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New Data on Miocene Neotropical Provinciality from Cerdas, Bolivia

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Abstract We provide the first faunal report for the early/middle Miocene fauna of Cerdas, Bolivia (16.5–15.3 Ma; 20° 52′ S, 66° 19′ W), based primarily on new specimens collected in 2007. As many as twelve species of mammals in nine families are represented. Notoungulates include *Palyeidodon obtusum* (Toxodontidae), *Protypotherium* cf. *attenuatum* and *Protypotherium* sp. nov. (Interatheriidae), '*Plesiotypotherium*' *minus* and possibly *Microtypotherium choquecotense* (Mesotheriidae), and *Hegetotherium*? sp. nov. (Hegetotheriidae). Xenarthrans include *Stenotatus planus* and *Prozaedyus* sp. (Cingulata: Dasypodidae), Peltephilidae gen. et sp. nov. (Cingulata), and *Xyophorus* cf. *bondesioi* (Pilosa: Nothrotheriidae). A new species of litoptern is also present (Macraucheniidae) as well as an unidentified rodent (Chinchillidae: Lagostominae). Two of these Cerdas species occur in Friasian sensu stricto/Colloncuran SALMA faunas of Patagonia, and perhaps one in Santacrucian SALMA faunas. Among middle latitude localities, Cerdas resembles Chucal, Chile (late early Miocene, Santacrucian SALMA) in community composition (e.g., abundant mesotheriids, few rodent species), but has no species in common; it shares one species with Quebrada Honda, Bolivia (middle Miocene, Laventan SALMA), and perhaps as many as three more. These observations indicate that Cerdas is not referable to the Santacrucian, and that the upper limit of this SALMA in the middle latitudes falls somewhere between 17.5 Ma (the top of Chucal) and 16.5 Ma (the base of Cerdas). Based on the range of dates proposed for the youngest Santacrucian intervals in Patagonia, a diachronous offset of up to 2.1 Ma may exist at this point in the SALMA sequence between middle and high latitude faunas.

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Introduction

The Neotropics is a region of high conservation priority (Ricketts et al. 2005; Shi et al. 2005), and creating sound strategies for preserving Neotropical faunas requires understanding their historical development (Webb 1999; Wilson 1999; MacFadden 2006). This historical perspective can best be gained through study of the fossil record—ideally one based on thorough temporal and geographic sampling. Regrettably, such sampling in the Neotropics has lagged far behind that in the Southern Cone (e.g., Patagonia) for many years; although roughly 80% of South America is in the tropics, most Tertiary mammal localities come from temperate, southern high latitudes (Flynn and Wyss 1998). A geographically biased record such as this is inadequate for elucidating past species diversities and distributions, and understanding the development of modern Neotropical faunas.

Among South American countries at low and intermediate latitudes, Bolivia holds perhaps the greatest potential for improved sampling of Cenozoic paleofaunas due to its abundant exposures of continental sediments deposited in basins with relatively high rates of sedimentation. Many fossil localities have been documented in these basins, and those that have been targeted for field projects have proved well worth the effort (Marshall and Sempere 1991; MacFadden 2006). For example, the early Paleocene locality of Tiupampa has provided unparalleled insights into the early stages of Cenozoic mammal evolution in South America (Marshall and Muizon 1988; Muizon 1991; Muizon and Cifelli 2000; Muizon and Argot 2003; Gelfo et al. 2009). The late Oligocene fauna of Salla documents the earliest platyrrhine primate and is likely the richest South American terrestrial fossil assemblage of that age (Hoffstetter 1969; MacFadden et al. 1985; Shockey 1997; Kay et al. 1998, 2002; Shockey and Anaya 2008). The middle Miocene locality of Quebrada Honda has produced beautifully preserved specimens representing many clades, about half pertaining to new species (Frailey 1987, 1988; Sánchez-Villagra et

al. 2000; Goin et al. 2003; Croft and Anaya 2006; Forasiepi et al. 2006; Croft 2007). Tarija preserves a remarkable snapshot of a Pleistocene Neotropical mammal community prior to the megafaunal extinction (Hoffstetter 1963, 1986; MacFadden and Shockey 1997; Zurita et al. 2009).

Nevertheless, these few faunas spread across 65 million years of mammal evolution provide only a very coarse view of evolving species, habitats, and paleocommunities in South America. Our research aims to supplement the number of well-characterized Neotropical paleofaunas through multidisciplinary geological and paleontological studies, thereby facilitating investigations of evolving paleocommunities and species/clade distributions. The present report provides an initial description of one of these paleofaunas, Cerdas, located in south-central Bolivia (Fig. 1). This fossil locality was first reported several decades ago by Carlos Villarroel, but only two specimens had ever been described (Villarroel 1978). Our investigations, based primarily on new specimens and data collected in 2007 by our joint US-Bolivian team, represent the first report of a fauna from this locality. In addition to documenting the specimens and taxa recovered thus far from Cerdas, we discuss its temporal and geographic relationships to other important Miocene South American faunas.
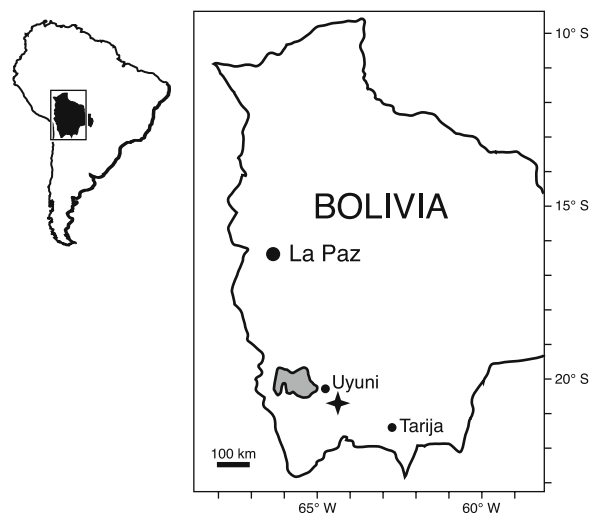
Fig. 1 Location of Cerdas (*star*) in Bolivia (*inset box*), southeast of Uyuni.

Materials and methods

All referred specimens are from the Cerdas beds (see below), province of Nor Chichas, department of Potosí, Bolivia. Locality and horizon data refer to locality numbers recorded in the field notes of DC (available upon request). Metric data not taken from the literature were collected firsthand using a digital calipers to the nearest 0.1 mm. Unless otherwise indicated, dental dimensions provided in the text are mesiodistal × buccolingual and osteoderm dimensions are anteroposterior × mediolateral × dorsoventral. Cingulate osteoderm terminology follows Vizcaíno et al. (2003); see also Croft et al. (2007). Dental terminology for toxodontids follows Madden (1997) and that for litopterns follows Soria (2001). Taxonomic nomenclature for insecurely identified specimens follows recommendations of Bengston (1988).
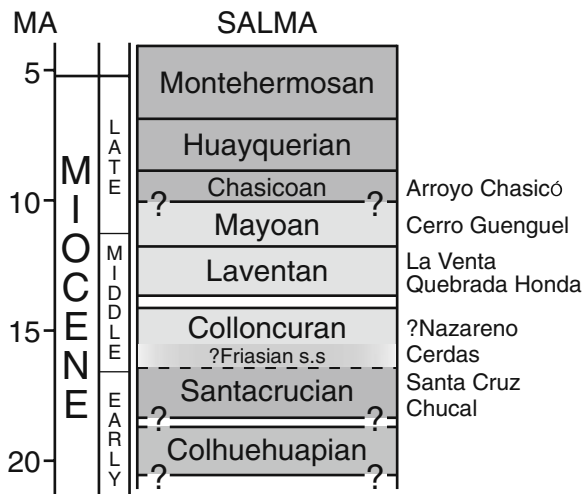
Friasian (Sensu Lato) Faunas Few parts of the South American Land Mammal 'Age' (SALMA) sequence have proven as puzzling as the late early Miocene to early late Miocene interval, the Friasian sensu lato (Flynn and Swisher 1995; Madden et al. 1997; Scillato-Yané and Carlini 1998; Fig. 2). This span has been divided into three to four intervals, typified by faunas of: (1) Río Frías Formation, region XI, Chile (Friasian SALMA sensu stricto; Kraglievich 1930; Madden 1990); (2) Collón-Curá Formation, Neuquén and Río Negro provinces, Argentina (Colloncuran SALMA; Bondesio et al. 1980b; Vucetich et al. 1993; Kay et al. 1998); (3) Honda Group, La Venta, Colombia (Laventan Stage, generally treated as a SALMA although not formally proposed as such; Kay et al. 1997); and (4) Río Mayo Formation, Chubut and Santa Cruz provinces, Argentina (Mayoan SALMA; De Iuliis et al. 2008). As noted by Flynn and Swisher (1995:325), these biochronological units "may be temporally sequential and continuous, sequential but with hiatuses between them, overlapping, or even equivalent."

Given the uncertain correlations among these localities, the ages and distributions of taxa provided below are based on geological units and their contained faunas—as reported in scientific publications—rather than on temporal intervals such as SALMAs (following Croft et al. 2004). This serves three main purposes. First, it links occurrences with particular specimens (collections) so that temporal and geographic ranges of taxa can be modified when specimens are re-identified. Second, it links occurrences with geological units so that the temporal ranges can be updated when absolute age determinations and/or SALMA correlations for these geological units change. Finally, by linking occurrences with specific specimens from specific rock units, it minimizes loss of information that can result from lumping together faunas thought to be contemporaneous based only on biochronologic correlations that may later prove to be incorrect. Nevertheless, we continue to use the Friasian sensu stricto, Colloncuran, Laventan, and Mayoan SALMAs in discussions because they succinctly refer to particular intervals (albeit potentially overlapping ones) of the Miocene.

Fig. 2 Miocene South American Land Mammal 'Ages' (SALMAs) and approximate ages of localities discussed in the text. *Light shading* indicates the Friasian sensu lato. *Dashed line* indicates SALMAs that may overlap based on current dating. *Question marks* indicate uncertain boundaries. Modified from Croft (2007).

Anatomical Abbreviations Upper tooth loci are indicated by upper case letters (e.g., I1, P2, M1) and lower tooth loci by lower case letters (e.g., i1, p2, m1). Sloth caniniform and molariform teeth are also abbreviated as c, m1, m2, etc., even though the homologies of these teeth relative to those of other groups are unclear. AP, anteroposterior; ML, mediolateral; MT metatarsal.

Institutional Abbreviations AMNH, American Museum of Natural History, New York; GB, Servicio

Fig. 3 Stratigraphic section at Cerdas indicating fossiliferous levels (bone icons) and localities (in B-07-X format) cited in text. Stratigraphic level of B-07-12 is uncertain. Radioisotopic dates (^{40}Ar/^{39}Ar) are from MacFadden et al. (1995). Upper dated bed (ca. 205 m) is the yellow-green tuffaceous sandstone noted in the text.
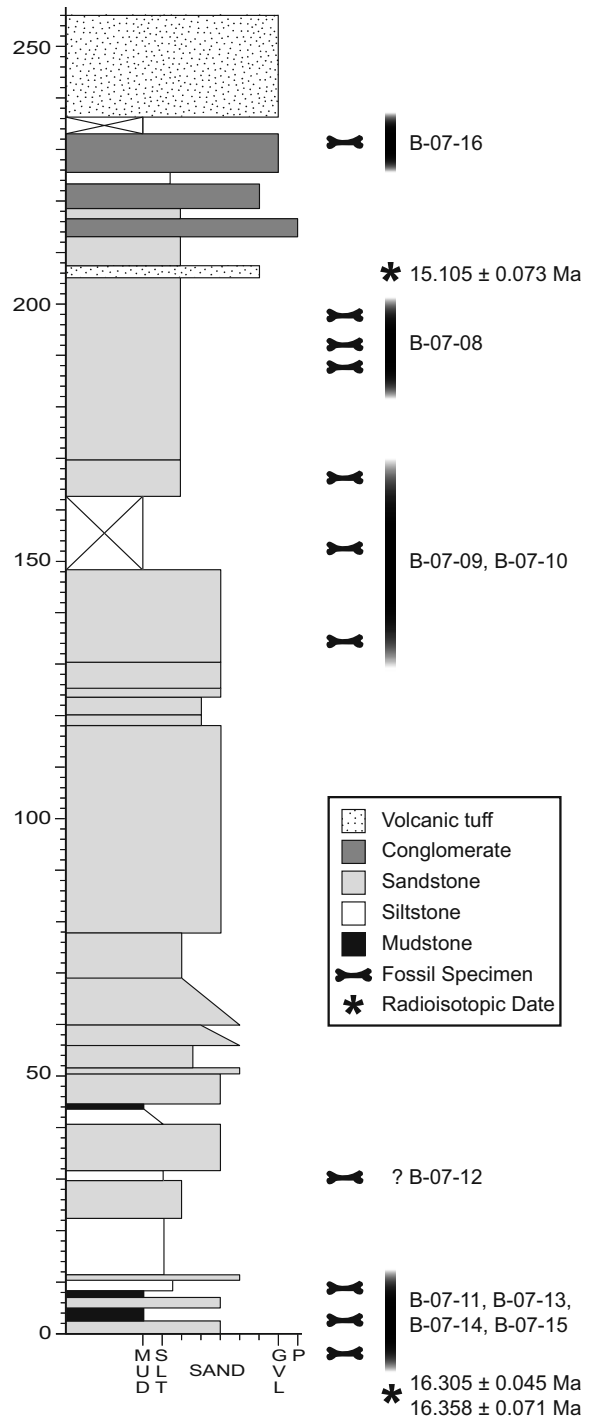
Geológico de Bolivia, La Paz; MLP, Museo de La Plata, Argentina; MNHN, Museum National d'Histoire Naturelle, Paris, France; UATF, Universidad Autónoma Tomás Frías, Potosí, Bolivia; UF, Florida Museum of Natural History, Gainesville, Florida.

