Huayquerian, Montehermosan, and Chapadmalalan SALMAs), and *Mesotherium* (Pliocene–Pleistocene Uquian [Marplatan stage/age, Cione and Tonni, 1995] and Ensenadan SALMAs). There are six potentially valid mesotheriine genera—the four just listed plus *Microtypotherium* (Villarroel, 1974b; middle Miocene ?Friasian and/or ?Colloncuran SALMAs) and *Plesiotypotherium* (Villarroel, 1974a; middle-late Miocene ?Friasian, ?Colloncuran, ?Mayoan, and/or ?Chasicoan SALMAs)—a number likely to increase with the analysis of recently discovered faunas (e.g., Chucal). Regardless of the taxonomic details, all mesotheriines clearly possess diagnostic dental attributes of the loss of upper I2–P2 and lower i3–p3, among other characteristics (Francis, 1965; Villarroel, 1974a; Cerdeño and Montalvo, 2001; Flynn et al., 2002a).

The presence of both upper and lower dentitions in SGO PV 4004 (Salinas et al., 1991) permits direct comparisons
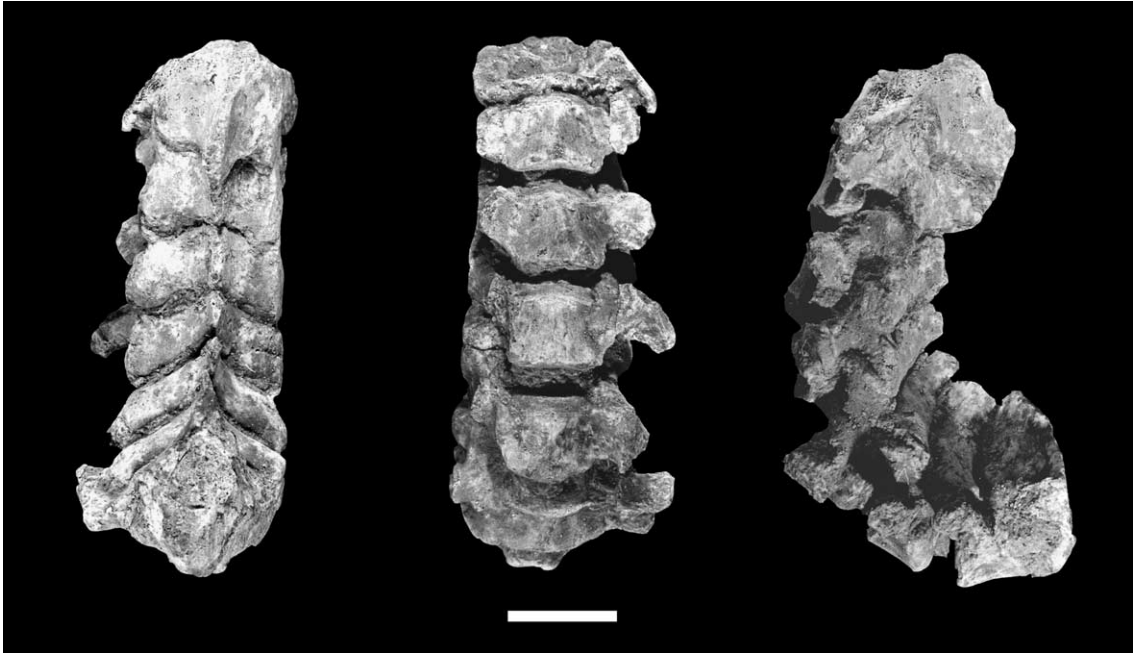
Fig. 5. Vertebrae of SGO PV 4004, holotype of *Caraguatypotherium munozi*. Axis and six subsequent vertebrae in dorsal (left), ventral (middle), and left lateral (right) views. Anterior is to the top. Scale bar equals 2 cm.

Fig. 6. Selected limb bones of SGO PV 4004, holotype of *Caraguatypotherium munozi*. (A) Left distal humerus and articulated ulna and radius in internal (top) and external (bottom) views. (B) Left hand in dorsal view. (C) Right hand and distal forearm in lateral view. Scale bars equal 2 cm.

with both MLP 86-VII-10-1 (Bargo and Reguero, 1989) and SGO PV 4056 (the new partial maxilla). These three specimens exhibit no clear discrete morphological differences, and their metric differences fall within the expected ranges of variation for a single mesothere species. Comparisons of the Caragua material with other mesotheriines indicate that the Caragua species possesses a unique combination of primitive and derived character states that differentiate it from all previously described mesotheriids. Salinas et al. (1991) recognized aspects of its distinctiveness but elected to assign it to *Typotheriopsis*. A preliminary phylogenetic analysis of mesotheriines reveals no synapomorphies shared by the Caragua form and *Typotheriopsis*; we therefore refer the Caragua material to a new taxon.

We use several abbreviations in our discussion; they are as follows: FMNH = Field Museum of Natural History, Chicago; MLP = Museo de La Plata, Argentina; OTU = operational taxonomic unit; and SGO PV = vertebrate paleontology collections of the Museo Nacional de Historia Natural, Santiago, Chile. We indicate upper tooth loci by uppercase letters (e.g., I1, P2, M1) and lower tooth loci by lowercase letters (e.g., i1, p2, m1).

2. Geographic location and stratigraphy

The Caragua area is located in the Precordillera, on the western flank of the Altiplano (Fig. 1). It is situated west of the Western Cordillera (the present-day volcanic arc) and thus west of the Chapiquiña-Belén Ridge, which formed between the west-vergent thrust system developed along the Precordillera (Muñoz and Charrier, 1996) and the east vergent thrust-system (Chucal system) along the Western Cordillera (Charrier et al., 1999, 2000, 2002, 2004; Hérail and Riquelme, 1997; Riquelme and Hérail, 1997).

Our new mesotheriid specimen derives from the same stratigraphic unit and the same general area as previous specimens, but the name 'Caragua,' as used in prior studies, does not appear on standard geologic or topographic maps of the region, and the geographic information in the prior reports is less precise than that available to us (using global positioning systems (GPS)). Bargo and Reguero (1989) provided only a general location for the Caragua locality at the confluence of the Lupica and Belén quebradas (ca. 18°25′S, 69°35′W), did not specify its position relative to the flanks of either quebrada, and considered it derived from the Formación Oxaya (likely from the middle member). Their usage reflects a broadly conceived 'Formación Oxaya' that spans 18.0–2.9 Ma and includes strata that have been partitioned more finely into multiple, separate formations. Salinas et al. (1991) reported similar geographic coordinates (18°28′S, 69°34′W), more detailed locality position information (p. 314, north side of Quebrada Belén; their Fig. 1, north of the Quebrada Belén/Lupica confluence, NNW of Quebrada Belén), and a more refined stratigraphic position (informal 'Estratos de Caragua' above

the Oxaya Formation). The strata that lie unconformably (in angular and erosional discordance) above the distinctive red-colored (due to superficial alteration) volcaniclastic strata, with strong columnar jointing, of the Oxaya Formation (more narrowly defined than in Bargo and Reguero, 1989) can be assigned to the Huaylas Formation (García et al., 1996). Our observations along Quebrada Belén indicate that the Huaylas Formation in this area is a largely conglomeratic, gray-colored sedimentary unit with sporadic finer intervals, especially in the basal levels that crop out in the western exposures. The mesotheriid specimens from the various Caragua localities all appear to be from within the lowest part of the formation in the finer sediments (sands to conglomeratic sands). Salinas et al. (1991) noted that the unit varies widely in facies but crop out only in a discontinuous band along the lower courses of the Quebradas Belén and Lupica. The westernmost parts are massive, moderately consolidated siltstones and sandstones with sporadic gravel interbeds in the form of paleochannels; in the central portions, gravels with angular and subangular clasts and sandy matrix dominate; and in the east, immature to mature gravels with conglomerate, sandstone, and siltstone layers appear (Salinas et al., 1991). The lowest levels of the Huaylas Formation south of Quebrada Belén (and SE of the Quebradas Belén/Lupica confluence), including the sandy pebble conglomerate that produced the new specimen, appear coarser than those that yielded the more complete specimen reported by Salinas et al. (1991). Muñoz and Charrier (1996; Muñoz discovered SGO PV 4004) indicated that SGO PV 4004 came from lacustrine beds of the lower Huaylas Formation. We provide the general location of the Caragua region and a schematic stratigraphic column in Figs. 1 and 2.