Geographic and geologic setting

The small village of Cerdas is located near the eastern edge of the Bolivian Altiplano at an elevation of roughly 4,000 m, ca. 60 km southeast of Uyuni (Fig. 1). The fossiliferous badlands several kilometers southeast of Cerdas were discovered by C. Martínez and T. Subieta in 1972 and later prospected by R. Hoffstetter, M. Servant, and C. Villarroel (Villarroel 1978). Two partial mesotheriid notoungulate mandibles were recovered during this expedition (Villarroel 1978; see also below). Two decades later, in 1991 and 1992, F. Anaya, B. MacFadden, and colleagues visited Cerdas to study the geology and geochronology of the area (MacFadden et al. 1995) and to collect fossil mammals. They produced a paleomagnetic section with associated high precision ^{40}Ar/^{39}Ar dates indicating that the fossiliferous horizons at Cerdas span ca. 16.5–15.3 Ma (early middle Miocene; Figs. 2, 3). The expedition also collected several dozen vertebrate fossils, mostly mesotheriid notoungulates, which were accessioned into collections at UF and the Museo Nacional de Historia Natural in La Paz. Our study also provides the first descriptions of the UF specimens.

Sedimentology The Cerdas sedimentary section (20° 52′ S, 66° 19′ W) sits at a modern elevation of ~4,000 m. The total stratigraphic section consists of more than 250 m of mostly fluvo-lacustrine claystones, siltstones, and silty sandstones (Fig. 3), informally referred to as the "Cerdas beds" (estratos de Cerdas) (Villarroel 1978; MacFadden et al. 1995).

The lower ~80 m of the section contains a mixture of finer (mud to very fine-grained sand) and coarser (fine-grained to very coarse-grained sand) siliciclastic lithologies. Coarser sediments rarely show horizontal laminations, ripple-scale cross-strata, and lateral accretion elements, which all indicate traction transport. Individual beds are laterally extensive over tens of

meters, and these coarse-grained beds stack to form sand bodies that are continuous over hundreds of meters. Reddish-brown, massive mudstones that show rare root traces and well-developed nodular carbonate horizons are interpreted as paleosols formed in flood-plain depositional settings. We interpret this part of the section as fluvial braided stream deposits, including both overbank (finer) and channel (coarser) environments. Fossils occur primarily at the base of this 80 m interval.

The upper ~150 m of section are primarily composed of poorly sorted, sand-sized volcaniclastic material with granule- to pebble-sized volcanic clasts floating in a silt- to clay-sized matrix. Beds pinch out laterally over tens to hundreds of meters. Some beds display crude internal horizontal organization. Occasional thin (tens of cm to 2 m) units of tuff and conglomerate are interbedded with the volcaniclastics. We interpret this upper lithology to represent water-rich sediment gravity flows of pyroclastic volcanic material (e.g., lahars). Such flows would have been very effective at trapping and preserving animal remains, and indeed, many of our fossil specimens come from these upper beds (also noted by MacFadden et al. 1995). A thick (~20 m), regionally extensive ash-flow tuff caps the section. A thinner (~1 m), yellow-green tuffaceous sandstone, lower in the section (205 m), was dated by MacFadden et al. (1995) at 15.105±0.073 Ma. Most of the fossils that we collected are from the upper part of the section, below this tuff. The material in the volcaniclastic units was presumably sourced from Cerro Chorolque—a nearby 16.2±0.3 Ma volcano (Grant et al. 1979; Schneider and Halls 1986)—or a similar local eruptive center.

Systematic paleontology

Mammalia Linnaeus, 1758
Xenarthra Cope, 1889
Cingulata Illiger, 1811
Dasypodoidea Gray, 1821
Dasypodidae Gray, 1821
Euphractinae Winge, 1923
Eutatini Bordas, 1933

Stenotatus Ameghino, 1891

Type species *Stenotatus patagonicus* (Ameghino, 1887).

Included species The type, *Stenotatus centralis* (Ameghino, 1902), *Stenotatus hesternus* (Ameghino, 1889), *Stenotatus ornatus* (Ameghino, 1897), *Stenotatus planus* Scillato-Yané and Carlini, 1998.

Age and distribution Deseado Formation, Santa Cruz and Chubut provinces, Argentina, late Oligocene age, Deseadan SALMA (Ameghino 1897); Sarmiento Formation, Chubut province, Argentina, early Miocene age, Colhuehuapian SALMA (Ameghino 1902); Chichinales Formation, Río Negro province, Argentina, early Miocene age, Colhuehuapian SALMA (Barrio et al. 1989); Santa Cruz Formation, Santa Cruz province, Argentina, late early Miocene age, Santacrucian SALMA (Scott 1903; Vizcaíno et al. 2006); Chucal Formation, region I, Chile, late early Miocene age, Santacrucian SALMA (Croft et al. 2004, 2007); indeterminate formation, Neuquén, Argentina, ?early Miocene age, ?Santacrucian SALMA (Tauber et al. 1999); Cerdas beds, department of Potosí, Bolivia, early to middle Miocene age, Friasian/Colloncuran SALMA (present study); Collón-Curá Formation, Neuquén and Río Negro provinces, Argentina, early middle Miocene age, Colloncuran SALMA (Roth 1899); Cerro Boleadoras Formation, Santa Cruz province, Argentina, early to middle Miocene age, ?Colloncuran SALMA (Scillato-Yané and Carlini 1998).

Diagnosis See Scillato-Yané and Carlini (1998) and Croft et al. (2007).

Stenotatus planus
Scillato-Yané and Carlini, 1998
(Fig. 4a)

Holotype MLP 91-I-10-54, disarticulated mobile band and buckler osteoderms from a single individual.

Type Locality CB-025, Cerro Boleadoras, Argentina.

Age and distribution Cerdas beds, department of Potosí, Bolivia, early to middle Miocene age, Friasian/Colloncuran SALMA (present study); Cerro Boleadoras Formation, Santa Cruz province, Argentina, early to middle Miocene age, ?Colloncuran SALMA (Scillato-Yané and Carlini 1998).
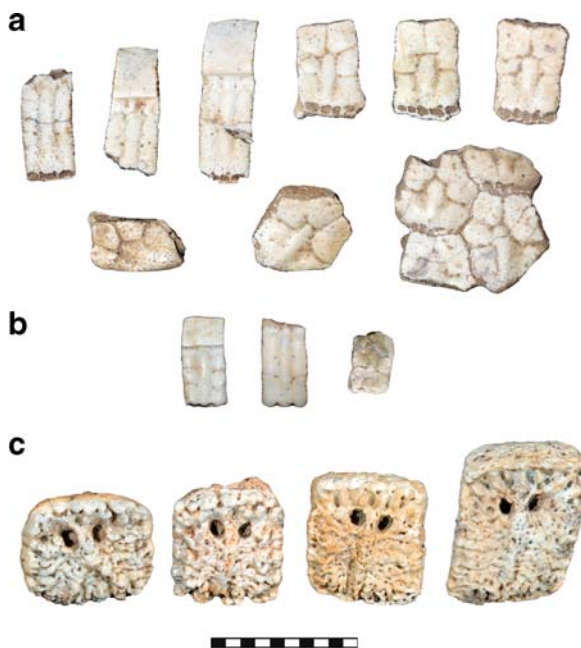
Referred Material UATF-V-000869, partial carapace (mostly disarticulated) and some bones of the

forelimb, including a partial humerus and various phalanges.

Locality and Horizon B-07-15, east side of large ridge east of river valley, in grayish sandstones near base of section (Fig. 3).

Amended Diagnosis Differs from *S. patagonicus* primarily in having a wider, flatter primary figures. Lacks the large, conspicuous piliferous pits present in longitudinal sulci of *S. hesternus* (Ameghino 1889). Distal row of piliferous pits in moveable band osteoderms smaller than those of *S. ornatus* and *S. centralis* (Ameghino 1897, 1902).

Description: Both moveable band and buckler osteoderms of UATF-V-000869 are characterized by a single row of large piliferous pits (generally 4–5, but sometimes more) along the posterior border (Fig. 4a). Like the holotype of *S. planus*, the superficial texture of the osteoderms shows little relief compared to other species of *Stenotatus*. Moveable band osteo-

derms of UATF-V-000869 bear two longitudinal sulci and two pairs of transverse sulci that together define an elongate central figure and two pairs of peripheral figures. Small piliferous pits (3–4 pairs) are present in the longitudinal sulci. Four complete moveable band osteoderms are 18.3 mm, 19.0 mm, 19.8 mm and 22.5 mm long and 7.3–7.7 mm wide. Buckler osteoderms of UATF-V-000869 bear a convex central figure with five short radiating sulci (one anterior, two lateral pairs); small piliferous pits are present at the intersections of these sulci. Buckler osteoderms are 12–15 mm long and 7.5–11.5 mm wide.

Euphractini Winge, 1923

Prozaedyus Ameghino, 1891

Type species Prozaedyus proximus (Ameghino, 1887).

Included species The type, *Prozaedyus exilis* (Ameghino, 1887*), Prozaedyus impressus* Ameghino, 1897, *Prozaedyus planus* Ameghino, 1897, *Prozaedyus humilis* Ameghino, 1902, *Prozaedyus tenuissimus* Ameghino, 1902.

Age and distribution Deseado Formation, Santa Cruz and Chubut provinces, Argentina, late Oligocene age, Deseadan SALMA (Ameghino 1897; Loomis 1914); Sarmiento Formation, Chubut province, Argentina, early Miocene age, Colhuehuapian SALMA (Ameghino 1902); Cerro Bandera Formation, Neuquén province, Argentina, early Miocene age, Colhuehuapian SALMA (Kramarz et al. 2005); Santa Cruz Formation, Santa Cruz province, Argentina, late early Miocene age, Santacrucian SALMA (Scott 1903; Vizcaíno et al. 2006); Río Frías Formation, region XI, Chile, early to middle Miocene age, Friasian SALMA (Kraglievich 1930); Cerdas beds, department of Potosí, Bolivia, early to middle Miocene age, Friasian/Colloncuran SALMA (present study); Collón-Curá Formation, Neuquén and Río Negro provinces, Argentina, early middle Miocene age, Colloncuran SALMA (Roth 1899; Kay et al. 1998); Choquecota Formation, department of Oruro, Bolivia, early middle Miocene age, ?Colloncuran SALMA (Hoffstetter et al. 1972); Quebrada Honda beds, department of Tarija, Bolivia, late middle Miocene age, Laventan SALMA

Fig. 4 Representative osteoderms of Cerdas armadillos. **a**, *Stenotatus planus*, UATF-V-000869; **b**, *Prozaedyus* sp., from *left* to *right*, UATF-V-000831, UATF-V-000820, UATF-V-000855; **c**, Peltephilidae, gen.? et sp. nov., UF 225047. *Scale bar* equals 10 mm.

(Hoffstetter 1977; Scillato-Yané and Carlini 1999);
?Río Mayo Formation (Laguna Blanca = Lago Blanco
and Río Fenix faunas), Chubut and Santa Cruz
provinces, Argentina, middle to late Miocene age,
Mayoan SALMA (Kraglievich 1930).

Diagnosis (Osteoderms) As for other euphractins,
characterized by: osteoderms with relatively narrow
and straight-sided primary figure; relatively small
piliferous foramina; and foramina often present along
sides of the osteoderm in addition to posterior edge.
Distinguished from other euphractins primarily by
small size (typically≤15–20 mm×5–6 mm for move-
able band osteoderms and 8–10 mm×5–6 mm for
buckler osteoderms; Scott 1903; Tauber 1994).
Lateral figures divided into variable number of
smaller figures (usually four to five).

Prozaedyus sp.
(Fig. 4b)

Referred Material UATF-V-000820, partial moveable
band osteoderm; UATF-V-000831, moveable band
osteoderm; UATF-V-000855, buckler osteoderm; UF
225720, partial moveable band osteoderm; UF
225723, partial moveable band osteoderm, partial
buckler osteoderm, ?marginal osteoderm.

Localities and Horizons B-07-8 (UATF-V-000820,
UF 225720) and B-07-9 (UATF-V-000831), north-
west area of badlands, high in section (mostly≤50 m
below dated tuff), in beige-brown sandstones (Fig. 3);
B-07-11 (UATF-V-000855), west of river valley, in
grayish sandstones near base of section.

Description UATF-V-000831 is a complete, well-
preserved moveable band osteoderm that measures
12.9 mm×6.4 mm×2.4 mm (Fig. 4b, left). Two
longitudinal sulci on the superficial surface of the
osteoderm divide it approximately into thirds. The
lateral thirds are further subdivided by two transverse
sulci each, resulting in three pairs of small lateral
figures bordering an elongate central (primary) figure.
Very small foramina are present at the intersections of
the sulci, and slightly larger foramina border the
posterior edge. The posterior foramina are much
smaller than those of eutatins. The pairs of lateral
figures are subequal in size, with the anteriormost pair
slightly longer anteroposteriorly than the other two.

UATF-V-000820 is a partial moveable band osteo-
derm lacking the anterior third (i.e., the region
overlapped anteriorly) (Fig. 4b, center). The relief
on its superficial surface is less pronounced, but
resembles UATF-V-000820. It measures 12.2 mm×
6.4 mm×2.2 mm, and therefore would have been
longer than UATF-V-000831 in its unbroken state
(probably 15–16 mm). UATF-V-000855, a complete
buckler osteoderm, preserves little ornamentation but
likely pertains to this species based on its small size
(8.6 mm×5.6 mm×3.0 mm) and lack of prominent
posterior foramina (Fig. 4b, right). Two specimens
from the Florida collections, UF 225720 and UF
225723, probably also pertain to this species.