Another unit in Pampa El Muerto, near the Caragua area, the Zapahuira Formation, has bearing on the age of the Huaylas Formation. García (1996) and García et al. (1996) defined and discussed this lenticular, up to 600 m thick, mainly andesitic unit, noting its interposition between the Oxaya Formation and the coarse gravels of the Huaylas Formation wherever it occurs. On the basis of 10 ^{40}K–^{40}Ar whole-rock dates from various flows (separated from one another by ≥20 km; García, 1996, 2001; García et al., 1996) that range from 11.4±0.3 Ma (G-45 from Pampa El Muerto) to 15.7±0.6 Ma (G-25), as well as a ^{40}Ar/^{39}Ar whole-rock date (slightly disturbed spectrum) of 15.1±0.1 Ma (Wörner et al., 2000), the lavas of the Zapahuira Formation are considered to span ∼16–12 Ma (middle Miocene; García, 2001; García et al., 2002). Although the east-dipping Oxaya and Zapahuira formations are progressively onlapped in a low-angle progressive unconformity (García et al., 2002) by the Huaylas Formation, the Zapahuira Formation does not appear to be directly overlain anywhere by the fine-grained deposits that are characteristic of the lower parts of the Huaylas Formation. García (1996) and García et al. (1996) also pointed out that the Zapahuira Formation is composed

largely of volcanics that represent distal lava flows derived from stratovolcanoes in the surrounding region. Because there are many different volcanoes of middle Miocene age in the region, it is likely that the laterally discontinuous lenticular flows are derived from separate sources and may have widely different ages. This conclusion is supported by the distinctly different dates and relatively wide age range of the dated flows, though they have generally similar petrographic features. It might be preferable to identify and name each individually (associating it with its particular source stratovolcano) rather than lumping them into a single formation, but sedimentary cover (e.g., Huaylas Formation) and faulting would make this difficult. Because of the short, rapid phase of deformation associated with the Zapahuira–Huaylas transition, as we discuss subsequently, such fine-scale local analyses of age, structural relations, and stratigraphic contacts should make it possible to determine whether all Zapahuira Formation lavas underlie the Huaylas Formation or if some intertongue with, or are lateral equivalents to, Huaylas sediments, which would thereby better constrain the tectonosedimentary history of these units.

García (2001) noted that lavas of the Zapahuira Formation are parallel to, but erosionally unconformable with, the underlying Oxaya Formation strata, indicating a minor episode of erosion but no significant regional tectonism between the deposition of those units. García (2001) also observed that, in the Caragua region, strata of both the Oxaya and Zapahuira formations are inclined to the east, and the lower part of the Huaylas Formation (Copaquilla sequence) covers those units with a slight progressive unconformity and an onlap fan geometry, which indicates that deformation began after $\sim$11.4 Ma (the youngest Zapahuira date). The basal Huaylas levels progressively tilt, which indicates syntectonic deposition, whereas the younger, thickest, and most widespread parts of the Huaylas Formation dip gently and thus postdate the deformation. The syndepositional deformation of Huaylas Formation strata and the angular discordance between the coarse conglomeratic units of the upper Huaylas Formation and all underlying units document an intraformational unconformity in the Huaylas Formation. This unconformity appears to represent a continuation of deformation of the Oxaya and Zapahuira formations, as well as formation of the Oxaya Anticline through movement along the Ausipar fault near the central depression (Fig. 1). This phase of deformation ceased by the time of deposition of the gently dipping upper Huaylas beds, so integration of refined age constraints for the Huaylas Formation and bracketing units could provide a more precise estimate of fault activation and the timing of initiation and maximum deformation of the Oxaya anticline.

Our new Caragua mesotheriid specimen comes from S 18°27.829′, W 69°34.647′, 2923 $\pm$ 24 m elevation (using provincial South America 1956 datum), slightly above the Oxaya/Huaylas Formation contact (the Zapahuira Formation is absent), on west-facing slopes on the south side of Quebrada Belén, SE of the Quebradas Belén/Lupica confluence. The site appears to be situated slightly farther south and east of the site reported in Salinas et al. (1991). Our GPS coordinates, however, indicate a slightly more northerly position for our site than the coordinates given for it in Salinas et al. (1991). Assuming that the positions relative to major topographic features (e.g., quebradas) are correct and that our site lies slightly SE, the coordinate discrepancy likely reflects minor differences in maps or GPS base geoids. We therefore tentatively conclude that the new specimen is derived from the same area as those previously reported (herein termed the Caragua area) and the same general stratigraphic horizon near the base of the Huaylas Formation but likely is from a different locality than is the previous material.

3. Systematic paleontology

Mammalia Linnaeus, 1758
Notoungulata Roth, 1903
Typotheria Zittel, 1892
Mesotheriidae Alston, 1876
Mesotheriinae Simpson, 1945
Caraguatypotherium munozi Taxon novum
Figs. 3–7, Tables 1–3

Type species. Caraguatypotherium munozi

Holotype. SGO PV 4004, an articulated partial skeleton including a largely complete skull and mandibles (Figs. 3 and 4); eight vertebrae (all cervicals and first thoracic; Fig. 5); left distal humerus, left ulna and radius (Fig. 6A); right distal ulna and radius; and moderately complete hands (both sides, right manus in articulation with distal ulna and radius; Figs. 6B and C).

Hypodigm. MLP 86-VII-10-1, right mandibular fragment with m1–3 (Fig. 7A); SGO PV 4056, partial left maxilla with P4 and alveolus for P3 (Figs. 7B and C), likely associated with two vertebrae and bone pieces found in close proximity.

Type locality. Lower Huaylas Formation, Caragua area, northernmost Chile (Figs. 1 and 2). Two or three Caragua area localities yielded the three specimens assigned to this taxon: the north side of Quebrada Belén with geographic coordinates of ca. 18°25′S, 69°35′W (Bargo and Reguero, 1989) and 18°28′S, 69°34′W (Salinas et al., 1991; the holotype specimen locality). The third specimen was recovered from Loc. C-ALT-01-1 (Loc. JJF 9-5-01-1; S 18°27.829′, W 69°34.647′, 2923 $\pm$ 24 m elevation, using provincial South America 1956 datum), SE of the confluence of Quebradas Belén and Lupica and the locality(s) yielding the other specimens.

Age and distribution. Middle to late Miocene, pre-Huayquerian and post-Friasian SALMA, $\sim$10–15 Ma; radioisotopic dates likely constrain this as narrowly as $\sim$10.8–11.7 Ma (see text).
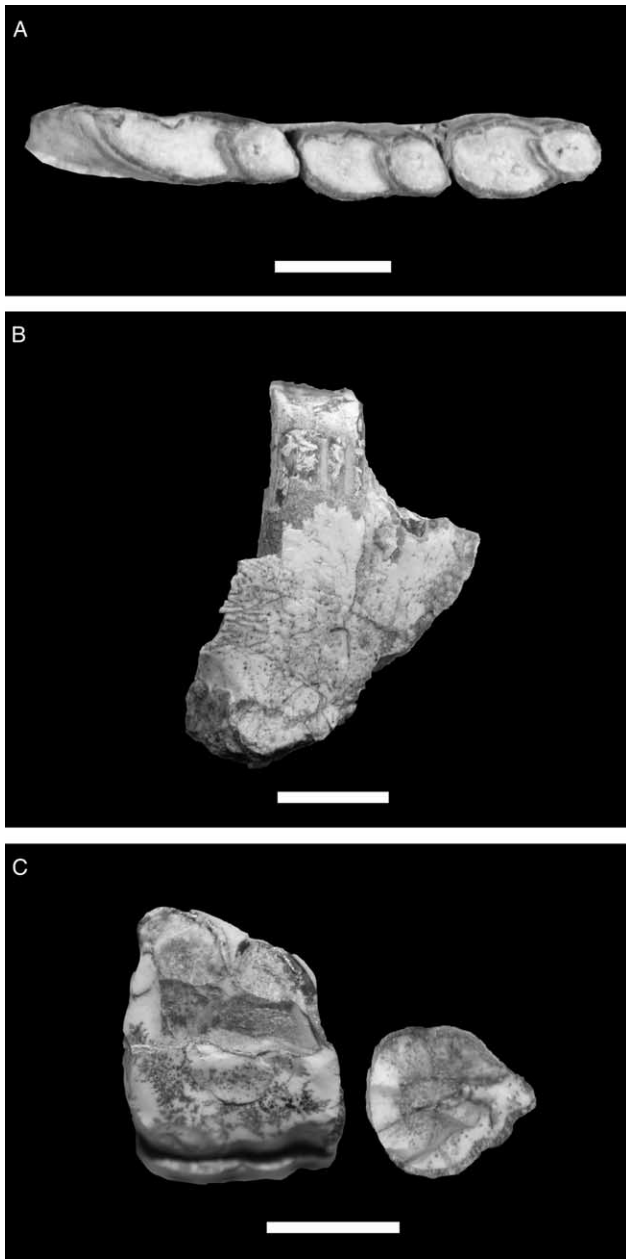
Fig. 7. Specimens referred to *Caraguatypotherium munozi*. (A) MLP 86-VII-10-1, partial right mandible with m1-3, occlusal view. Scale bar equals 1 cm. (B) SGO PV 4056, partial left maxilla with P4 and the alveolus of P3 in labial view. Scale bar equals 1 cm. (C) SGO PV 4056, partial left maxilla with P4 and the base of P3 in occlusal view. Scale bar equals 5 mm.

Etymology. After the area (*Caragua*) in which the holotype and all referred specimens were discovered and in reference to the familiar root (*typotherium*) used in mesothere names. Also in honor of geologist Nelson Muñoz, who discovered SGO PV 4004 and has contributed significantly to understanding the geology and tectonics of the region.

Diagnosis. Differs from trachytheriine mesotheriids on the basis of the presence of hypselodont cheek teeth; presence of three persistent lobes in upper molars; absence of I2-P2/i3–p3. Craniodental measurements for this taxon are

given in Tables 1–3, and molar 'imbrication' is illustrated in Fig. 8. Differs from all previously described mesotheriines in the presence of two pronounced lingual sulci on m3 talonid. Differs from other mesotheriine taxa as follows:

Differs from *Eutypotherium* in possessing character states (see Table 4 for this and subsequent taxa) 3(1); 4(2); 7(1); 9(2); 13(1); 22(1); and 29(1).

Differs from *Microtypotherium* in much larger size (approximately 50% larger, based on linear dental measurements) and in possessing character states 4(2); 9(2); 13(1); 16(2); 19(2); 29(1); 30(1); and 31(0).

Differs from *Plesiotypotherium* in possessing character states 6(1); 9(2); 13(1); 21(2); and 22(1).

Differs from *Typotheriopsis* in possessing character states 3(1); 6(1); 9(2); 19(2); and 27(0).

Differs from *Pseudotypotherium* in possessing character states 6(1); 9(2); 13(1); 22(1); 23(2); 28(0); and 31(0).

Differs from *Mesotherium* in possessing character states 3(1); 6(1); 13(1); 19(2); 21(2); 22(1); 23(2); 28(0); 29(1); and 31(0).

Description. We provide the first dental, cranial, and postcranial metrics for SGO PV 4004 and augment the preliminary morphological descriptions by Salinas et al. (1991). Description of the postcranial material is beyond the scope of this brief taxonomic report but would be useful in a more detailed analysis of mesotheriid anatomy, phylogeny, and diversification. We give approximate measures of the dentition and various skull and jaw features in Table 1. In addition, we describe the two other specimens (MLP 86-VII-10-1, Fig. 7A, Table 2; SGO PV 4056, Fig. 7B and C, Table 3) that we refer to this new taxon and discuss both similarities (including taxon synapomorphies) and differences (either within-species variability or features that indicate they belong to different species).

SGO PV 4004 represents a medium-sized mesothere (M1 length = 16.5 mm; range for family is approximately 9.5–24.5 mm). Its teeth are moderately to heavily worn, portions of some are broken, and the buccal borders of the right upper cheekteeth are eroded. Nevertheless, tooth crowns are moderately well preserved, and many morphological details of the crowns and exterior faces remain visible. The dental formula is 1.0.2.3/2.0.2.3. Homologies of the incisors can be determined only through comparisons with other typotheres, reconstruction of the phylogenetic transformations of the loss of incisors in particular loci, and great expansion of the remaining incisors. On the basis of previous analyses (e.g., Francis, 1965; Villarroel, 1974a), we presume the incisors in this taxon (as in all other mesotheriines) are I1 and i1–2. The upper and lower canines are absent, as are P1–2/p1–3 (the remaining upper premolars almost certainly are P3–4, and the sole lower premolar is p4). All teeth are hypsodont, and their roots appear quite elongate. We cannot determine whether some or all of the teeth are hypselodont without removing the surrounding bone near the root tips or X-raying the specimen, but it seems likely that this is the case, as it is for all other mesotheriines.

Table 1

Craniodental measurements (in mm) for SGO PV 4004, the holotype of *Caraguatypotherium munozi*

Mandible and lower dentition	
Jaw length (anterior edge i1 to back of jaw)	∼160.0
Mandible depth (below m2 trigonid)	36.75/37.30
Mandible depth (below m3 trigonid)	36.85/37.00
i1 (tip) to m3, along toothrow axis	91.20/89.80
i1–p4 diastema	18.70/17.70
p4–m3	57.20/55.75
i1 length	10.20/10.00
i1 width	5.95/6.65
i2 length	∼5.55/∼7.30
i2 width	5.40/5.20
p4 length	10.00/9.95
p4 width (trigonid)	4.50/4.90
p4 width (talonid, maximum)	6.40/6.35
m1 length	14.35/13.70
m1 width (trigonid)	5.95/5.95
m1 width (talonid, maximum)	7.10/7.15
m2 length	13.75/14.35
m2 width (trigonid)	∼5.50/6.10
m2 width (talonid, maximum)	6.15/6.15
m3 length	18.20/18.10
m3 width (trigonid, maximum)	5.85/5.80
m3 width (talonid)	5.50/5.40
Skull and upper dentition	
Skull length (tip nasals-back of skull)	163.00
Skull length (tip premax.- back of skull)	165.30
Palate length (along midline)	93.40
I1–P3 diastema length	20.40/20.45
Width across zygomatic arches	106.90
Zygomatic arch height (below orbit)	13.40
Orbit diameter (max.)	32.00
Skull height (tip of tooth row to top of skull)	67.10
Skull height (alveolar border to top of skull)	58.95
Snout height (top of incisor to top of nasals)	33.75
Nasal dorsal breadth	∼29.10
Maximum breadth of palate, internal (between inner borders M2 or M3)	40.50
Maximum breadth of palate, external (between outer borders M2 or M3)	∼59.00
Palate breadth at diastema	27.90
I1 length	17.40/17.10
I1 width (0.870 at tooth tip)	9.80/8.95
P3 length	9.65/10.50
P3 width	7.05/7.00
P4 length	10.85/∼11.00
P4 width	8.65/8.80
M1 length	16.45/∼14.40
M1 width	9.60/10.10
M2 length	∼16.10/∼15.25
M2 width	∼8.75/–
M3 length	17.10/∼15.50
M3 width	∼9.45/–

Measurements are provided for both left and right sides of the specimen (L/R) where applicable.

The skull and lower jaws are both ∼16 cm long (16.3 cm for nasals-posterior margin of the skull, 16.5 cm for tip of premaxilla-posterior margin of the skull). In comparison with its length, the skull is relatively narrow (≥10.7 cm bizygomatic breadth) and moderately high (6.7 cm).

The dorsal surface of the skull is smooth and gently arcuate, with maximum height above the orbits, tapering anteriorly to only 3.4 cm at the snout (incisor alveolus to top of nasals). Although the dorsal surface of the skull is worn, it appears to lack a pronounced sagittal crest. The dorso-ventrally thin nasals project far forward and reach the anterior end of the premaxillae, creating a deeply incised/retracted narial fossa. A heavy layer of cementum is present on all the teeth, encrusting all but their occlusal surfaces, including their roots. The zygomatic arch below the orbit is moderately robust (≥1.3 cm high). A shallow, suborbital fossa occurs on the dorsal surface of the maxilla that differs strongly from the deep, transversely oriented suborbital fossa present in *Typotheriopsis*. The dorsal surface of the braincase is eroded or missing, revealing some details of the endocast.

The mandible is deep with a markedly curved lower border. It is deepest below m2–3 (∼3.7 cm) and becomes progressively shallower anteriorly until it becomes inclined much more steeply dorsally (and thus very shallow) from the region below the diastema to the incisors. The mandibular rami are conjoined at the fused symphysis, which extends posteriorly to the m1 trigonid. In dorsal view, the jaws are uniformly narrow from the incisors to the anterior border of the premolars, then each ramus diverges posterolaterally, forming a V-shaped cheektooth row arcade. The snout and palate generally mirror this morphology, with a narrow snout (2.9 cm nasal breadth, 2.8 cm palate breadth at diastema) and straight lateral borders of the premaxilla-maxilla from the greatly enlarged pair of incisors, along the diastema, to the anterior edge of P3. The cheektooth row curves outward, first rapidly, then more gently, giving the palate a wide breadth and the upper cheektooth battery a U-shaped arc. The palate is moderately elongate (9.3 cm) and broad (maximum breadth of 5.9 cm [external, across outer edges of posterior molars] or 4.1 cm [internal, across inner edges]). The lower incisor–premolar diastema is slightly shorter than the upper diastema (∼1.8 versus 2.04 cm).