Discussion The genus *Prozaedyus* has been recorded
in many post-Santacrucian faunas (see above), but we
are unaware of any specific identifications that have
been published for such specimens. This no doubt
partly stems from the poor material available at some
localities (e.g., Kraglievich 1930), but also indicates
that a revision of the genus—or at least the younger
material referred to the genus—is needed. In such a
context, a reliable identification of the sparse material
from Cerdas is not possible.

Peltephilidae Ameghino, 1894

Gen.? et sp. nov.
(Fig. 4c)

Referred Material UF 225047, five mostly complete
and one partial osteoderm.

Locality and Horizon B-07-8, northwest area of
badlands, high in section (10–20 m below dated tuff),
in beige-brown sandstones (Fig. 3).

Description Of the six osteoderms pertaining to UF
225047, four are complete (Fig. 4c), one lacks its
posterior corner, and one lack its anterior half. The
superficial surface of each is very rugose and bears a
pair of large, oval pits (ca. 1.5–2.0 mm×2.0–3.0 mm;
not preserved in the least complete osteoderm); these
pits lie closer to the anterior border of each osteoderm
than to the posterior border, and to either side of the AP
median axis. The osteoderms vary in size, 16–22 mm
AP×16–18 mm ML. They also vary in the degree to
which they were overlapped by more anterior osteo-

derms, as indicated by the size of the articular surface along the anterior edge. This area is most developed in the largest (AP) osteoderm and is least developed in the smallest. The development of a median AP ridge also is correlated with osteoderm size, being most pronounced in the longest and least developed (as well as angled posterolaterally) in the smallest.

Discussion Croft et al. (2007) provided a concise review of the taxonomy and stratigraphic range of peltephilids, as well as a discussion of diagnostic osteoderm characters. Although UF 225047 clearly represents a peltephilid, the large, rugose osteoderms do not closely resemble those of any previously described species, including *Epipeltephilus* Ameghino, 1904. Examination of additional specimens of this latter genus subsequent to our preliminary report (Croft and Anaya 2008) revealed that *Epipeltephilus* is characterized by osteoderms similar in size to those of *Peltephilus* Ameghino, 1887 (generally smaller than those of Cerdas), bearing two to four superficial pits that are larger and more rounded than those of the Cerdas species. We therefore judge the material from Cerdas to be distinct from that referred to *Epipeltephilus*, but insufficient for establishing a new species at this time.

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Phyllophaga Owen, 1842
Megatherioidea Gray, 1821
Nothrotheriidae Ameghino, 1920
Xyophorus Ameghino, 1887

Xyophorus cf. *bondesioi* Scillato-Yané, 1979
(Fig. 5a–c)

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Holotype MLP 32-IV-20, partial left mandible bearing bases of c and m2 and nearly complete m1 and m3.

Age and distribution ?Quebrada Honda beds, department of Tarija, Bolivia, late middle Miocene age, Laventan SALMA (see below); Cerdas beds, department of Potosí, Bolivia, early to middle Miocene age, Friasian/Colloncuran SALMA (present study); Arroyo Chasicó Formation, Buenos Aires province, Argentina, late Miocene age, Chasicoan SALMA (Scillato-Yané 1979); ?Toro Negro Formation, La Rioja province, Argentina, ?early Pliocene age, ?Montehermosan SALMA (Rodríguez Brizuela and Tauber 2006).

Referred Material UATF-V-000871, partial right mandible and predental spout bearing complete dentition, separate and mostly complete molariform (possibly upper); UATF-V-0008850, manual ungual ?I.

Questionably Referred Material UATF-V-0008825, pedal ungual.

Localities and Horizons B-07-8, northwest area of badlands, high in section (10–20 m below dated tuff), in beige-brown sandstones (Fig. 3).

Diagnosis (lower dentition) Larger than *Xyophorus rostratus* Ameghino, 1887, but smaller than *Xyophorus atlanticus* Ameghino, 1891, *Xyophorus andinus* Ameghino, 1891, *Xyophorus crassissimus* Ameghino, 1894, and *Xyophorus villarroeli* Saint-André, 1996; differs from all other species of *Xyophorus* except *X. villarroeli* in its more reduced lower caniniform and deeper lingual longitudinal sulcus in m1–2 (Scillato-Yané 1979; Saint-André 1996); differs from *X. villarroeli* in more equidimensional caniniform (see below).

Description UATF-V-000871 is a heavily weathered specimen, although some areas are in reasonably good state of preservation. It measures ca. 120 mm in greatest length. The predental spout accounts for 25% of this distance, extending ca. 30 mm anterior to the caniniform. The spout is v-shaped in anterior view and is 12.6 mm wide where both left and right superior edges are preserved. The buccal surfaces of the spout are rugose, especially near the superior edge and midway between the superior and inferior surfaces. Several small foramina ≤1.1 mm in diameter are present on the lingual surface. The lingual surface is horizontal anterior to the caniniform and begins to dip steeply ventrally behind the mandibular symphysis at a point ca. 6 mm anterior to the caniniform; the mental foramen sits at approximately this level on the buccal surface of the mandible. The base of the symphysis is directly inferior and medial to the caniniform. The horizontal ramus of the mandible is ca. 24 mm deep at m1, measured parallel to the long axis of the tooth. The posterior external opening of the mandibular canal is visible near the dorsal edge of the horizontal ramus near its juncture with the ascending ramus, just posterior to the last molariform (Fig. 5a, below).
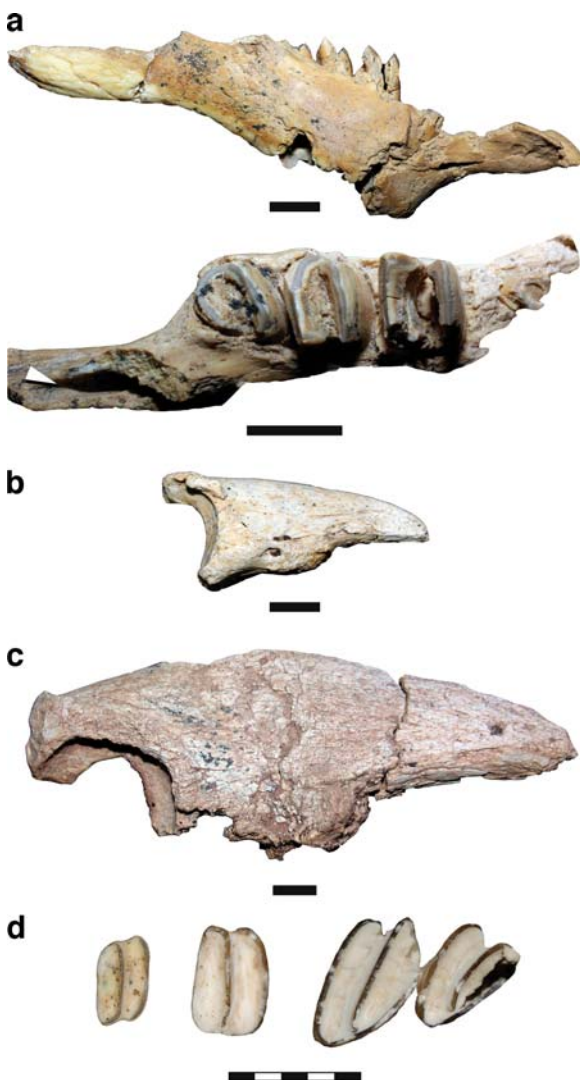
Fig. 5 Sloth and rodent specimens from Cerdas. **a**, Partial right mandible of *Xyophorus* cf. *bondesioi*, UATF-V-000871, in lateral (*above*) and occlusal (*below*) views; *arrow* in occlusal view indicates posterior external opening of mandibular canal; **b**, manual ungual ?I of *Xyophorus* cf. *bondesioi*, UATF-V-000850; **c**, pedal ungual, UATF-V-000825, possibly referable to *Xyophorus* cf. *bondesioi*; **d**. indeterminate lagostomine teeth in occlusal view (mesial to right), including right M1 or M2 (UATF-V-000851, left), left M1 or M2 (UATF-V-000864, center), and left p4-m1 (UATF-V-000864, right). *Scale bars* equal 10 mm in **a**–**c** and 5 mm in **d**.

The preserved portion of the caniniform is peglike and elliptical in section, measuring 5.5×4.1 mm. The ratio of its axes (AP diameter / ML diameter=1.34) more closely resembles that of *X. bondesioi* (holotype= 1.38) than that of *X. villarroeli* (1.74; Saint-André

1996). The caniniform is separated from m1 by a diastema of ca. 3.5 mm. In occlusal view, m1–2 are roughly quadrangular, and each bears two transverse lophs of orthodentine. The first molariform measures ≤7.0 mm×9.1 mm; the second measures ≥6.6× 9.6 mm. Because both teeth have split longitudinally between the two transverse lophs, the AP diameter of each is an estimate; in m1 the two parts have diverged slightly whereas in m2 they appear to have been compressed. Both bear evidence of a lingual sulcus, but its exact depth and morphology cannot be ascertained. The third molariform is irregular in occlusal view; the lingual face is broad and rounded, the buccal face is short and essentially flat, and the greatest diameter (ca. 10 mm) is oriented obliquely. It measures 8.6×7.5 mm relative to the axis of the toothrow. The buccal surface is not well preserved but the orthodentine certainly was thin or absent on this face. Total toothrow length is ca. 37.5 mm, very close to that of *X. bondesioi* (38.0 mm; Scillato-Yané 1979) and smaller than that of *X. villarroeli* (43.9 mm; Saint-André 1996). The relative size of the caniniform (= c AP diameter / m1 AP diameter) is ca. 0.8, similar to that of other *Xyophorus* species and greater than that of younger nothrotheriids such as *Pronothrotherium* (Saint-André 1996:102).

Two unguals may also pertain to this species. UATF-V-0008850 (Fig. 5b), a manual ungual, is probably from digit I. It is 56.4 mm long, 17.5 mm wide proximally, 6.7 mm wide distally, and 25.5 mm high at its proximal end. UATF-V-0008825 (Fig. 5c) is a pedal ungual. It is 120.4 mm long, 31.8 mm wide proximally, 10.8 mm wide distally, and has a maximum height of 47.3 mm.

Discussion The presence of a buccal longitudinal sulcus in m3 has been cited as a character differentiating *X. villarroeli* and *X. bondesioi* from other species of *Xyophorus* (Scillato-Yané 1979; Saint-André 1996) but we were unable to verify the presence of such a sulcus in the holotype of *X. bondesioi* or the specimen from Cerdas. For that reason, it has been excluded from the above diagnosis.

Frailey (1988) referred a sloth specimen from the middle Miocene locality of Quebrada Honda (UF 26668) to *Hapalops angustipalatus* Ameghino, 1891. Scillato-Yané and Carlini (1999) noted the reduced caniniform and the longitudinal sulci on the molariforms of UF 26668 and referred it instead to *X.*

villarroeli. Although these characters support the specimen's referral to *Xyophorus*, it appears to more closely resemble *X. bondesioi* (and the specimen from Cerdas) than *X. villarroeli*; the caniniform sectional ratio of UF 26668 is very close to that of *X. bondesioi* (1.42 based on Frailey's measurements) and toothrow length is nearly identical (ca. 37 mm based on Frailey 1988:fig. 2b). Given the importance of toothrow length and caniniform morphology in distinguishing *X. villarroeli* from other species of the genus, including *X. bondesioi* (Saint-André 1996:102), this specimen more likely pertains to *X. bondesioi*. Additional craniodental specimens from Achiri, Cerdas, Quebrada Honda, and/or Arroyo Chasicó would permit an assessment of population variation and clarify the utility of size, molariform shape, and other characters for distinguishing *X. bondesioi* and *X. villarroeli*.

Rodentia Bowdich, 1821
Caviomorpha Wood and Patterson in Wood, 1955
Chinchilloidea Bennett, 1835
Chinchillidae Bennett, 1835
Lagostominae Wiegmann, 1832

Gen. et sp. indet.
(Fig. 5d)

Referred Material UATF-V-000851, right M1 or M2; UATF-V-000864, left M1 or M2, partial left mandible bearing partial incisor and p4 and complete m1, and bone fragments.

Localities and Horizons B-07-10, northwest area of badlands, high in section (ca. 50 m below dated tuff), in beige-brown sandstones; B-07-15, east of large ridge east of river valley, in grayish sandstones near base of section (Fig. 3).

Description UATF-V-000851 is an isolated upper right cheek tooth, probably M1 or M2. It consists of two parallel, transverse lophs and measures 3.1×2.1 mm (Fig. 5d). The enamel of each loph is thin relative to the dentin, and is restricted to the mesial and lingual faces of each loph. The tooth is covered by a thin layer of cement. UATF-V-000864 includes a left M1 or M2 and a partial left mandible in addition to some small postcranial fragments. The upper molar generally resembles UATF-V-000851

but is much larger (4.2×3.2 mm) and bears little cement (Fig. 5d). The mandible is poorly preserved, and a portion of the incisor is visible inferolateral to the cheek teeth. The occlusal surfaces of p4 and m1 are slightly damaged mesiolingually. Both teeth consist of two thick enamel/dentin lophids. As is typical for lower teeth, the two lophids are oriented more obliquely relative to the long axis of the toothrow than they are in upper teeth, and the enamel is more extensive along the buccal face. In occlusal view, the premolar approximates a rounded right triangle with distal and lingual legs; the hypotenuse bears a shallow sulcus where it intersects the enamel plate separating the two lophids. The tooth is ca. 4.4 mm wide. The occlusal surface of m1 is elliptical, and the buccal face is more acute than the lingual one. It measures ca. 5.7×3.5 mm.

Discussion Lagostomine chinchillids are easily recognized by their characteristic hypselodont cheek teeth composed of two closely appressed, subparallel plates (Scott 1905; Vucetich 1984, 1989; Flynn et al. 2002). Miocene lagostomines are primarily represented by species of *Prolagostomus* Ameghino, 1887, and *Pliolagostomus* Ameghino, 1887, and the material from Cerdas almost certainly is referable to one of these genera. Nevertheless, a definitive identification cannot be made confidently at the present time because of the scant material available for study.

Litopterna Ameghino, 1889
Macraucheniidae Gervais, 1855

Discussion The Cerdas litoptern specimens described below are referred to Macraucheniidae rather than Proterotheriidae based on: (1) the lack of a diastema between p1 and c; and (2) the lack of lateral metatarsal reduction. Although dental and postcranial material referred to this species are not associated, the compatible morphology and close correspondence in size of these elements favor referral to the same species.
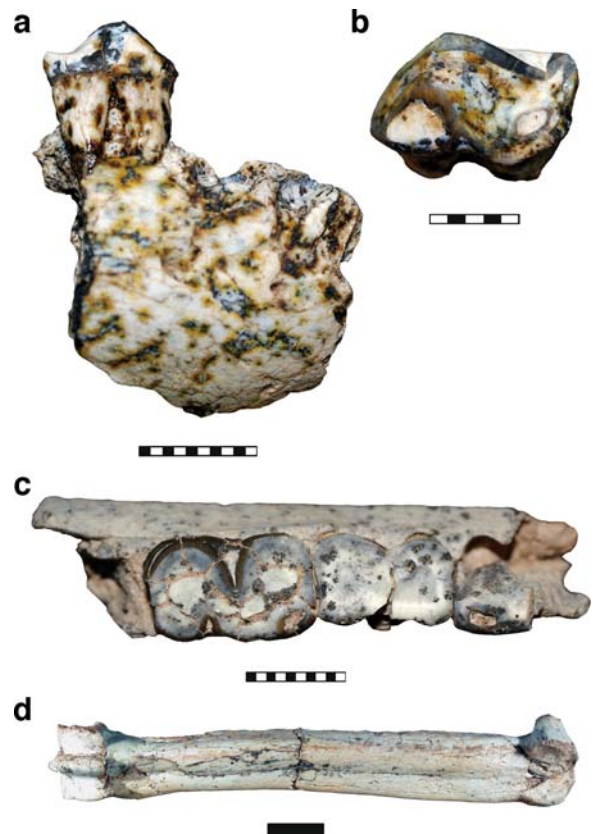
Gen. et sp. nov.
(Fig. 6)

Referred Material UATF-V-000881, partial right mandible bearing p2 and roots of c, p1; MNHN BLV 148, left mandible fragment bearing ?m1–2 and partial ?p4; UF 225719, left fourth metatarsal.

Localities and Horizons B-07-8 (UF 225719), northwest area of badlands, high in section (10–20 m below dated tuff), in beige-brown sandstones; B-07-16 (UATF-V-000881), northwest area of badlands, very high in section, above dated tuff (Fig. 3); "Gisement 1" (MNHN BLV 148, more specific geographic and stratigraphic provenance not known).

Description UATF-V-000881 is ca. 25 mm in total length and preserves one complete brachydont tooth (p2) and the roots of two others (c, p1) (Fig. 6a, b). The superior edge of the horizontal ramus has eroded away, exposing the roots of p2 buccally and distally; the distal root measures ca. 11 mm from its base to its tip. The roots of p1 and c are exposed in cross section. Both are roughly circular with a diameter of 4.7 mm. Their centers are ca. 7 mm apart. A large mental foramen is present between p2 and the root of p1, about halfway between the superior and inferior borders of the mandible. A second, smaller foramen is present just below the distal edge of the canine root.

The premolar is moderately worn, relatively broad for its length, and measures 11.9×6.4 mm. In buccal view, the high, sloping trigonid is dominated by the protoconid, and the low, flat talonid rises slightly in the region of the hypoconid. The trigonid is much longer anteroposteriorly than the talonid. The lingual face of the trigonid bears a shallow sulcus (metaflexid) that is partly filled by cement. The buccal surface of the trigonid also is partially covered by cement. A sharply-defined buccal sulcus (ectoflexid) separates the trigonid from the talonid, defining a buccally-projecting hypoconid. An elliptical, cement-filled fossettid is present in the talonid basin; it lies slightly closer to the lingual face than the buccal one, and its long axis oriented is mesiolingually. The tooth is broadest just mesial to this fossettid.

MNHN BLV 148 includes two very heavily worn teeth and a more mesial fragment of a third (Fig. 6c). The mesial tooth (?m1) is most worn, and only tiny slivers of enamel are present along some edges; no occlusal morphology is discernable. It measures 13.9×8.8 mm. The distal tooth (?m2) bears enamel along its buccal and lingual faces, and a buccal cingulum is present. The deep ectoflexid is partly filled with cement. A small fossettid is present near the mesiolingual corner (the remains of the metaflexid), and the shallow hypoflexid almost has been similarly isolated. The tooth measures $15.9 \times$

Fig. 6 Macraucheniidae gen. et sp. nov. **a**, UATF-V-000881, partial right mandible bearing p2 and roots of c, p1 in lateral view (anterior to *right*); **b**, close-up of p2 from **a** in oblique occlusal view (anterior to *left*); **c**, MNHN BLV 148, heavily worn partial left mandible bearing ?m1–2 and partial ?p4 (anterior to right); **d**, UF 225719, left fourth metatarsal with proximal and distal halves slightly offset. *Scale bars* equal 10 mm in **a**, **c**, **d**, and 5 mm in **b**.

10.0 mm. The tooth fragment (p4?) is merely the distolingual corner of the talonid, but it bears a small enamel fossettid. The tooth is apparently less worn than the following tooth, more similar in this regard to the distal one. Given that the adult tooth eruption sequence in some (perhaps all) macraucheniids is apparently m1>m2>m3>p4>p3 (Scott 1910; Cifelli and Guerrero 1997), a molariform flanked by two less worn teeth—as in MNHN BLV 148—supports their identification as p4–m2.

UF 225719 (MT IV) is ca. 10.5 cm long. It consists of three pieces that have been glued together (Fig. 6d). The two pieces of the diaphysis fit together well, indicating that little bone is missing. The distal epiphysis has been rotated laterally (counterclock-

wise) in proximal view relative to the rest of the metatarsal prior to gluing; this implies that the fit was not precise and that some small amount of bone may be missing between it and the diaphysis. The proximal articular surface of MT IV is gently convex and approximates a 'T' in proximal view. The dorsoplantar dimension is slightly greater than the mediolateral one (ca. 17 mm vs. 15 mm), and the medial articular surface (for articulation with MT III) is larger in the dorsoplantar dimension than the lateral surface (for articulation with MT V). The distal articular surface bears a well-defined median keel.

Discussion The litoptern from Cerdas differs markedly from previously described species both in its small size and in its robust, cement-covered dentition. Typical Miocene macraucheniids are much larger (e.g., species of *Theosodon* Ameghino, 1887; see Scott 1910; Cifelli and Guerrero 1997; Croft et al. 2004). Only the diminutive *Cullinia laevis* Cabrera and Kraglievich, 1931, from the late Miocene of Arroyo Chasicó resembles the Cerdas species in size; the MT IV of the holotype (MLP 29-IX-1-78) is longer than UF 225719 (13.4 cm vs. 10.5 cm) but the inferred length of p2 is comparable (p2 is incompletely preserved in the holotype of *C. laevis*, but p1= 10.2 mm and p3=12.9 mm; an isolated ?p2 from a separate specimen, MLP 28-X-11–36, is 11.3 mm long). MNHN BLV-148 is from an equally small litoptern, comparable to or even smaller than *C. laevis*; left and right m2 of the holotype of *C. laevis* are 18.4 mm and 18.6 mm long, respectively, and that of a referred specimen, MLP 29-IX-1–77, is 18.0 mm (vs. 15.9 mm in MNHN BLV 148). The relatively long, gracile proportions of UF 225719 compare favorably with *Cullinia* and contrast with *Theosodon* and other macraucheniids (Cabrera and Kraglievich 1931; Bond and López 1995). Interestingly, a macraucheniid metapodial noted by Hoffstetter (1977) in his original description of Quebrada Honda is also quite small, and may pertain to the Cerdas species. Another small macraucheniid has been reported from the ?early Miocene Kollukollu Formation south of La Paz, but may not preserve enough detail for a secure identification (Huxley 1860; Hoffstetter and Paskoff 1966; Marshall and Sempere 1991).

In terms of morphology, we have observed no closely similar p2. The corresponding tooth of the holotype of *C. laevis* and of MLP 28-X-11–36 lacks a thick covering of cement, a pronounced buccal sulcus between the trigonid and talonid, and a talonid fossettid. *Theosodon* specimens preserving p2 from the early/middle Miocene of Collón-Curá (e.g., MLP 73-VII-6-2) and the early Miocene of Santa Cruz (e.g., MLP 12–378) are equally dissimilar. Cement is rare in litopterns, occurring only in some late Miocene and younger species (Bond 1999; Bond et al. 2001). We are unaware of any litoptern characterized by an enclosed talonid fossettid in p2. We have observed a fossettid-like basin in the p2 talonid of MLP 12–345, a specimen from the early Miocene of Santa Cruz referred to the proterotheriid *Diadiaphorus majusculus* Ameghino, 1887, but it appears it would not have become isolated with wear. With the caveat that well-preserved litoptern p2s are relatively uncommon in museum collections, UATF-V-000881 appears to be unique. The morphology of MNHN BLV 148 appears to be compatible with UATF-V-000881, given that fossettes are present, as well as cement. We defer formal naming of this new species until more complete material has been collected.

Notoungulata Roth, 1903
Toxodontia Owen, 1853
Toxodontidae Owen, 1845

Palyeidodon Roth, 1899

Type Species Palyeidodon obtusum Roth, 1899.

Included Species The type only.

Age and Distribution ?Chucal Formation, region I, Chile, late early Miocene age, Santacrucian SALMA (Bond and García 2002; Croft et al. 2004); Río Frías Formation, region XI, Chile, early to middle Miocene age, Friasian SALMA (Kraglievich 1930; Madden 1990); Collón-Curá Formation, Neuquén province, Argentina, early middle Miocene age, Colloncuran SALMA (Roth 1899; Bondesio et al. 1980b; Madden 1990); unknown formation (Aguada La Escondida), Chubut province, Argentina (Pascual 1954).

Diagnosis (Upper Cheek Teeth) Differs from *Proadinotherium* Ameghino, 1887, *Adinotherium* Ameghino,

1895, and *Nesodon* Owen, 1846, in much larger size, presence of hypselodont M2-3, and more simplified tooth crowns (among other character states; see Madden 1990). Differs from all other "advanced" toxodontids (see below) except *Pericotoxodon* Madden, 1997, in the presence of a prominent, bifurcate, primary enamel fold in all molars and a persistent M3 distolingual fold. Differs from *Pericotoxodon* in having a more persistent M3 distolingual fold (variably present in *Pericotoxodon*) and quadrangular distal premolars (rather than teardrop-shaped).

Discussion Toxodontids are a monophyletic group of mostly Neogene, generally large to very large notoungulates (100–1,000 kg) that are abundant in most faunas of appropriate age (Cifelli 1985; Bond 1986). Among extant mammals, toxodontids most resemble rhinocerotids, hippopotamids, and/or large bovids in overall morphology. Middle Miocene and younger members of the clade are characterized by hypselodont (ever-growing) anterior and buccal dentitions (Madden 1990; Nasif et al. 2000). The group ranged throughout South America, dispersed into southern Central America in the late Neogene, and persisted until the Pleistocene megafaunal extinction (Webb 1991; MacFadden 2005).

As discussed recently by Bond et al. (2006) and Croft (2007), the number of valid toxodontid genera and their phylogenetic relationships are unclear. Although the late Oligocene and early Miocene *Proadinotherium*, *Adinotherium*, and *Nesodon* are universally recognized as basal forms, no consensus has been reached on the relationships among middle Miocene and younger species (e.g., Madden 1990; McKenna and Bell 1997; Nasif et al. 2000). Early to middle Miocene *Palyeidodon* has long been recognized as morphologically intermediate between these two groups (e.g., Pascual 1954, 1965; Paula Couto 1982; Madden 1990). Madden (1990) provided very useful, detailed comparative descriptions of *Palyeidodon obtusum* Roth, 1899, based on new material collected from the Río Frías Formation in the 1980s and concluded that: (1) *P. obtusum* is the most basal "advanced" toxodontid (i.e., toxodontid with at least one hypselodont molar); and (2) *Prototrigodon rothi* Kraglievich, 1930, is a junior synonym of *P. obtusum*. The basal position of *P. obtusum* among "advanced"

toxodontids also has been supported by the phylogenetic analysis of Nasif et al. (2000).

Palyeidodon obtusum Roth, 1899
(Fig. 7)

Holotype MLP 12–3171, damaged skull with poorly preserved upper molars.

*Type Locality* Unknown (from Collón-Curá Formation, Neuquén, Argentina).

Age and Distribution As for genus.

Referred Material UATF-V-000870, associated right M3, right ?P4, enamel fragments from upper molar ectolophs (probably M1–2).

Locality and Horizon B-07-8, northwest area of badlands, high in section (10–20 m below dated tuff), in beige-brown sandstones (Fig. 3).

Diagnosis As for genus.