The total lower toothrow length (anterior tip of first incisor to posterior edge of m3, along toothrow axis) is ∼9 cm. The first lower incisor is larger than the second, especially in mesio-distal length. The lower cheekteeth are roughly equivalent in maximum breadth, though the talonid is wider than the trigonid on p4–m2 (only slightly on m2), and the reverse is true for m3. The lower cheekteeth all are

Table 2

Mandibular and dental measurements (in mm) for MLP 86-VII-10-1

Mandible depth (below m1)	31.50
Mandible depth (below m2)	37.00
m1 length	12.40
m1 width (talonid, maximum)	7.30
m2 length	12.30
m2 width (talonid, maximum)	6.30
m3 length	16.90
m3 width (trigonid, maximum)	6.40

Table 3
Dental measurements (in mm) for SGO PV 4056

P3 length	~7.3
P3 width	~6.4
P4 length	8.1
P4 width	~7.1

longer than wide (roughly 2–3 times), and in length, p4 ≪ m1 ∼ m2 ≪ m3. As is common in mesotheriids, the trigonids are much shorter than the talonids, especially on m3.

There is a single pair of upper incisors. Each is gliriform, chisel-tipped, and huge (∼1.73 cm mesio-distal length × ∼0.95 cm maximum bucco-lingual width). The upper incisors are comma-shaped in crown-view (long axis at 46° angle to midline, Salinas et al., 1991), and the occlusal surface of the incisor crowns slope steeply dorso-posteriorly from the sharp, arcuate anterior tip. In contrast to the lower dentition with its single premolar, two upper premolars are present, with P4 slightly larger than P3. The upper molars are significantly larger than the premolars, especially in length. M3 is longer than M1 and M2. Both M1 and M2 are approximately equal in length, but M1 is substantially broader than the other upper cheekteeth (width P4 < M1 > M2 < M3); M3 is the second widest.

P3 is present and is the smallest upper cheektooth. It is subtriangular in shape, with its apex situated antero-labially and its posterior edge forming the base, making the tooth longer than wide. The ectoloph has two prominent labial grooves, one between the parastyle and paracone and the other between the paracone and metacone. The occlusal surface of the tooth is simple and displays no enamel fossettes or sulci. P4 resembles P3 in being longer than wide but it is larger than P3, submolariform in form, and more
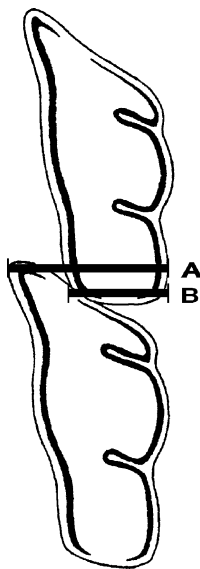

Fig. 8. Diagram of imbrication as used herein (modified from Villarroel, 1974a). Imbrication equals A (width from M2 parastyle to M1 hypocone)/B (width of M1 distal face).

quadrangular in shape. A shallow internal sulcus or enamel fold is present lingually, dividing the lingual side of the crown into two lobes. The fold is visible as a slight indentation in the lingual (cementum-covered) wall of the tooth, extending across approximately one-third the breadth of the crown.

The upper molars are moderately imbricated, more so than in *Eutypotherium* and more closely resembling *Typotheriopsis*. The middle of the three lobes on M1 is larger than the anterior but smaller than the posterior, and its sides are essentially parallel (possibly slightly convergent lingually).

In the lower cheekteeth, the m2 trigonid is significantly smaller (in length and area) than the talonid, and a pronounced internal enamel sulcus appears on the lingual side of the m3 talonid. The m3 talonid sulcus is observable on both the crown and the lingual wall of enamel, forming pillar-like lingual lobes (the anterior spans approximately one-third the lingual length of the talonid and the posterior the remaining two-thirds). An additional lingual sulcus, much less pronounced, is present near the posteriormost extent of the talonid.

MLP 86-VII-10-1 (Bargo and Reguero, 1989) consists of a partial right mandible preserving m1–3 and the posterior portion of the alveolus of p4 (Fig. 7A). We present the measurements in Table 2. SGO PV 4004 and MLP 86-VII-10-1 are similar morphologically; the trigonid comprises approximately 35% of tooth length in m1 and 40% of tooth length in m2. Both specimens also possess two sulci on the lingual side of the m3 talonid. SGO PV 4004 is slightly larger than MLP 86-VII-10-1, but the greatest difference in size (m1 length) represents a difference of only 0.2 log units, the minimum difference Gingerich and Winkler (1979, 1985) considered necessary to differentiate sympatric species on the basis of size alone. The same range of size variation (0.2 log units) occurs in a sample of mesotheriines (*Plesiotypotherium* sp.) from Nazareno, Bolivia (Oiso, 1991), suggesting this difference is typical for the group. Although the molars of SGO PV 4004 are proportionately narrower than those of MLP 86-VII-10-1, the variation also falls within the range exhibited by the Nazareno mesotheriines.

The most recently recovered specimen, SGO PV 4056, consists of a partial maxilla with left P4 and alveolus for P3 (Fig. 7B and C), likely associated with two vertebrae and bone pieces found in close proximity (the only other fossils found in this area). We present the measurements in Table 3. The crown of P3 is not preserved, but the base of the tooth is present in the alveolus, enabling comparison with SGO PV 4004. The outline of P3 is similar in the two specimens: subtriangular with a mesial apex, distal base, and two prominent grooves on the labial face. The tooth is absolutely larger in SGO PV 4004 but similarly proportioned. In both specimens, P3 is approximately 90% the length of P4. SGO PV 4004 and SGO PV 4056 share the presence of a lingual sulcus and two prominent labial sulci on P4; one of the sulci

Table 4
List of characters and character states used in phylogenetic analyses of mesothere relationships

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

Character 9, state 2, was listed as '3' by Cerdeño and Montalvo (2001) but not included in their table as such. Characters with multiple derived character states are ordered unless denoted by an asterisk (*).

is located directly opposite the lingual sulcus and the other near the anterior edge of the tooth. P4 is both relatively and absolutely longer in SGO PV 4004 than in SGO PV 4056 and exhibits an unusual pattern of wear in SGO PV 4056, but these differences are not atypical for mesotheriines.

4. Discussion

4.1. Taxonomy and phylogeny

Although there are slight metric differences between the three specimens from Caragua, they fall within the range of variation exhibited by what is presumed to be a single-species assemblage of mesotheriines from Nazareno, Bolivia (Oiso, 1991). Even if these metric differences are viewed as taxonomically significant, they traditionally

would be considered, at most, 'species'-level distinctions. Even so, it seems unlikely that two closely related sympatric species of very similar size and morphology would be present at Caragua, given the probable overlap in diet, habitat, and other attributes. We therefore consider it most likely that the three specimens are referable to a single species.

To determine the taxonomic affinities of the material from Caragua, we performed a phylogenetic analysis of mesotheriines based primarily on a modified, emended version of the data matrix of Cerdeño and Montalvo (2001). To their matrix of 13 OTUs and 25 characters, we add seven original characters gathered from our observations (characters 26–32) and two additional OTUs (*Caraguaty-potherium munozi* and *Microtypotherium choquecotense*). In addition, we quantify and redefine two of Cerdeño and Montalvo's (2001) characters (13, degree of dental

imbrication; 22, relationship of i1/i2) to reduce ambiguity in scoring character states. We present the list of characters we use in our preliminary analysis in Table 4 and the complete data matrix in Table 5. The phylogeny was generated using the heuristic search option in PAUP 3.11 for the Macintosh® computer. Archaeohyracidae and Trachytheriinae were considered outgroups for the analysis (following Cerdeño and Montalvo, 2001), and OTUs with multiple character states were considered polymorphic. The analysis resulted in 63 equally most-parsimonious trees, each with a length of 88 steps; we present the strict consensus of these trees in Fig. 9 and a temporally calibrated phylogeny in Fig. 10.