Description UATF-V-000870 includes portions of at least four highly weathered teeth. The largest, a right M3, preserves its ectoloph and most of its occlusal morphology, but most of the dentin surface has been eroded away (Fig. 7a, c). It is a very large tooth, its ectoloph measuring ca. 67 mm at the crown and ca. 74 mm at the base. The perpendicular width cannot be measured due to incomplete preservation. The ectoloph is saddle-shaped, gently convex from its occlusal edge to its base, but more sharply concave mesiodistally; its maximal lingual inflection is closer to the mesial end of the tooth than the distal end. The enamel of the mesial face of the protoloph is not preserved and neither is the expanded lingual portion of the protoloph (i.e., the column). The primary enamel fold between the protoloph and metaloph is shallow and bifurcate buccally, demarcating a gently rounded intermediate lobe. The metaloph is roughly rectangular, about twice the mesiodistal length of the intermediate lobe, and is slightly wider near its distal edge. A well-defined enamel fold distal to the metaloph separates it from a long, tapering, fourth lobe. Enamel is absent along the lingual surface of the fourth lobe.
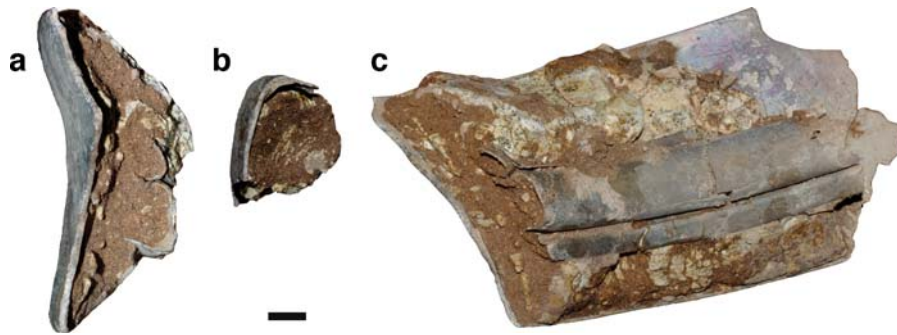
Fig. 7 Right M3 (**a**, **c**) and right ?P4 (**b**) of *Palyeidodon* sp., UATF-V-000870, in occlusal (**a**, **b**) and oblique lingual (**c**) views. *Scale bar* equals 1 cm.

A very poorly preserved right premolar may represent P4 (Fig. 7b). It includes the enamel of the ectoloph and that of an adjacent portion of the mesial face, which are oriented at a right angle to each other. No enamel fossettes or folds are present on the occlusal surface of the tooth or are visible along its faces. It measures ca. 40 mm×30 mm.

Two large pieces of enamel likely represent the ectolophs of right M1 and M2. They measure ca. 42 mm and 54 mm in mesiodistal length, respectively.

Discussion Despite the relatively poor condition of UATF-V-000870, key morphological features fortuitously have been preserved. The occlusal morphology of M3 matches that of *P. obtusum* in having a bifurcate primary enamel fold and a quadrangular metaloph distally demarcated by a persistent lingual enamel fold. (This fold extends to the base of the tooth in UATF-V-000870.) The length of M3 falls in the middle range of that of *P. obtusum* from Río Frías (Madden 1990:164), much larger than typical values for *Nesodon imbricatus*, the largest "nesodontine" (Scott 1912; Croft et al. 2003). The closely similar *Pericotoxodon platignathus* Madden, 1997 is similar in size to *P. obtusum*, but lacks the well-defined metaloph and persistent distolingual fold. Moreover, the poorly preserved premolar of UATF-V-000870 clearly preserves a 90° angle between the ectoloph and the protoloph; this differs from the acute angle present in premolars of *P. platignathus*, which results in its characteristic "teardrop" shape.

Typotheria Zittel, 1893
Interatheriidae Ameghino, 1887
Interatheriinae Ameghino, 1887

Protypotherium Ameghino, 1882
(Fig. 8a–c)

Referred Material UATF-V-000860, partial left mandible and symphysis bearing p3–m3 and bases of i1–p2, partial right mandible bearing p4–m1 and partial m2; UATF-V-000861, partial right maxilla bearing P2–M2 and partial left mandible bearing m2–3.

Locality and Horizon B-07-14, east side of river valley, in grayish sandstones near base of section.

Description UATF-V-000860 includes two partial mandibles. The left includes five complete teeth (p3–m3) and the bases of the remainder of the lower dentition (Fig. 8a, b). In size and morphology, the specimen resembles the smallest Santacrucian interatheriid, *Protypotherium attenuatum* Ameghino, 1887 (Sinclair 1909; Tauber 1996), although the premolar talonids are relatively smaller in UATF-V-000860. Given that such premolar characters can vary within populations (Tauber 1996), this may be of little taxonomic significance. The associated right mandible is similar in size and morphology and probably pertains to the same individual.

UATF-V-000861 includes a partial upper and lower dentition (Fig. 8c). The specimen is much smaller than UATF-V-000860—approx. 25% smaller based on linear dental measurements—more di-
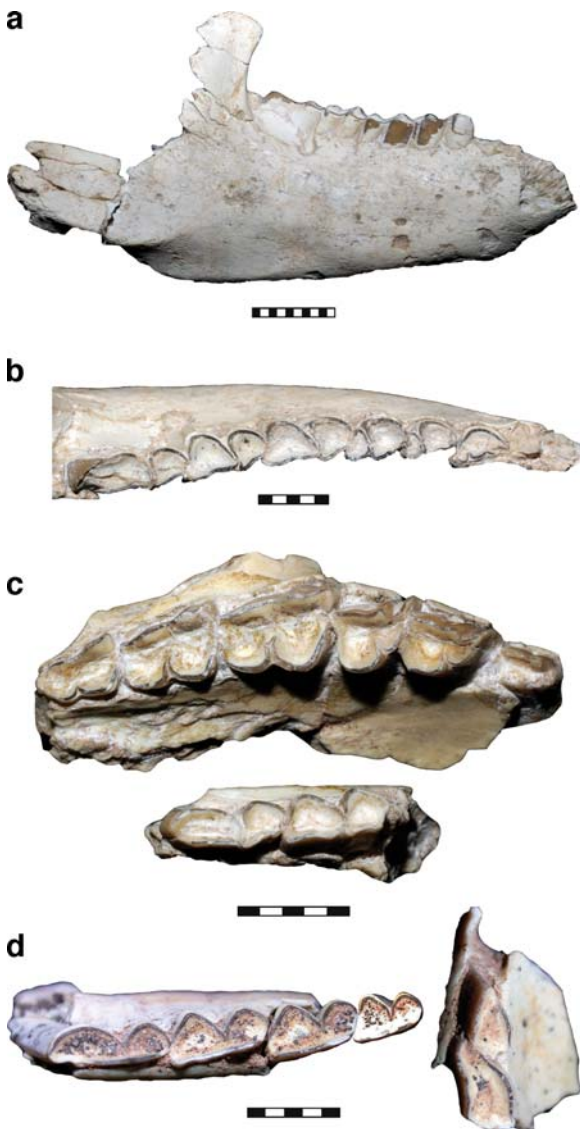
Fig. 8 Small typotheres of Cerdas. Left mandible of *Protypotherium* cf. *attenuatum*, UATF-V-000860, in **a**, lateral view (reversed) and **b**, occlusal view (only c–m3 visible); **c**, partial right maxilla bearing P2–M3 (*above*) and partial left mandible bearing m2–3 (*below*) of *Protypotherium* sp. nov., UATF-V-000861, in occlusal view; **d**, *Hegetotherium*? sp. nov., UATF-V-000856, partial right mandible bearing m1–3 and separate p4 (both reversed, p4 in life position, left), and partial right maxilla bearing ?P2–3 (right), all in occlusal view. Anterior is to the right in all views except for maxilla in **d** (in which it is toward the top). *Scale bars* equal 10 mm in **a** and 5 mm in **b–d**.

minutive than even Chasicoan *Protypotherium minutum* Cabrera and Kraglievich, 1931 (Bond and López 1996). It differs from other members of the genus in its complete lack of a buccal sulcus on the

talonid of m3, and the presence of a tiny middle lobe in M1 (as in *Miocochilius federicoi* Croft, 2007).

Discussion Given the differences in size and morphology between these two specimens, it appears that at least two interatheriids are present at Cerdas. Both appear to pertain to *Protypotherium*, although it should be noted that no phylogenetic analysis has tested whether all *Protypotherium* species—which together span the Miocene (Ameghino 1885; Bordas 1939; Bond and López 1998)—form a monophyletic clade exclusive of other species.

As has been noted previously, interatheriids are common in most early to middle Miocene South American faunas, with the exception of those at intermediate latitudes (e.g., Bolivia, northern Chile and Argentina; Croft et al. 2004; Croft and Anaya 2006; Croft 2007). The presence of interatheriids at Cerdas is noteworthy in this regard, being only the second report of early or middle Miocene interatheriids from Bolivia. Given that interatheriids are also present at the early/middle Miocene locality of Nazareno (pers. obs.; not reported by Oiso 1991), their absence from other localities of similar age may reflect small population sizes rather than true absences. A more detailed study of the interatheriids (and hegetotheriids) of Cerdas and Nazareno is currently underway (Croft and Anaya, in prep.).

Mesotheriiidae Alston, 1876
Mesotheriinae Simpson, 1945

'*Pesiotypotherium*' *minus* Villarroel, 1978

Holotype GB-226, partial left mandible with complete dentition; right i1, p4 also present.

Type Locality Cerdas beds, ca. 3 km southeast of the town of Cerdas, department of Potosí, Bolivia (Villarroel 1978).

Age and Distribution Cerdas beds, department of Potosí, Bolivia, early to middle Miocene age, Friasian/Colloncuran SALMA (Villarroel 1978; MacFadden et al. 1995); ?Nazareno Formation, department of Potosí, Bolivia, ?middle Miocene age, ?Colloncuran SALMA (Oiso 1991); Quebrada Honda beds, department of Tarija, Bolivia, late middle Miocene age, Laventan SALMA (Croft 2007).

Referred Material More than 60 specimens from UATF and UF collections, including several skulls and many partial dentitions (detailed in Townsend and Croft in review).

Discussion The holotype of '*P.*' *minus* comes from Cerdas and most (perhaps all) subsequently collected specimens also are referable to this species (Townsend and Croft in review). The species occurs throughout the stratigraphic section. Although '*P.*' *minus* appears to be a valid species, it probably is not closely related to *Plesiotypotherium achirense* Villarroel, 1974 (the type species), and therefore should be referred to a different genus (Townsend and Croft in review).

Hegetotheriidae Ameghino, 1894
Hegetotheriinae Ameghino, 1894

Hegetotherium? sp. nov.
(Fig. 8d)

Referred Material UATF-V-000838, right m2–3; UATF-V-000856, partial left mandible bearing m1–2, right p4, partial right mandible bearing m1–3, ?left i1, partial right maxilla bearing ?P2–3; UATF-V-000873, partial left mandible bearing ?m2, right m3, upper molar.

Localities and Horizons B-07-9 (UATF-V-000873) and B-07-10 (UATF-V-000838), northwest area of badlands, high in section (40–60 m below dated tuff), in beige-brown sandstones (Fig. 3); B-07-12 (UATF-V-000856), west of river, approximately in middle of section.

Description The three hegetotheriid specimens from Cerdas are all fragmentary dental remains from a small species of hegetotheriine. As illustrated by UATF-V-000856, p4–m3 are bilobed, with a flat lingual face and a deep buccal sulcus that separates the trigonid from the talonid (Fig. 8d). The teeth are very imbricated, and relatively thick cement covers the buccal faces. The trigonids are rounded in all teeth and are smaller mesiodistally and buccolingually than the talonids in p4–m2; in m3, the trigonid and talonid are of similar breadth. The talonids are triangular in p4–m2, whereas m3 has a semicircular talonid. No buccal sulcus is present in the m3 talonid of any specimen. The partial maxilla (UATF-V-000856) preserves two teeth, probably P2–3 (Fig. 8d). They

are triangular, but the lingual face of ?P3 is slightly concave mesially and convex distally.

Discussion Several derived character states distinguish pachyrukhines from more basal hegetotheriids such as *Hegetotherium* Ameghino, 1887, but most of these pertain to the anterior dentition, cranium, or postcranium (Cifelli 1993; Cerdeño and Bond 1998; Croft et al. 2004; Croft and Anaya 2006; Reguero et al. 2007). A strongly trilobed m3 (i.e., one with a pronounced buccal talonid sulcus) was an unequivocal synapomorphy of pachyrukhines within Hegetotheriidae prior to the description of *Hemihegetotherium trilobus* Croft and Anaya, 2006—a non-pachyrukhine with a clearly trilobed m3 (Croft and Anaya 2006). No pachyrukhine has yet been described with a bilobed m3, however, indicating that the Cerdas hegetotheriid is not referable to this clade, despite its very small size; it is smaller than any previously described hegetotheriine, ca. 25% smaller than *Hegetotherium mirabile* Ameghino, 1887. Although it most closely resembles species of *Hegetotherium* in dental morphology, its small size and complete lack of a buccal sulcus on m3 indicates it represents a new species. The same species likely is represented at Nazareno, Bolivia (pers. obs.; see also Oiso 1991).

Cerdas fauna

Twelve species of mammals from nine families are currently represented at Cerdas (Table 1), including six species (four families) of notoungulates, three species (two families) of armadillos, one sloth, one chinchillid rodent, and one litoptern. Glyptodontids, marsupials, and other families of rodents almost certainly were present at Cerdas during the early to middle Miocene, but have not yet been recorded. These absences can partly be attributed to the relatively small size of the collections from Cerdas (ca. 100 specimens) and may also reflect a taphonomic and/or collecting bias against very small mammals. The smallest mammals currently known from Cerdas are interatheriid and hegetotheriid notoungulates and the armadillo *Prozaedyus*, all of which are larger than many unrecorded rodents (e.g., octodontoids) and marsupials (e.g., caenolestids, argyrolagids). Screenwashing sediment would likely

Table 1 Faunal list for the Cerdas beds near Cerdas, Bolivia

| Higher classification	Family	Species
Xenarthra: Cingulata	Dasypodidae	*Stenotatus planus*
		Prozaedyus sp.
	Peltephilidae	Gen.? et sp. nov.
Xenarthra: Phyllophaga	Nothrotheriidae	*Xyophorus* cf. *bondesioi*
Rodentia: Caviomorpha	Chinchillidae	Lagostominae sp. indet.
Litopterna	Macraucheniidae	Gen. et sp. nov.
Notoungulata	Toxodontidae	*Palyeidodon obtusum*
	Interatheriidae	*Protypotherium* cf. *attenuatum*
		Protypotherium sp. nov.
	Mesotheriidae	*'Plesiotypotherium' minus*
		Microtypotherium cf. *choquecotense*
	Hegetotheriidae	*Hegetotherium*? sp. nov.

improve representation of smaller species, but no suitable sites have yet been encountered at Cerdas. No significant changes in faunal composition are observable between the base and the top of the section.