The phylogenetic analysis places *Caraguatypotherium munozi* in a polytomy that includes *Plesiotypotherium*, *Typotheriopsis*, and a clade of later diverging mesotheriines (*Mesotherium* and *Pseudotypotherium* species; Figs. 9 and 10). Members of this polytomy are characterized by long, posteriorly directed postorbital processes (character four, state 2; unknown in *P. exiguum*); deep suborbital fossa and large infraorbital foramen (ACCTRAN optimization only; character 6, state 2; reversed in *Mesotherium* and in *Caraguatypotherium munozi*, unknown in *P. exiguum* and *M. hystatum*); zygomatic arches orientated perpendicular to M1 (character 7, state 1; reversed in *M. hystatum*, absent in *M. cristatum*, independently derived in *Microtypotherium*, variably present in *T. chasicoensis*); ratio of i1/i2 greater than 1.50 (character 22; reversed in *Plesiotypotherium*, unknown in *T. silveyrai*); and a middle lobe of M1 with anterior and posterior faces parallel or lingually divergent (character 29; unknown in *M. hystatum*).

Caraguatypotherium munozi is excluded from the *Pseudotypotherium*/*Mesotherium* clade by the absence of the following derived character states: upper molar imbrication greater than 1.50 (character 13, state 2); bilobed P4 with well-developed and patent plication (character 19, state 3; variably present in *P. subinsigne*); M3 with middle lobe only partially enclosed but still shorter than the other two lobes (character 21, state 3; variably present in *P. subinsigne*, independently derived in *Plesiotypotherium* and *E. superans*); ratio of i1/i2 greater than 2.00 (character 22, state 2; unknown in *M. hystatum*, independently derived (but variable) in *T. chasicoensis*); section of i1 trapezoidal with well demarcated lingual sulcus (character 23, state 3; absent in *M. maendrum*, unknown in *P. exiguum*, *M. hystatum*, and *M. pachygnathum*); P4 length/width ratio ≥ 1.50 (character 28); and m2 length/width ratio greater than 2.30 (character 31, state 1).

Salinas et al. (1991) noted the presence of a labial sulcus on P4 of SGO PV 4004 and interpreted it as a potential synapomorphy of a clade within Mesotheriidae. According to those authors, this character is infrequently present in *Eutypotherium* (except *E. roveretoi*), *Plesiotypotherium*, *Microtypotherium*, and *Typotheriopsis* and always present in *Pseudotypotherium* and *Mesotherium*. According to Francis (1965), however, this feature is not observed in *Typotheriopsis*; study of a large collection of *Typotheriopsis chasicoensis* specimens in collections at the Museo de La Plata confirms Francis' statement. In addition, neither the type of *Microtypotherium* nor any specimen attributed to that taxon known to us possesses a sulcus on P4. Because *Trachytherus*, the nearest outgroup to the Mesotheriinae, possesses a P4 sulcus that is lost with wear, this character state appears to be ancestral for the Mesotheriinae and therefore is a potential symplesiomorphy, not a synapomorphy. Its

Table 5
Matrix of characters used in phylogenetic analyses of mesotheriine relationships

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Archaeohyracidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	1
Trachytheriinae	1	0	1	0	1	2	0	1	1	1	0	1	0	1	1	1	1	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0
Eutypotherium lehmannnitchei	2	1	?	1	?	1	0	2	1	1	?	2	0	0	1	2	2	2	2	2	0	2	1	1	1	0	0	0	1	0	0	0
Eutypotherium superans	2	1	2	1	?	1	0	2	1	1	?	2	0	0	1	2	2	2	1	2	3	?	?	?	0	1	0	0	0	1	?	0
Typotheriopsis chasicoensis	2	1	?	2	2	2	0	2	0	1	1	2	0	0	1	2	2	2	1	2	2	1	2	1	1	1	1	0	1	1	0	0
Typotheriopsis silveyrai	2	1	2	2	2	2	1	2	0	1	1	2	0	?	1	?	2	2	1	2	2	?	?	?	?	1	1	0	1	1	?	0
Pseudotypotherium subinsigne	2	1	?	2	1	2	1	2	0	1	1	2	2	0	1	?	2	2	2	2	2	2	3	1	1	1	0	1	1	1	1	0
Pseudotypotherium exiguum	2	?	?	?	1	?	1	2	1	?	?	2	2	?	?	?	?	?	3	2	3	2	?	1	1	1	0	1	1	1	1	0
Mesotherium hystatum	2	1	2	3	1	?	0	2	0	1	1	2	2	?	1	?	2	2	3	2	3	?	1	1	1	0	1	?	1	1	1	0
Mesotherium cristatum	2	2	3	3	2	0	2	2	2	1	1	2	2	0	2	2	2	2	3	2	3	3	3	1	1	1	0	1	2	1	1	0
Mesotherium pachygnathum	2	1	?	2	2	0	2	2	3	1	1	2	2	0	2	2	2	2	3	3	3	3	?	1	1	1	0	1	2	1	1	0
Mesotherium maendrum	2	2	2	3	2	0	1	2	2	1	1	2	2	0	2	3	2	2	3	2	3	3	4	1	1	1	0	1	2	1	1	0
Plesiotypotherium achirense	2	1	1	2	2	1	2	1	1	1	2	0	0	1	2	2	2	1	2	3	0	2	1	1	1	0	0	1	1	0	0	0
Microtypotherium choquecotense	2	?	?	1	?	?	1	2	0	1	?	2	0	0	1	1	2	2	1	2	2	?	?	?	?	1	1	0	0	0	2	0
Caraguatypotherium munozi	2	1	1	2	?	1	1	2	2	1	1	2	1	0	1	2	2	2	2	2	2	1	2	1	1	1	0	0	1	1	0	1

Note: The original matrix also shows polymorphic secondary-state digits (printed as smaller digits below certain cells): Archaeohyracidae (characters 10 and 13, state 1); Trachytheriinae (characters 20 and 26, state 1); *Typotheriopsis chasicoensis* (character 5, state 1; character 14, state 1; character 23, state 2); *Pseudotypotherium subinsigne* (character 9, state 1; character 19, state 3; character 21, state 3); *Plesiotypotherium achirense* (character 21, state 2).
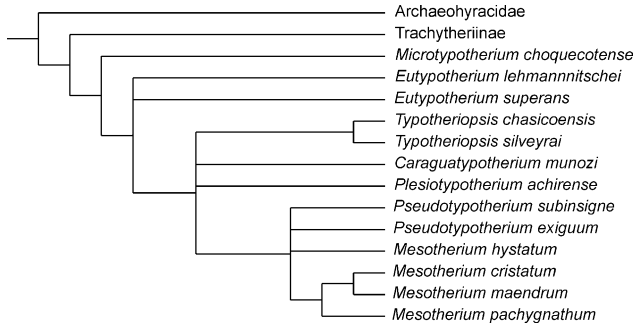
Fig. 9. Strict consensus tree of mesotheriine relationships as indicated by the preliminary phylogenetic analysis. Tree length=81 steps; CI=0.75; RC=0.60; and RI=0.79.

persistence in *Pseudotypotherium* and *Mesotherium* may be a derived condition, partly depending on whether the variable presence of a P4 sulcus in other taxa is variable among individuals in a population or due to ontogenetic (wear-related) changes. An assessment of the phylogenetic utility of this character must await more detailed studies of individual mesotheriine specimens, but it seems likely that the absence of a sulcus on P4 is an apomorphic condition unique to *Typotheriopsis* and perhaps *Microtypotherium*.

Our addition of 2 taxa and 7 characters to Cerdeño and Montalvo's (2001) matrix results in a significant loss of phylogenetic resolution relative to the tree presented in that study, which can be attributed to several factors. Although Cerdeño and Montalvo's (2001) original matrix includes 25 characters and 13 OTUs, 10 characters are invariant within Mesotheriinae (the ingroup for Cerdeño and Montalvo's analysis). Thus, the interrelationships of the 11 mesotheriines were determined from optimization of only 15 (of the original 25) characters. Even with our addition of 2 new OTUs and 7 new characters (5 of which are variable and non-autapomorphic among mesotheriines), our phylogeny of the 13 OTUs still is determined by only 20 characters.

Two other factors appear to be more important than the number of characters in the analysis, however: (1) variability within taxa and (2) the unusual combination of primitive and derived character states in *Caraguatypotherium munozi*. Our recoding of two of Cerdeño and Montalvo's (2001) characters illustrates that mesothere taxa often cannot be adequately described using simple terms. Our observations of the distributions of both recoded characters (9, upper molar imbrication; 22, relationship of i1/i2) reveal that the taxa originally coded as monomorphic by Cerdeño and Montalvo (2001) are, in reality, polymorphic for these characters.
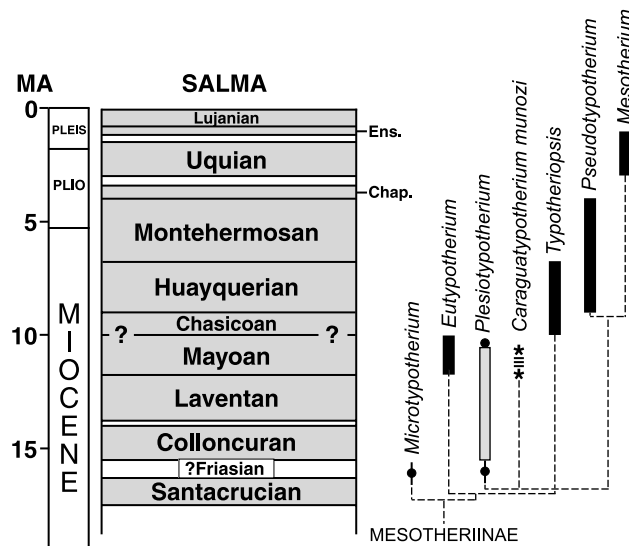

Fig. 10. Calibrated phylogeny for mesotheriines showing the phylogenetic position of *Caraguaytotherium munozi* and its probable stratigraphic temporal position (indicated by wide dashed bar). Age constraints for *Caraguaytotherium munozi* are indicated by asterisks (*). Upper age constraint for the fossil-bearing part of the Huaylas Formation is 10.7±0.3 Ma (mean of ^{40}Ar/^{39}Ar dates from three sites in the same ignimbrite in the Huaylas Formation; García et al., 2002; 10.8±0.4 Ma in García, 2001), and lower age constraint is 11.4±0.3 Ma (youngest Zapahuira Formation date [whole-rock, K–Ar] in tilted strata below the unconformity on which the Huaylas Formation was deposited; García et al., 1996; 1997). At Caragua, the fossil-bearing Huaylas Formation is in direct, unconformable contact with the Oxaya Formation, the uppermost ignimbritic flow (Sucuna ignimbrite) which has been dated at 19.3±0.8 Ma (weighted mean of five dates, García et al., 1999; see also Salinas et al., 1991) and 18.9±1.3 Ma (García, 2001); Wörner et al. (2000, Table 1) report similar dates (19.72± 0.90 Ma and 19.38±0.20 Ma, ^{40}Ar/^{39}Ar plateau ages on sanidine) for the 'Top Ignimbrite' of the Oxaya Formation in two different locations. Solid bars indicate stratigraphic occurrences of Argentine taxa based on data from Francis (1965); McKenna and Bell (1997) and temporal spans of SALMAs in Flynn and Swisher (1995). Gray bar indicates presumed range of *Plesiotypotherium* based on first and last occurrences; dots indicate occurrences of Bolivian taxa that have not been correlated with the SALMA sequence; Bolivian taxa are positioned according to bracketing dates presented in Marshall et al. (1992); MacFadden et al. (1995).

This finding may be due to intraspecific variability, the presence of unrecognized species, and/or misidentified specimens. It also may indicate that certain characters are not useful for phylogenetic analyses at this hierarchical level. If the other characters in the analysis can be examined as rigorously in future systematic revision of mesotheres, additional variation should become evident; however, the potential impact of this variation in terms of either further obscuring or possibly clarifying phylogenetic relationships is uncertain.

Finally, the presence of a combination of primitive and derived character states in *Caraguatypotherium munozi* demonstrates that character evolution in the Mesotheriinae is more complicated than originally thought. For example, though the presence of a little-pronounced suborbital fossa and a small infraorbital foramen would indicate that *Caraguatypotherium munozi* is a basal mesotheriine (resembling *Eutypotherium*), the structure of the postpalatal notch, by contrast suggests affinities with members of the very young *Pseudotypotherium-Mesotherium* clade. The ratio of i1/i2 in *Caraguatypotherium munozi* more closely resembles that in *Typotheriopsis* (and later mesotheriines), but the morphology of P4 more closely resembles some *Plesiotypotherium* specimens (and later mesotheriines), to the exclusion of *Typotheriopsis*. With the mosaic of character states in *Caraguatypotherium munozi*, the strict consensus tree places all these groups in a single polytomy, thus indicating that *Caraguatypotherium munozi* is neither a basal mesotheriine (as suggested by the retention or reappearance of primitive characters) nor a member of the *Pseudotypotherium–Mesotherium* clade (as indicated by the apparently homoplasious occurrence of some derived features). Until each of these taxa has been better differentiated, important new material from the Chilean Altiplano has been analyzed (Flynn et al., 2002a; Croft et al., 2003, 2004[1]), and a comprehensive analysis and systematic revision of all mesotheriids have been undertaken, the precise phylogenetic position of *Caraguatypotherium munozi* (and other mesotheriines) will remain unclear.

4.2. Biochronologic implications for the lower Huaylas formation at Caragua

Prior to the discovery of the Chucal Fauna, mesotheriines had been reported definitively only from Friasian s.l. (Mayoan SALMA) or younger faunas (e.g., Flynn et al., 2002a; Marshall and Sempere, 1991; see also Marshall

[1] Although the publication date of the present study postdates that of Croft et al. (2004), the analyses presented herein were completed and submitted for review prior to the submittal of Croft et al. (2004); the discrepancy in publication dates, and the apparent inconsistency in the named taxa included in each, results simply from differences in processing and publication time between the two journals.

et al., 1983; Pascual and Bondesio, 1985; Pascual et al., 1996; McKenna and Bell, 1997). This report left a marked temporal gap in the record of mesotheriids; trachytheriines, though reported from the temporally unconstrained Divisaderan SALMA (Simpson et al., 1962; Reguero, 1994) and possibly the Tinguiririran SALMA (Bond et al., 1997; Croft et al., 2003; Flynn et al., 2003), are unknown in any post-Deseadan SALMA faunas (Reguero and Castro, 2002).

Fiandraia (Roselli, 1976; McKenna and Bell, 1997) is reported from Miocene deposits of Uruguay, but this taxon does not appear to be a mesotheriine (more closely resembles a toxodontid); regardless, the nonspecific age assignment provides no additional information on the presence or absence of mesotheriids in Colhuehuapian or Santacrucian faunas. A variety of new mesotheriines are known from Bolivian faunas, but none has been considered as old as the Santacrucian (the oldest is considered Colloncuran [or 'Friasian' *sensu lato*]).

Initial study of the Chucal Fauna, which includes at least three mesotheriines, suggested an age no younger than Friasian s.l. and perhaps as old as Santacrucian or Colhuehuapian (Flynn et al., 2002a). A single toxodontid specimen from the upper Chucal Formation, identified as *Palyeidodon*, led Bond and García (2002) to suggest that the Chucal Fauna is Colloncuran in age, yet their new radioisotopic age determination (17.5 ± 0.4 Ma) from a level above the *Palyeidodon*-bearing horizon (and above all the sites from which the Chucal Fauna has been collected; Flynn et al., 2002a; Charrier et al., 2002) appears to favor a Santacrucian, or older, SALMA assignment (see the most recent compilation of SALMA time spans, Flynn and Swisher, 1995). Refined identifications of Chucal taxa (based on specimens collected in 2001), support a Santacrucian age for the Chucal Fauna (Charrier et al., 2002; Croft et al., 2004), which would extend the temporal range of the various Chucal taxa, including mesotheriines (and thus the first appearance of Mesotheriinae), earlier than the Friasian s.l. to the Santacrucian SALMA (Croft et al., 2003).

Bargo and Reguero (1989) and Salinas et al. (1991) reached very different conclusions regarding the likely age of the lower Huaylas Formation at Caragua. Both noted the broad constraints placed on the age of the Huaylas Formation by bracketing radioisotopic dates (18.7–2.9 Ma, middle Miocene–Pliocene, Bargo and Reguero, 1989; younger than early Miocene 19.3 ± 0.8 Ma from underlying Oxaya Formation west of Caragua, Salinas et al., 1991). However, the taxa to which these authors assigned the two previously reported Caragua mesotheriine specimens have different age ranges elsewhere, leading to divergent opinions regarding a more precise biochronologic age estimate for the fossil-bearing strata. Salinas et al. (1991) assigned SGO PV 4004 to *Typotheriopsis* sp. (possibly a new species); though *Typotheriopsis* ranges from Chasicoan to Huayquerian SALMAs in Argentina, Salinas et al. (1991) selected the younger end of the range for the Caragua

deposits because of the more advanced features of SGO PV 4004 relative to Chasicoan (late Miocene) species. Bargo and Reguero (1989), in contrast, favored a middle Miocene age on the basis of the assumed affinities of MLP 86-VII-10-1 to *Eutypotherium*.