Of the identifiable specimens collected at Cerdas, the vast majority are typothere notoungulates (i.e., interatheriids, mesotheriids, and hegetotheriids; Fig. 9). Most of these specimens (93%) are mesotheriids. In this regard, Cerdas resembles the late early Miocene fauna of Chucal and many less well sampled Bolivian localities; just over half of the specimens from Chucal are typotheres, and most (83%) are mesotheriids (Fig. 9; see also Croft et al. 2004, 2007). Typotheres are much less common in the slightly younger middle Miocene fauna of Quebrada Honda (only 9%) and nearly all of these are hegetotheriids

(Croft and Anaya 2006); only one interatheriid and one mesotheriid specimen are known from Quebrada Honda, both collected prior to our 2007 expedition (Croft 2007). Toxodontian notoungulates (thus far exclusively toxodontids) are moderately abundant at both Cerdas and Chucal, and relatively uncommon at Quebrada Honda. The reverse is true for litopterns (Fig. 9).

For xenarthran specimens, Cerdas (11%) is intermediate between Chucal (4%) and Quebrada Honda (28%). Most of these are cingulates (i.e., armored forms). In all faunas, sloths are relatively uncommon or have not been recorded.

For rodents, only two specimens have been collected from Cerdas, both lagostomine chinchillids. Little can be said about this aspect of the fauna other
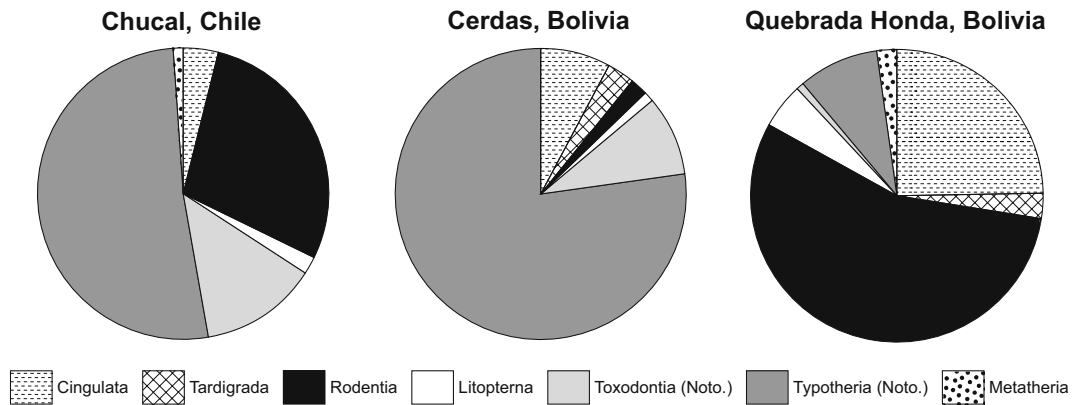
Fig. 9 Number of identified specimens (NISP) coded by higher taxonomic group for Chucal, Cerdas, and Quebrada Honda. Data for Cerdas are from UATF and UF collections (*N*=90).

Data for Chucal are from DAC (unpubl. data; *N*=251). Data for Quebrada Honda are from UATF collections only (*N*=151).

than that chinchillids also are the most abundant group of rodents at Chucal (Croft et al. 2004, 2007) and at Quebrada Honda (MacFadden and Wolff 1981; Chick et al. 2008). It is noteworthy that the chinchillids of Cerdas and Quebrada Honda are lagostomines, whereas the chinchillids of Chucal are chinchillines (Flynn et al. 2002; Croft et al. 2007; Chick et al. 2008). It is not known whether the difference in subfamilial representation reflects temporal or geographic differences between Chucal and Cerdas/Quebrada Honda. Rodents are by far the most abundant group overall at Quebrada Honda (Fig. 9); they likely also are the most diverse (Croft 2007; Chick et al. 2008).

Marsupials (metatherians) are uncommon or absent in all three faunas, though they are relatively diverse and represented by excellent material at Quebrada Honda (Sánchez-Villagra et al. 2000; Goin et al. 2003; Forasiepi et al. 2006; Croft 2007). At Chucal, only a caenolestid has been recovered to date (Croft et al. 2007). The scarcity of marsupials may partly be attributed to taphonomic and/or collecting biases against small-sized mammals, but this should not apply to the carnivorous marsupials (sparassodontants), most of which were at least as large as smaller notoungulates and cingulates and medium-sized rodents (Marshall 1977, 1978, 1981; Argot 2004; Wroe et al. 2004). More likely, the scarcity of sparassodont specimens reflects actual rarity of individuals in paleocommunities, an attribute that may have contributed to (or be a reflection of) their relatively low species diversity (Croft 2006).

Few of the species present at Cerdas have been recorded previously in Bolivia: only the mesotheriids 'P.' minus and M. choquecotense. The toxodontid P. obtusum occurs at Río Frías in Chile and in Colloncuran faunas in Argentina. Given the inferred temporal overlap between these localities and the Cerdas beds (see below), the presence of P. obtusum illustrates the general value of toxodontids for biostratigraphic correlation. The armadillo Stenotatus planus is otherwise known only from its type locality of Cerro Boleadoras, probably of Colloncuran age (Scillato-Yané and Carlini 1998). Its presence at Cerdas may represent a slight increase in temporal range, but would be a ca. 3,000 km northward extension of its geographic range (more than 25° latitude). Temporal and geographic range extensions of similar magnitude would apply to the interatheriid

notoungulate P. cf. attenuatum, otherwise known from the Santacrucian of Patagonia. The greatest temporal range extension appears to be for the sloth, X. cf. bondesioi, recorded previously only from the late Miocene of Buenos Aires Province (Arroyo Chasicó), more than 2,000 km and 18° of latitude south and east of Cerdas (Bondesio et al. 1980a). If this species also occurs at Quebrada Honda (see discussion above), then X. bondesioi and X. villarroeli may represent temporally disjunct species, with the latter occurring only in latest Miocene (and potentially younger) faunas.

Four species at Cerdas described herein likely are new: the peltephilid, the macraucheniid litoptern, one species of Protypotherium, and an hegetotheriid. We refrain from naming these new species pending recovery of more complete material from Cerdas and study of specimens from nearby localities such as Nazareno. None of these species represents a temporal range extension for their family (nor their genus, in the case of the notoungulates). Peltephilids previously have been reported from the late Oligocene of Bolivia (Hoffstetter 1968; Marshall and Sempere 1991; Carlini and Scillato-Yané 1999; Shockey and Anaya 2008) and the early Miocene of northern Chile (Croft et al. 2007), but the Cerdas occurrence would be the youngest in the middle latitudes of South America (though a peltephilid has recently been collected from the late Miocene of Caragua, northern Chile; pers. obs.; Montoya Sanhueza and Moreno 2008). Macraucheniids are present throughout the Neogene of Bolivia (Hoffstetter 1986; Marshall and Sempere 1991), but are mostly represented in the Miocene by sparse material of limited taxonomic utility. As noted above, the small macraucheniid of Cerdas may also be present in other Bolivian localities. The two new typothere notoungulates from Cerdas may also occur at Nazareno, Bolivia (Croft and Anaya, in prep.), but are not closely related to species reported from other faunas of Bolivia and northern Chile.

Based on associated radioisotopic dates and magnetostratigraphy, most of the fossiliferous levels at Cerdas span 16.5–15.3 Ma (early middle Miocene; MacFadden et al. 1995). The fauna is thus younger than Chucal (18.8–17.5 Ma; Wörner et al. 2000; Charrier et al. 2005; Croft et al. 2007) and older than Quebrada Honda (13.0–12.7 Ma; MacFadden et al. 1990; see also Fig. 2). Cerdas may overlap the youngest Santacrucian deposits from Argentina, which have been estimated to

be as young as 16.5 Ma (Fleagle et al. 1995), 16.3 Ma (Flynn and Swisher 1995), 16.05 Ma (Bown and Fleagle 1993), or 15.4 Ma (Madden et al. 1997). Cerdas apparently overlaps the fauna of Río Frías/Cisnes, based on a preliminary $^{40}Ar/^{39}Ar$ date of "about 16.5 Ma" near the base of the section (Flynn and Swisher 1995:325). Cerdas also overlaps deposits of the Collón-Curá Formation, whose Pilcaniyeu Ignimbrite— within the fossiliferous levels—has been dated to 15.7 Ma (Madden et al. 1997; Kay et al. 1998).

In sum, the Cerdas beds record a particularly problematic slice of time at the intersection of the Santacrucian, Friasian sensu stricto, and Colloncuran SALMAs. The moderately diverse fauna of Cerdas— combined with those from other middle latitude localities—thus provides an opportunity to test faunal differences among these biochronologic intervals. This slice of time also is of particular interest for understanding the relationships between climate and habitat/faunal change in South America, because it falls within the middle Miocene climatic optimum (17–15 Ma; Zachos et al. 2001).

Unfortunately, among the faunas of Patagonia, only Santacrucian faunas are known in some detail. The few taxonomic groups from Río Frías that have been revised recently (toxodontids and marsupials; Madden 1990; Marshall 1990) overlap little with those so far recovered from Cerdas (xenarthrans, litopterns, toxodontids, typotheres). The one commonality is the toxodontid, which at both sites is referred to *Palyeidodon obtusum*, a species that also occurs in the Colloncuran (see above). Collón-Curá is slightly better characterized than Río Frías (e.g., Vucetich et al. 1993; Kay et al. 1998; Scillato-Yané and Carlini 1998), and shares at least one additional species with Cerdas, *Stenotatus planus*. One species from Cerdas may be shared with Santacrucian faunas (*Protypotherium* cf. *attenuatum*). Another species may be shared with Arroyo Chasicó (*Xyophorus* cf. *bondesioi*), but this obviously would represent a temporal range extension for the species. The other taxa from Cerdas presently are not biochronologically informative.

Compounding these challenges is the effect of latitudinal provinciality; the classic localities for the Santacrucian, Friasian sensu stricto, and Colloncuran SALMAs lie some 25° and 3,000 km south of those in northern Chile and southern Bolivia. Given that significant provinciality was present in South Amer-

ica at least by the early Miocene, one would expect large faunal differences to be present between Cerdas and Patagonia that might obscure temporal patterns. Comparisons with faunas at similar latitudes as Cerdas should help minimize these effects. No faunas in this area are unequivocally referable to the Colloncuran or Friasian sensu stricto (Nazareno may correspond to this interval in whole or part but is not well constrained temporally), but Quebrada Honda pertains to the next youngest interval, the Laventan. The Santacrucian is represented by Chucal, though this fauna appears to be slightly older than some typical localities in Santa Cruz.

As noted above, Cerdas resembles Chucal at above-species taxonomic levels and in relative abundance of ordinal and family-level taxonomic groups. Unexpectedly, the two faunas have no species in common. In contrast, even though Cerdas and Quebrada Honda differ in community composition, they share one species (*P. minus*) and potentially as many as three others (*Xyophorus* cf. *bondesioi*, *Prozaedyus* sp., Lagostominae sp. indet.). This may reflect the closer proximity of Quebrada Honda to Cerdas, but serves to highlight the differences between Cerdas and Chucal, the latter of which includes many typical Santacrucian taxa (e.g., *Nesodon imbricatus*, *Hegetotherium mirabile*, *Theosodon* sp., *Neoreomys* sp., *Peltephilus* sp.; Croft et al. 2004, 2007).

In sum: (1) the age of the Cerdas beds partly overlaps that of the Río Frías, Collón-Curá, and perhaps Santa Cruz formations of southern South America; (2) the fauna of Cerdas includes two Friasian sensu stricto/Colloncuran species, and perhaps one Santacrucian species; (3) compared to middle latitude faunas of western South America, Cerdas is more similar to the younger (Laventan) fauna of Quebrada Honda than to the older (Santacrucian) fauna of Chucal. These observations imply that—at least in the middle latitudes—the particular interval of time represented by the Cerdas beds is more appropriately grouped with the Friasian sensu stricto/Colloncuran interval than the Santacrucian. The boundary between these SALMAs must therefore occur between 17.5 Ma (the youngest levels at Chucal) and 16.5 Ma (the base of the Cerdas beds). This hypothesis is testable through additional investigations at Cerdas as well as study of other middle latitude faunas with associated radioisotopic dates. If

further supported, this would indicate that a diachroneity of up to 2.1 Ma may exist in the early Miocene SALMA sequence between middle and high latitude faunas, with the top of the Santacrucian ranging from 17.5–16.5 in the middle latitudes (the gap between Chucal and Cerdas) and from 16.5–15.4 in the southern cone (the range of dates cited above). Such a diachroneity would pose obvious difficulties for intra-continental biochronologic age determinations based solely on fossil mammals, at least for faunas spanning many degrees of latitude.