There are obvious risks in formulating an age assignment for a stratigraphic unit on the basis of a single taxon (Flynn et al., 1984). These risks are exacerbated when biochronologic correlations must be made across large geographic ranges (e.g., from Patagonia to the Altiplano), especially if there is uncertainty about whether the sites pertain to the same paleobiogeographic regions. Nevertheless, one mammalian species currently is known from the Huaylas Formation. Any biochronologic correlation must use the known temporal distributions of this taxon and its nearest relatives, but age inferences must be interpreted with appropriate caution and viewed as tentative. As we noted previously, the ages of the broadly bracketing volcanic units and stage of evolution biochronologic correlations for SGO PV 4004 were used to infer a young and very narrow range (8–9 Ma, late Miocene) for the age of the Huaylas Formation at Caragua (Salinas et al., 1991), though that range conflicted with the older age estimates derived from the identification of the second mesothere specimen (Bargo and Reguero, 1989). Our taxonomic revisions, phylogenetic analysis, and phylogenetic bracketing improve the constraints on the estimated divergence age of the Caragua mesothere (Fig. 10). These analyses better resolve the relationships of the taxon and provide different constraints on the age inferences indicated by the known ranges of its closest mesotheriine relatives from elsewhere in the Altiplano and higher latitudes (Patagonia and other parts of Argentina).

The single mesotheriine that occurs in the Huaylas Formation at Caragua is clearly distinct from *Typotheriopsis* and definitely does not represent an advanced/younger species of that taxon. Thus, the range of *Typotheriopsis* cannot be used to support a Huayquerian age for the Huaylas Formation. Our preliminary phylogenetic analysis instead indicates that the Caragua mesotheriine represents a new taxon that diverged prior to the appearance of the most recent common ancestor of *Pseudotypotherium* and *Mesotherium* (a clade that is Huayquerian and younger) but subsequent to the earliest divergences in the Mesotheriinae (i.e., the basal mesotheriine *Microtypotherium* and *Plesiotypotherium* [an early-occurring member of the clade that includes *Caraguatypotherium munozi*], both of which appeared first in the Friasian [sensu stricto] or Colloncuran). Depending on the resolution of the interrelationships of the polytomy in Fig. 10, the first appearances of possible nearest relatives would indicate a minimum age for *Caraguatypotherium munozi* of either (1) Friasian-Colloncuran, especially if *Plesiotypotherium* is the nearest relative to or later diverging than

Caraguatypotherium munozi; (2) pre-Chasicoan, if *Typotheriopsis* is most closely related to *Caraguatypotherium munozi* or the *Pseudotypotherium* and *Mesotherium* clade (with *Caraguatypotherium munozi* more basal); or (3) pre-Huayquerian, if *Caraguatypotherium munozi* is most closely related to the *Pseudotypotherium* and *Mesotherium* clade. As we noted, an age conclusion based on phylogenetic bracketing of a single taxon is necessarily insecure and must be viewed as tentative. Nevertheless, the revised taxonomic and phylogenetic analyses of the Caragua mesothere provide a reasonably well-constrained age estimate for the fossil-bearing unit. Even with some ambiguity in the interrelationships of *Caraguatypotherium munozi* with other members of the polytomy in Fig. 10, the most conservative revised biochronologic age estimate for the Huaylas Formation—post-Friasian and pre-Huayquerian (9–15 Ma)—is fully consistent with the large and growing suite of bracketing radioisotopic dates from both below and above (in the Huaylas Formation) the horizons that contain *Caraguatypotherium munozi*.

4.3. Geochronology

Radioisotopic dating of a horizon that directly overlies the Caragua fossil-bearing horizons, more dates from underlying or interfingering units nearby, and additional tectonostratigraphic studies provide extensive and reliable chronologic calibration of the Huaylas Formation. These new dates and refined understanding of stratigraphic relationships yield more accurate age estimates than those based solely (or largely) on single-species biochronologic inferences, with precision similar to that possible even with the future discovery of more extensive faunas and use of SALMA correlations (most Miocene SALMAs span 1–3 million years, Flynn and Swisher, 1995; Kay et al., 1997). Thus, the age estimate for the Huaylas Formation is best constrained by the radioisotopic dates, and the fossil data can be used as independent tests of consistency and reliability.

The Huaylas Formation is one of the main later Cenozoic conglomerate-dominated sedimentary units in the Precordillera that appears to have been syntectonically deposited and deformed. Refinement of its age and stratigraphic relations with nearby sedimentary and volcanic units constrains the timing and duration of tectonic events in this region. García (1996) and García et al., (1996, Fig. 1) regarded the Huaylas and Joracane formations as syntectonic conglomerates. Constraining ages for the conglomerates came mainly from bracketing volcanic units, such as the basalts/andesites of the Zapahuira Formation (complemented by several dates in the Joracane Formation; García et al., 1996). These bracketing units, however, typically are geographically restricted (particularly the Zapahuira Formation), occur only in thrust instead of depositional contact, and may interfinger with rather than superpositionally

bracket all or parts of the sedimentary sequences. Previously available bracketing age ranges for the sedimentary sequences imply that the Huaylas Formation ($\sim$2.7–11 Ma) overlies and is temporally distinct from the Joracane Formation (12–18 Ma), though these two formations rarely if ever occur in direct superpositional contact. As we noted previously, Salinas et al. (1991) used a single Caragua mesotheriid specimen from basal Huaylas Formation horizons to suggest an age of 8–9 Ma. Not only has this age estimate been widely accepted, it also has been viewed as applying to the entire formation (e.g., García, 1996; García et al., 1996; Muñoz and Charrier, 1996 [unnamed syntectonic stratigraphic unit, containing lacustrine beds with late Miocene, 8–9 Ma, *Typotheriopsis* sp. interfingering with alluvial fan deposits]; Riquelme and Hérail, 1997; Charrier and Muñoz, 1997 [late Miocene age for Estratos de Caragua, discussed independently of the Huaylas Formation]; Riquelme, 1998; Charrier et al., 1999 [7–9 Ma for lower Huaylas based on the Huayquerian age range of 6.8–9.0 Ma in Flynn and Swisher, 1995] and 2000 [again 7–9 Ma but also more conservative estimate of 'post-11 Ma and pre-5 Ma'].

More recent dating of both bracketing units and the Huaylas Formation permit much more precise age determinations for these sequences and related tectonic events. The Oxaya Formation has not been dated near Caragua, though dates from the unit in nearby regions indicate that it is comprised of a series of ignimbritic flows ranging in age from $\sim$22 Ma in the lower flows to $\sim$19 Ma in the upper flows, with minor sedimentary units interbedded with the ignimbrites (Muñoz and Charrier, 1996; García et al., 1996), or $\sim$25–19 Ma (see new dates and summaries in García et al., 1999, 2000; Wörner et al., 2000; García, 2001). At Caragua, a thin ignimbritic intercalation in the upper part of the Huaylas Formation, where it is covered by the regionally extensive Pliocene Huaylas Ignimbrite, has been dated at 10.7 ± 0.3 Ma (García et al., 2002; mean of dates from three sites in the same ignimbrite; ^{40}Ar/^{39}Ar on biotite; given as 10.8 ± 0.4 Ma in García, 2001, Fig. 6.10, Table A5). This date represents the first direct radioisotopic dating of any part of the Huaylas Formation. The fossil-bearing sediments of the lower Huaylas Formation are separated from the immediately underlying volcanic Oxaya Formation by an erosional and angular unconformity. The fossil-bearing levels were syndepositionally deformed and are separated from the relatively flat-lying upper parts of the Huaylas by an intraformational unconformity. The nearly horizontal, $\sim$30 m thick Huaylas Ignimbrite, dated at 4.4 ± 0.3 and 4.8 ± 0.3 Ma (Naranjo and Paskoff, 1985), overlies with strong erosional unconformity the Huaylas Formation conglomerates near Caragua (e.g., on hills on the north side of Quebrada Belén). Recent authors have suggested that the Lauca Ignimbrite (Lauca-Pérez Ignimbrite of Wörner et al., 2000) corresponds to the same flow as the Huaylas

Ignimbrite (Wörner et al., 2000; García, 2001; García et al., 2002). Three ^{40}Ar/^{39}Ar dates on sanidine crystals (2.72 ± 0.1, 2.7 ± 0.2, and 2.4 ± 0.4 Ma) and one ^{40}K–^{40}Ar date on biotite (3.0 ± 0.4 Ma) from this ignimbrite in the Lauca area indicate that the Huaylas Ignimbrite is late Pliocene in age. The Lupica ($\sim$23–18 Ma) and Joracane (18.2 and 16.8 Ma, $\sim$18–12 Ma, García et al., 1996; 10.55 ± 0.1 Ma, Wörner et al., 2000) formations do not occur at Caragua and thus are of limited utility in constraining the age of the fossil-bearing portions of the lower Huaylas Formation. Thus, the broad age constraints from units in direct super-position with the fossil deposits at Caragua most conservatively indicate an age somewhere between $\sim$19 Ma (the youngest Oxaya Ignimbrite dates) and 2.7 Ma (the Huaylas Ignimbrite dates in the Lauca area) but more likely between 16 and 10 Ma (the age of the youngest dated Zapahuira lavas overlying the Oxaya Formation in areas near Caragua and the 10.7 Ma date from within the upper Huaylas Formation at Caragua).