References

Ameghino F (1885) Nuevos restos de mamíferos fósiles oligocenos recogidos por el Profesor Pedro Scalabrini y pertenecientes al Museo Provincial de la ciudad de Paraná. Bol Acad Nac Cien Córdoba 8: 5–207

Ameghino F (1887) Enumeración sistemática de las especies de mamíferos fósiles coleccionados por C. Ameghino en los terrenos eocenos de la Patagonia austral. Bol Mus La Plata 1: 1–24

Ameghino F (1889) Contribución al conocimiento de los mamíferos fósiles de la República Argentina. Actas Acad Nac Cien, Córdoba 6: 1–1027

Ameghino F (1895) Première contribution à la connaissance de la faune mammalogique des couches à *Pyrotherium*. Bol Inst Geogr Arg 15: 501–602

Ameghino F (1897) Les mammifères crétacés de l'Argentine. Deuxième contribution à la connaissance de la faune mammalogique des couches à Pyrotherium. Bol Inst Geogr Arg 18: 406–521

Ameghino F (1902) Première contribution à la connaissance de la faune mammalogique des couches à *Colpodon*. Bol Acad Nac Cien Córdoba 17: 71–138

Argot C (2004) Evolution of South American mammalian predators (Borhyaenoidea): anatomical and palaeobiological implications. Zool J Linn Soc 140: 487–521

Barrio C, Carlini AA, Goin FJ (1989) Litogénesis y antigüedad de la Formación Chinchinales de Paso Córdoba (Río Negro, Argentina). Actas, IV Cong Arg Pal Bioestrat 4: 149–156

Bengtson P (1988) Open nomenclature. Palaeontol 31: 223–227

Bond M (1986) Los ungulados fósiles de Argentina: evolución y paleoambientes. Actas, IV Cong Arg Pal Bioestrat 2: 173–185

Bond M (1999) Quaternary native ungulates of southern South America. A synthesis. Quat South Am Antarct Penins 12: 177–206

Bond M, García M (2002) Nuevos restos de toxodonte (Mamalia, Notoungulata) en estratos de la Formación Chucal, Mioceno, Altiplano de Arica, norte de Chile. Rev Geol Chile 29: 81–91

Bond M, López G (1995) Los Macraucheniidae (Mammalia, Litopterna) de la Formación Arroyo Chasicó (Partido de Villarino, Pcia de Buenos Aires). Actas, IV Jor Geol Geof Bonaer 1: 23–27

Bond M, López G (1996) Las espécies de *Protypotherium* (Notoungulata, Interatheriidae) de la Formación Arroyo Chasicó (Mioceno superior), provincia de Buenos Aires, Argentina. Ameghiniana 33: 460

Bond M, López G (1998) "*Notopachyrukhos tambuttoi*" Rusconi, 1933, un Interatheriidae (Mammalia, Notoungulata) del "Puelchense" de la provincia de Buenos Aires, Argentina. Actas, X Cong Lat Geol y VI Cong Nac Geol Econ 1: 280–283

Bond M, Madden RH, Carlini AA (2006) A new specimen of Toxodontidae (Notoungulata) from the Urumaco Formation (upper Miocene) of Venezuela. J Syst Palaeontol 4: 285–291

Bond M, Perea D, Ubilla M, Tauber A (2001) *Neolicaphrium recens* Frenguelli, 1921, the only surviving Proterotheriidae (Litopterna, Mammalia) into the South American Pleistocene. Palaeovertebr 30: 37–50

Bondesio P, Laza JH, Scillato-Yané GJ, Tonni EP, Vucetich MG (1980a) Estado actual del conocimiento de los vertebrados de la Formación Arroyo Chasicó (Plioceno temprano) de la Provincia de Buenos Aires. Actas, II Cong Arg Pal Bioestrat y I Cong Lat Pal 3: 101–127

Bondesio P, Rabassa J, Pascual R, Vucetich MG, Scillato-Yané GJ (1980b) La Formación Collón Curá de Pilcaniyeu Viejo y sus alrededores (Río Negro, República Argentina). Su antigüedad y las condiciones ambientales según su distribución, su litogénesis y sus vertebrados. Actas, II Cong Arg Pal Bioestrat y I Cong Lat Pal 3: 85–99

Bordas AF (1939) Diagnosis sobre algunos mamíferos de las capas con *Colpodon* del Valle del Río Chubut (República Argentina). Physis 14: 413–433

Bown TM, Fleagle JG (1993) Systematics, biostratigraphy, and dental evolution of the Palaeothentidae, later Oligocene to early-middle Miocene (Deseadan-Santacrucian) caenolestoid marsupials of South America. J Paleontol 67: 1–76

Cabrera A, Kraglievich L (1931) Diagnosis previas de los ungulados fósiles del Arroyo Chasicó. Notas Prelim Mus La Plata 1: 107–113

Carlini AA, Scillato-Yané GJ (1999) Cingulata del Oligoceno tardío de Salla, Bolivia. Resúmenes, Cong Int Evol Neotrop Cenozoico, La Paz, pp 15

Cerdeño E, Bond M (1998) Taxonomic revision and phylogeny of *Paedotherium* and *Tremacyllus* (Pachyrukhinae, Hegetotheriidae, Notoungulata) from the late Miocene to Pleistocene of Argentina. J Vertebr Paleontol 18: 799–811

Charrier R, Chávez A, Elgueta S, Hérail G, Flynn JJ, Croft DA, Wyss A, Riquelme R, García M (2005) Rapid tectonic and paleogeographic evolution associated with the development of the Chucal anticline and the Chucal-Lauca Basin in the Altiplano of Arica, northern Chile. J South Am Earth Sci 19: 35–54

Chick J, Croft DA, Anaya F (2008) Middle Miocene rodents from Quebrada Honda, Bolivia. J Vertebr Paleontol 28: 63A

Cifelli RL (1985) South American ungulate evolution and extinction. In: Stehli FG, Webb SD (eds) The Great American Biotic Interchange. Plenum, New York, pp 249–266

Cifelli RL (1993) The phylogeny of the native South American ungulates. In: Szalay FS, Novacek MJ, McKenna MC (eds) Mammal Phylogeny: Placentals. Springer-Verlag, New York, pp 195–216

Cifelli RL, Guerrero J (1997) Litopterns. In: Kay RF, Madden RH, Cifelli RL, Flynn JJ (eds) Vertebrate Paleontology in the Neotropics: the Miocene Fauna of La Venta, Colombia. Smithsonian Institution Press, Washington, pp 289–302

Croft DA (2006) Do marsupials make good predators? Insights from predator-prey diversity ratios. Evol Ecol Res 8: 1193–1214

Croft DA (2007) The middle Miocene (Laventan) Quebrada Honda Fauna, southern Bolivia, and a description of its notoungulates. Palaeontol 50: 277–303

Croft DA, Anaya F (2006) A new middle Miocene hegetotheriid (Notoungulata: Typotheria) and a phylogeny of the Hegetotheriidae. J Vertebr Paleontol 26: 387–399

Croft DA, Anaya F (2008) A new early/middle Miocene fauna from southern Bolivia. J Vertebr Paleontol 28: 67A

Croft DA, Flynn JJ, Wyss AR (2004) Notoungulata and Litopterna of the early Miocene Chucal Fauna, northern Chile. Fieldiana: Geol (NS) 50: 1–52

Croft DA, Flynn JJ, Wyss AR (2007) A new basal glyptodontid and other Xenarthra of the early Miocene Chucal Fauna, northern Chile. J Vertebr Paleontol 27: 781–797

Croft DA, Radic JP, Zurita E, Charrier R, Flynn JJ, Wyss AR (2003) A Miocene toxodontid (Mammalia: Notoungulata) from the sedimentary series of the Cura-Mallín Formation, Lonquimay, Chile. Rev Geol Chile 30: 285–298

De Iuliis G, Brandoni D, Scillato-Yané GJ (2008) New remains of *Megathericulus patagonicus* Ameghino, 1904 (Xenarthra, Megatheriidae): information on primitive features of megatheriines. J Vertebr Paleontol 28: 181–196

Fleagle JG, Bown TM, Swisher C, Buckley G (1995) Age of the Pinturas and Santa Cruz Formations. Actas, VI Cong Arg Pal Bioestrat 1: 129–135

Flynn JJ, Croft DA, Charrier R, Hérail G, Wyss AR (2002) The first Cenozoic mammal fauna from the Chilean Altiplano. J Vertebr Paleontol 22: 200–206

Flynn JJ, Swisher CC, III (1995) Cenozoic South American Land Mammal Ages: Correlation to global geochronologies. In: Berggren WA, Kent DV, Aubry M-P, Hardenbol J (eds) Geochronology, Time Scales, and Global Stratigraphic Correlation. SEPM (Society for Sedimentary Geology) Special Publication No. 54, pp 317–333

Flynn JJ, Wyss AR (1998) Recent advances in South American mammalian paleontology. Trends Ecol Evol 13: 449–454

Forasiepi AM, Sánchez-Villagra MR, Goin FJ, Takai M, Shigehara N, Kay RF (2006) A new species of Hathliacynidae (Metatheria, Sparassodonta) from the middle Miocene of Quebrada Honda, Bolivia. J Vertebr Paleontol 26: 670–684

Frailey CD (1987) The Miocene vertebrates of Quebrada Honda, Bolivia. Part I. Astrapotheria. Occas Pap, Mus Nat Hist, Univ Kans 122: 1–15

Frailey CD (1988) The Miocene vertebrates of Quebrada Honda, Bolivia. Part II. Edentata. Occas Pap, Mus Nat Hist, Univ Kans 123: 1–13

Gelfo JN, Goin FJ, Woodburne MO, Muizon C de (2009) Biochronological relationships of the earliest South American Paleogene mammalian faunas. Palaeontol 52: 251–269

Goin F, Sánchez-Villagra MR, Kay RF, Anaya-Daza F, Takai M (2003) New palaeothentid marsupial from the middle Miocene of Bolivia. Palaeontol 46: 307–315

Grant JN, Halls C, Salinas WA, Snelling NJ (1979) K-Ar ages of igneous rocks and mineralization in part of the Bolivian tin belt. Econ Geol 74: 838–851

Hoffstetter R (1963) La faune Pléistocène de Tarija (Bolivie). Bull Mus Natl Hist Nat 35: 194–203

Hoffstetter R (1968) Un gisement de mammifères déséadiens (Oligocène infèrieur) en Bolivie. C R Acad Sci Paris, Série D 267: 1095–1097

Hoffstetter R (1969) Un primate de l'Oligocène infèrieurran sudamerica: *Branisella boliviana* gen. et sp. nov. C R Acad Sci Paris, Sèrie D 269: 434–437

Hoffstetter R (1977) Un gisement de mammifères miocènes à Quebrada Honda (Sud Bolivien). C R Acad Sci Paris, Série D 284: 1517–1520

Hoffstetter R (1986) High Andean mammalian faunas during the Plio-Pleistocene. In: Vuilleumier F, Munesterio M (eds) High Altitude Sub-Tropical Biogeography. Oxford University Press, Oxford, pp 218–245

Hoffstetter R, Martinez C, Tomasi P (1972) Nouveaux gisements de mammifères néogènes dans les couches rouges de l'Altiplano bolivien. C R Acad Sci Paris, Série D 275: 739–742

Hoffstetter R, Paskoff R (1966) Présence des genres *Macrauchenia* et *Hippidion* dans la faune pléistocène du Chili. Bull Mus Natl Hist Nat, Série 2 38: 476–490

Huxley TH (1860) On a new species of *Macrauchenia* (*M. Boliviensis*). Q J Geol Soc London 17: 73–84

Kay RF, Johnson D, Meldrum DJ (1998) A new pitheciin primate from the middle Miocene of Argentina. Am J Primatol 45: 317–336

Kay RF, Madden RH, Cifelli RL, Flynn JJ (1997) Vertebrate Paleontology in the Neotropics: the Miocene Fauna of La Venta, Colombia. Smithsonian Institution Press, Washington

Kay RF, Williams BA, Anaya F (2002) The adaptations of *Branisella boliviana*, the earliest South American monkey. In: Plavcan JM, Kay RF, Jungers WL, van Schaik CP (eds) Reconstructing Behavior in the Primate Fossil Record. Kluwer/Plenum, New York, pp 339–370

Kraglievich L (1930) La Formacíon Friaseana del Río Frías, etc., y su fauna de mamíferos. Physis 10: 127–166

Kramarz A, Garrido A, Forasiepi A, Bond M, Tambussi C (2005) Estratigrafía y vertebrados (Aves y Mammalia) de la Formación Cerro Bandera, Mioceno Temprano de la Provincia del Neuquén, Argentina. Rev Geol Chile 32: 273–291

Loomis FB (1914) The Deseado Formation of Patagonia. Runford, Concord

MacFadden BJ (2005) Diet and habitat of toxodont megaherbivores (Mammalia, Notoungulata) from the late Quaternary of South and Central America. Quaternary Res 64: 113–124

MacFadden BJ (2006) Extinct mammalian biodiversity of the ancient New World tropics. Trends Ecol Evol 21: 157–165

MacFadden BJ, Anaya F, Perez H, Naeser CW, Zeitler PK, Campbell KE Jr (1990) Late Cenozoic paleomagnetism and chronology of Andean basins of Bolivia: evidence for possible oroclinal bending. J Geol 98: 541–555

MacFadden BJ, Anaya F, Swisher CC III (1995) Neogene paleomagnetism and oroclinal bending of the central Andes of Bolivia. J Geophys Res 100: 8153–8167

MacFadden BJ, Campbell KE Jr, Cifelli RL, Siles O, Johnson NM, Naeser CW, Zeitler PK (1985) Magnetic polarity stratigraphy and mammalian fauna of the Deseadan (late Oligocene-early Miocene) Salla Beds of northern Bolivia. J Geol 93: 223–250

MacFadden BJ, Shockey BJ (1997) Ancient feeding ecology and niche differentiation of Pleistocene mammalian herbivores from Tarija, Bolivia: morphological and isotopic evidence. Paleobiol 23: 77–100

MacFadden BJ, Wolff RG (1981) Geological investigations of Late Cenozoic vertebrate-bearing deposits in southern Bolivia. Anais do II Congresso Latino-Americano de Paleontología 2: 765–778