Although not present below the fossil-bearing lower levels of the Huaylas Formation at Caragua, the Zapahuira Formation occurs to the north, where it is progressively onlapped by gravels of the upper parts of the Huaylas Formation. By combining dates from the Zapahuira Formation with the new radioisotopic dating of the upper Huaylas Formation at Caragua, we can tightly bracket the age of the fossil-bearing sediments of the lower Huaylas Formation and the duration of the syndepositional tectonic events. Deposition of the Huaylas Formation began after 11.4 ± 0.3 Ma (based on the youngest Zapahuira Formation ^{40}K–^{39}Ar whole-rock lava date from Pampa El Muerto, García, 1996; García et al., 1996) and before 10.7 ± 0.3 Ma (^{40}Ar/^{39}Ar date from the ignimbrite in the upper Huaylas Formation at Caragua, García, 2001; García et al., 2002), which suggests a total duration as short as 1–2 million years or less.

4.4. Tectonic implications

We complement the radioisotopic age constraints for the Huaylas Formation with an assessment of the inferred age of the new mesotheriine occurring at Caragua. Together, the biochronology and bracketing radioisotopic ages suggest that the entire Huaylas Formation and associated synsedimentary tectonic events span a range of only $\sim$1–2 m.y. (10.5–11.5 Ma or 10–12 Ma) and certainly occurred during less than 4–5 m.y. ($\sim$10–15 Ma). As noted by García (1996, 2001) and García et al. (1996), deposition of the upper Huaylas Formation conglomerates resulted from activity on the Copaquilla-Tignámar Fault in the eastern Precordillera, which took place after the Oxaya Anticline had formed (in response to activity on the Ausipar Fault in the western border of the Precordillera) and tilted (on its western back limb) the Zapahuira and lower Huaylas strata. The age of syntectonic deposition and deformation of this formation

preceded 10 Ma. It may have begun as early as 14–15 Ma but more likely started only after 12 Ma and lasted for fewer than 2 million years, because Zapahuira Formation lavas (the youngest is dated at ∼11.4 Ma) are conformable with Oxaya Formation strata, and both were deformed by this tectonic event. Uplift and erosion of the underlying Oxaya/Zapahuira units and syntectonic deposition of lower Huaylas Formation sediments (including the mesothere fossils described herein) also can be precisely constrained; the tectonic deformation and deposition occurred extremely rapidly within this post-11.4 Ma and pre-10.7 Ma window.

These results are consistent with the conclusions of Charrier et al. (2004) that the tectonic activity and subsequent deformation and paleogeographic evolution in the Precordillera and Western Altiplano (Chucal area of the Western Cordillera, approximately 50 km east of Caragua) occurred during a similar time interval. In that region, deformation occurred nearly continuously from at least the early Miocene to the early Pliocene. Deformation continued throughout the interval between deposition of the (1) upper Lupica Formation at 21.7 ± 0.8 Ma according to whole-rock ^{40}K–^{40}Ar in the Chucal sequence (Riquelme, 1998), 18.79 ± 0.11 Ma according to ^{40}Ar/^{39}Ar (Wörner et al., 2000), or 18.6 ± 0.7 Ma according to ^{40}K–^{40}Ar (García et al., 1996) from the surrounding area; (2) Chucal Formation at ∼19–17 Ma (Bond and García, 2002; Charrier et al., 2002; Flynn et al., 2002a; García et al., 2002); (3) Quebrada Macusa Formation at 11.2 ± 0.5 Ma and 11.4 ± 0.7 Ma according to whole-rock ^{40}K–^{40}Ar (García et al., in press) and 11.5 ± 0.4 Ma according to ^{40}Ar/^{39}Ar (Wörner et al., 2000), with the upper part at 10.4 ± 0.7 Ma according to whole-rock ^{40}K–^{40}Ar (Riquelme, 1998) and 10.3 ± 0.4 Ma according to whole-rock ^{40}K–^{40}Ar (Charrier et al., 2002; García et al., 2002); and (4) the lower Lauca Formation (∼5–1 Ma, García et al., 2002). On the eastern border of the Belén Ridge, deformation of the Chucal and lower Lauca Formations is characterized by progressive unconformities and the development of the Chucal growth fold (Hérail and Riquelme, 1997; Riquelme, 1998).

4.5. The Altiplano: a distinct biogeographic region and center of diversity for mesotheriines during the Miocene

Mesotheriids have long been known only from Patagonian and other Argentine assemblages, where they typically are uncommon and/or sporadic in temporal (SALMA) occurrence. In these temperate latitudes, no mesotheriids are known from the early Cenozoic (Tiupampan-Mustersan SALMAs), and trachytheriines (*Trachytherus* and other related but potentially distinct taxa) occur in Tinguiririran (Bond et al., 1997; though they are absent in the central Chilean Tinguiririca Fauna; Flynn et al., 2003), Divisaderan (Simpson et al., 1962; Reguero, 1994), and Deseadan (Patterson, 1934; Reguero, 1993; Reguero and Escribano, 1996; Reguero and Castro, 2002) SALMAs. Mesotheriids are unknown from the Colhuehuapian and Santacrucian

SALMAs, then reappear in the Friasian s.l. (Mayoan SALMA) and persist through the Pleistocene Ensenadan SALMA (Pascual et al., 1996; Croft et al., 2003).

This pattern changed dramatically when faunas began to be reported from the Altiplano of Bolivia and Chile. The trachytheriine mesotheriid *Trachytherus* is one of the most common mammals in the Deseadan assemblages of Salla, Bolivia (MacFadden et al., 1985), in contrast to its less common occurrence in Patagonian Deseadan faunas. Mesotheriines also are common and taxonomically diverse in middle-late Tertiary Altiplano assemblages, though the precise ages of some of the Bolivian faunas are uncertain (Villarroel, 1974a,b, 1978; Oiso, 1991; Marshall et al., 1992; MacFadden and Anaya, 1993; Anaya and MacFadden, 1995; Flynn and Swisher, 1995).

It is noteworthy that mesotheriines are diverse (at least three cooccurring species) and the most common taxa in the recently discovered Chucal Fauna of the Chilean Altiplano, and likely of Santacrucian age (Flynn et al., 2002a; Croft et al., 2003, 2004 Charrier et al., 2002, 2004). It is also striking that the three Caragua specimens, recovered from at least two (and possibly three) localities in the only other Tertiary mammal-bearing unit in northernmost Chilean Altiplano, are all mesotheriines. The abundance of mesotheriids throughout most assemblages in the Altiplano region, from the Deseadan (Salla) and Santacrucian through the Friasian s.l. (Chucal, Achiri) and from north-central Chile through the eastern Altiplano of Bolivia, contrasts markedly with their sporadic occurrence at higher latitudes, as well as with their complete absence from more equatorial tropic regions (e.g., Laventan La Venta Fauna of Colombia and correlative tropical faunas, Kay et al., 1997). In addition, according to the phylogenetic analysis we present, the taxon that is the outgroup to all other mesotheriines occurs only in Bolivia (Fig. 9, *Microtypotherium*). On the basis of the large post-Deseadan gap in the fossil record of mesotheriines in Argentina, Reguero and Castro (2002) hypothesized that trachytheriines may have become extinct only in more southerly latitudes and persisted in more northerly regions. Our results complement those of Reguero and Castro (2002) and indicate that intermediate latitudes, possibly more montane areas, may have been biogeographically distinct from both equatorial and Patagonian (and other higher latitude) regions (see also Bond and García, 2002) and may have served as a center of diversification for mesotheriines and other groups of indigenous South American mammals throughout much of the Cenozoic.

Acknowledgements

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