Madden RH (1990) Miocene Toxodontidae (Notoungulata, Mammalia) from Colombia, Ecuador and Chile. Ph.D. dissertation, Duke University

Madden RH (1997) A new toxodontid notoungulate. In: Kay RF, Madden RH, Cifelli RL, Flynn JJ (eds) Vertebrate Paleontology in the Neotropics: the Miocene Fauna of La Venta, Colombia. Smithsonian Institution Press, Washington, pp 335–354

Madden RH, Guerrero J, Kay RF, Flynn JJ, Swisher CC III, Walton AH (1997) The Laventan Stage and Age. In: Kay RF, Madden RH, Cifelli RL, Flynn JJ (eds) Vertebrate Paleontology in the Neotropics: the Miocene Fauna of La Venta, Colombia. Smithsonian Institution Press, Washington, pp 499–519

Marshall LG (1977) Evolution of the carnivorous adaptive zone in South America. In: Hecht MK, Goody PC, Hecht BM (eds) Major Patterns in Vertebrate Evolution. Plenum, New York, pp 709–721

Marshall LG (1978) Evolution of the Borhyaenidae, extinct South American predaceous marsupials. Univ Calif Publ Geol Sci 117: 1–89

Marshall LG (1981) Review of the Hathlyacyninae, an extinct subfamily of South American "dog-like" marsupials. Fieldiana: Geol (NS) 7: 1–120

Marshall LG (1990) Fossil Marsupialia from the type Friasian Land Mammal Age (Miocene), Alto Río Cisnes, Aisén, Chile. Rev Geol Chile 17: 19–55

Marshall LG, Muizon C de (1988) The dawn of the age of mammals in South America. Natl Geogr Res 4: 23–55

Marshall LG, Sempere T (1991) The Eocene to Pleistocene vertebrates of Bolivia and their stratigraphic context: a review. In: Suárez-Soruco R (ed) Fósiles y Facies de Bolivia–Vol I Vertebrados. Yacimientos Petrolíferos Fiscales Bolivianos, Santa Cruz, pp 631–652

McKenna MC, Bell SK (1997) Classification of Mammals Above the Species Level. Columbia University Press, New York

Montoya Sanhueza G, Moreno K (2008) Nuevos restos de mamíferos Miocenos de la localidad de Caragua, Formación Huaylas (norte de Chile). Resúmenes, III Cong Lat Pal Vert 1: 163

Muizon C de (1991) La Fauna de mamíferos de Tiupampa (Paleoceno Inferior, Formación Santa Lucía), Bolivia. In: Suárez-Soruco R (ed) Fósiles y Facies de Bolivia–Vol I Vertebrados. Yacimientos Petrolíferos Fiscales Bolivianos, Santa Cruz, pp 575–624

Muizon C de, Argot C (2003) Comparative anatomy of the Tiupampa didelphimorphs; an approach to locomotory habits of early marsupials. In: Jones M, Dickman C, Archer M (eds) Predators with Pouches: the Biology of Marsupial Carnivores. CSIRO Publishing, Collingwood, pp 43–62

Muizon C de, Cifelli RL (2000) The "condylarths" (archaic Ungulata, Mammalia) from the early Palaeocene of Tiupampa (Bolivia): implications on the origin of the South American ungulates. Geodiversitas 22: 47–150

Nasif NL, Musalem S, Cerdeño E (2000) A new toxodont from the late Miocene of Catamarca, Argentina, and a phylogenetic analysis of the Toxodontidae. J Vertebr Paleontol 20: 591–600

Oiso Y (1991) New land mammal locality of middle Miocene (Colloncuran) age from Nazareno, southern Bolivia. In: Suárez-Soruco R (ed) Fósiles y Facies de Bolivia–Vol I Vertebrados. Yacimientos Petrolíferos Fiscales Bolivianos, Santa Cruz, pp 653–672

Pascual R (1954) Los toxodóntidos del "Colloncurense" descriptos por Roth y su presencia en el Santacruciano. Notas Mus Eva Perón, Paleontología 17: 95–111

Pascual R (1965) Los Toxodontidae (Toxodonta, Notoungulata) de la Formación Arroyo Chasicó (Plioceno inferior) de la Provincia de Buenos Aires. Características geológicas. Ameghiniana 4: 101–132

Paula Couto C de (1982) Fossil mammals from the Cenozoic of Acre, Brazil. V. Notoungulata Nesodontinae (II), Toxodontinae and Haplodontheriinae, and Litopterna, Pyrotheria and Astrapotheria (II). Iheringia. Série Geol 7: 5–43

Reguero MA, Dozo MT, Cerdeño E (2007) A poorly known rodentlike mammal (Pachyrukhinae, Hegetotheriidae, Notoungulata) from the Deseadan (late Oligocene) of Argentina. Paleoecology, biogeography, and radiation of the rodentlike ungulates in South America. J Paleontol 81: 1301–1307

Ricketts TH, Dinerstein E, Boucher T, Brooks TM, Butchart SHM, Hoffmann M, Lamoreux JF, Morrison J, Parr M, Pilgrim JD, Rodrigues ASL, Sechrest W, Wallace GE, Berlin K, Bielby J, Burgess ND, Church DR, Cox N, Knox D, Loucks C, Luck GW, Master LL, Moore R, Naidoo R, Ridgely R, Schatz GE, Shire G, Strand H, Wettengel W, Wikramanayake E (2005) Pinpointing and

preventing imminent extinctions. PNAS USA 102: 18497–18501

Rodríguez Brizuela R, Tauber A (2006) Estratigrafía y mamíferos fósiles de la Formación Toro Negro (Neógeno), Departamento Vinchina, noroeste de la provincia de La Rioja, Argentina. Ameghiniana 43: 257–272

Roth S (1899) Apuntes sobre la geología y la paleontología de los territorios del Río Negro y Neuquén (diciembre de 1895 á junio de 1896). Rev Mus La Plata 9: 141–197

Saint-André P-A (1996) Deux nouveaux édentés (Mammalia, Xenarthra) *Trachycalyptoides achirense* nov. gen. et nov. sp. (Glyptodontidae, Sclerocalyptinae) et *Xyophorus villarroeli* nov. sp. (Megatheriidae, Nothrotheriinae) du Huayquérien (Miocène supérieur) de l'Alti. Bull Mus Natl Hist Nat, 4C 18: 79–106

Sánchez-Villagra MR, Kay RF, Anaya-Daza F (2000) Cranial anatomy and palaeobiology of the Miocene marsupial *Hondalagus altiplanensis* and a phylogeny of argyrolagids. Palaeontol 43: 287–301

Schneider A, Halls C (1986) Eruptive processes, mineralization and isotopic evolution of the Los Frailes Karikari region/ Bolivia. Geowiss Lateinamerika-Kolloquium, Berlin: 182–184

Scillato-Yané GJ (1979) Nuevo nothrotheriinae (Edentata, Tardigrada) de edad Chasiquense (Plioceno temprano) del sur de la prov. de Buenos Aires (Argentina): su importancia bioestratigráfica, filogenética y paleobiogeográfica. Actas, VII Cong Geol Arg 2: 449–457

Scillato-Yané GJ, Carlini AA (1998) Nuevos Xenarthra del Friasense (Mioceno medio) de Argentina. Stud Geol Salmant 34: 43–67

Scillato-Yané GJ, Carlini AA (1999) Nuevos Xenarthra del Mioceno de Quebrada Honda, Bolivia. Resúmenes, Cong Int Evol Neotrop Cenozoico, La Paz 1: 39

Scott WB (1903) Mammalia of the Santa Cruz Beds. Volume V, Paleontology. Part I, Edentata. 1. Dasypoda. In: Scott WB (ed) Reports of the Princeton University Expeditions to Patagonia, 1896–1899. Princeton University, E. Schweizerbart'sche Verlagshandlung (E. Nägele), Stuttgart, pp 1–106

Scott WB (1905) Mammalia of the Santa Cruz Beds. Volume V, Paleontology. Part III, Glires. In: Scott WB (ed) Reports of the Princeton University Expeditions to Patagonia, 1896–1899. Princeton University, E. Schweizerbart'sche Verlagshandlung (E. Nägele), Stuttgart, pp 384–490

Scott WB (1910) Mammalia of the Santa Cruz Beds. Volume VII, Paleontology. Part I, Litopt
erna. In: Scott WB (ed) Reports of the Princeton University Expeditions to Patagonia, 1896–1899. Princeton University, E. Schweizerbart'sche Verlagshandlung (E. Nägele), Stuttgart, pp 1–156

Scott WB (1912) Mammalia of the Santa Cruz Beds. Volume VI, Paleontology. Part II, Toxodonta. In: Scott WB (ed) Reports of the Princeton University Expeditions to Patagonia, 1896–1899. Princeton University, E. Schweizerbart'sche Verlagshandlung (E. Nägele), Stuttgart, pp 111–238

Shi H, Singh A, Kant S, Zhu ZL, Waller E (2005) Integrating habitat status, human population pressure, and protection status into biodiversity conservation priority setting. Conserv Biol 19:1273–1285

Shockey BJ (1997) Two new notoungulates (Family Notohippidae) from the Salla Beds of Bolivia (Deseadan: late Oligocene): systematics and functional morphology. J Vertebr Paleontol 17: 584–599

Shockey BJ, Anaya F (2008) Postcranial osteology of mammals from Salla, Bolivia (late Oligocene): form, function, and phylogenetic implications. In: Sargis EJ, Dagosto M (eds) Mammalian Evolutionary Morphology: A Tribute to Frederick S Szalay. Springer, New York, pp 135–157

Sinclair WJ (1909) Mammalia of the Santa Cruz Beds. Volume VI, Paleontology. Part I, Typotheria. In: Scott WB (ed) Reports of the Princeton University Expeditions to Patagonia, 1896–1899. Princeton University, E. Schweizerbart'sche Verlagshandlung (E. Nägele), Stuttgart, pp 1–110

Soria MF (2001) Los Proterotheriidae (Mammalia, Litopterna), sistemática, origen y filogenia. Monogr Mus Argent Cienc Nat 1: 1–167

Tauber A (1994) Estratigrafía y vertebrados fósiles de la Formación Santa Cruz (Mioceno Inferior) de la costa atlántica entre las rías del Coyle y de Río Gallegos, Provincia de Santa Cruz, República Argentina. PhD dissertation, Universidad Nacional de Córdoba

Tauber A (1996) Los representantes del género *Protypotherium* (Mammalia, Notoungulata, Interatheriidae) del Mioceno temprano del sudeste de la Provincia de Santa Cruz. Misc Acad Nac Cien Córdoba 95: 3–32

Tauber A, Garrido A, Tambussi C, Kramarz A, Saldivia S (1999) Una nueva localidad con vertebrados continentales del Mioceno, Departamento de Picún Leufú, Neuquén. Ameghiniana 36: 22R

Townsend KE, Croft DA (In review) Middle Miocene mesotheriine diversity at Cerdas, Bolivia and a reconsideration of *Plesiotypotherium minus*. Palaeontol Electron

Villarroel C (1978) Edades y correlaciones de algunas unidades litoestratigráficas del Altiplano boliviano y estudio de algunos representantes mesotériinos. Rev Acad Nac Cien Bolivia 1: 159–170

Vizcaíno SF, Bargo MS, Kay RF, Milne N (2006) The armadillos (Mammalia, Xenarthra, Dasypodidae) of the Santa Cruz Formation (early-middle Miocene): an approach to their paleobiology. Palaeogeogr Palaeoclimatol Palaeoecol 237: 255–269

Vizcaíno SF, Rinderknecht A, Czerwonogora A (2003) An enigmatic Cingulata (Mammalia: Xenarthra) from the late Miocene of Uruguay. J Vertebr Paleontol 23: 981–983

Vucetich M (1984) Los roedores de la Edad Friasense (Mioceno medio) de Patagonia. Rev Mus La Plata (NS) 8: 47–126

Vucetich MG (1989) Rodents (Mammalia) of the Lacayani fauna revisited (Deseadan, Bolivia). Comparison with new Chinchillidae and Cephalomyidae from Argentina. Bull Mus Natl Hist Nat 4C(11): 233–247

Vucetich MG, Mazzoni MM, Pardiñas UFJ (1993) Los roedores de la Formación Collón Cura (Mioceno medio), y la Ignimbrita Pilcaniyeu. Cañadón del Tordillo, Neuquen. Ameghiniana 30: 361–381

Webb SD (1991) Ecogeography and the Great American Interchange. Paleobiol 17: 266–280

Webb SD (1999) Isolation and interchange: a deep history of South American mammals. In: Eisenberg JF, Redford KH

(eds) Mammals of the Neotropics: The Central Neotropics. University of Chicago Press, Chicago, pp 13–26

Wilson EO (1999) The Diversity of Life. W. W. Norton & Company, New York

Wörner G, Hammerschmidt K, Henjes-Kunst F, Lezaun J, Wilke H (2000) Geochronology (40Ar/39Ar, K-Ar and He-exposure ages) of Cenozoic magmatic rocks from Northern Chile (18–22°S): implications for magmatism and tectonic evolution of the central Andes. Rev Geol Chile 27: 205–240

Wroe S, Argot C, Dickman C (2004) On the rarity of big, fierce carnivores and primacy of isolation and area: tracking large mammalian carnivore diversity on two isolated continents. Proc R Soc Lond 271: 1203–1211

Zachos J, Pagani M, Sloan L, Thomas E, Billups K (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292: 686–693

Zurita AE, Miño-Boilini AR, Soibelzon E, Carlini AA, Ríos FP (2009) The diversity of Glyptodontidae (Xenarthra, Cingulata) in the Tarija Valley (Bolivia): systematic, biostratigraphic and paleobiogeographic aspects of a particular assemblage. Neues Jahrb Geol Palaeontol, Abh 251: 225–237