

# 7. Postcranial Osteology of Mammals from Salla, Bolivia (Late Oligocene): Form, Function, and Phylogenetic Implications

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## 7.1 Introduction

### 7.1.1 General Overview

South America was a remote island continent throughout the greatest part of the Cenozoic. Such a “splendid isolation” (sensu Simpson, 1980) drove natural experiments in the organic evolution of terrestrial faunas on a continental scale. Thus, the fossil record of Cenozoic South America documents distinctive faunas, peculiar to that “lost” continent. These land mammal faunas were initially composed of primarily marsupials, xenarthrans, and native ungulates (“Stratum I” of Simpson, 1980). Somehow, in the mid-Tertiary, rodents and primates immigrated to South America (defining Simpson’s Stratum II). Then, in the late Tertiary, South America’s “splendid isolation” ended with the invasion of numerous North American land mammals upon the formation of the Panamanian land bridge (Stratum III: Simpson, 1980; see

Stehli and Webb, 1985 for an overview of this “Great American Biotic Interchange”). Now, all the native ungulate orders are extinct, as are the glyptodont and pampathere xenarthrans. Even the once spectacular diversity of sloths has been reduced to just a couple of genera of small, arboreal folivores.

For its species richness and early appearances of derived and immigrant taxa, the Deseadan South American Land Mammal “age” (SALMA, late Oligocene) is of considerable interest (Patterson and Pascual, 1972). It is characterized by numerous derived native South American ungulates of four orders, the first evidence of sloth diversity, some of the earliest records of rodents in South America, and the earliest record of primates on that continent (Ameghino, 1895, 1897; Gaudry, 1906; Loomis, 1914; Patterson and Pascual, 1972; Hoffstetter, 1969; MacFadden et al., 1985).

### 7.1.2 Historical Background

Carlos Ameghino discovered the classic Deseadan localities during expeditions to Patagonia from 1893 to 1896 (see Simpson, 1984). These localities range from Chubut down into Santa Cruz provinces of Argentina and include Cabeza

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Blanca, the Gran Barranca, and La Flecha, the later exposures lying near the Río Deseado, the inspiration for the name of the age (Gaudry, 1906). Also located in Patagonia, is the Deseadan “Scarritt Pocket”, discovered by Simpson and colleagues in their 1933–34 expedition to Patagonia (Marshall et al., 1984).

The first important Deseadan locality discovered outside of Patagonia was Salla (Hoffstetter, 1968). Other extra-Patagonian Deseadan localities include Taubaté of Brazil (Soria and Alvarenga, 1989), Fray Bentos Formation in Uruguay with exposures also in northern Argentina (Mones and Urbilla, 1978), and the newly discovered localities of Moquegua, Peru (Shockey et al., 2006). Salla is the best sampled of these extra-Patagonian localities, with collections held at MNHN-Paris, MNHN-Bol, PU, UF, and, now, UATF (see Methods section regarding abbreviations used).

The Salla Beds take their name from a mapmaker’s misspelling of the Aymaran village of Sahalla, Bolivia. Bolivian geologist G. Bejarano discovered fossils near Sahalla in 1962 (first announced by Baird et al., 1966). Leonardo Branisa, also a Bolivian geologist, and Robert

TABLE 7.1. Faunal list of mammals of the Salla Beds, late Oligocene (Deseadan SALMA).

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Cohort Marsupialia Illiger, 1811
Order Sparassodonta Ameghino, 1894
Family Borhyaenidae Ameghino, 1894
<i>Fredszalaya hunteri</i> gen. et sp. nov.
<i>Pharsophorus lacerans</i> Ameghino, 1897
<i>Notogale mitis</i> (Ameghino, 1897)
<i>Sallacyon hoffstetteri</i> Villarroel and Marshall, 1982
(= <i>Adinogale sallensis</i> Hoffstetter and Petter, 1983)
Unnamed genus
<i>Paraborhyaena boliviana</i> Hoffstetter and Petter, 1983
Order Paucituberculata Ameghino, 1894
Family Caenolestidae Trouessart, 1898
<i>Evolestes hadrommatus</i> Goin et al. 2007
<i>Palaeothenes boliviensis</i> Patterson and Marshall, 1978
Family Argyrolagidae Ameghino, 1894
<i>Proargyrolagus bolivianus</i> Wolff, 1984
Cohort Placentalia Owen, 1837
Order Cingulata Illiger, 1811
Family Dasypodidae Gray, 1821
Euphractini Wing, 1923
Eutatini Bordas, 1933
Family Peltephilidae Ameghino, 1894
Unnamed genus, cf. <i>Peltephilus</i> sp.
Family Glyptodontidae Gray, 1869
Glyptatelinae Castellanos, 1932
Family Palaeopeltidae Ameghino, 1895
Order Pilosa Flower, 1883
Suborder Folivora DeSulc et al., 2001
<i>Pseudoglyptodon sallaensis</i> Engelmann, 1987
Family Mylodontidae Gill, 1872
Unnamed genus, Shockey and Anaya, in preparation
Unnamed small “orophodontids” (2 spp.) Pujos and de Iulius, 2007.
Family Megalonychidae Gervais, 1855
Unnamed small species Pujos and de Iulius, 2007
Order Primates Linnaeus, 1758
Family Incerta Cedis

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(continued)

TABLE 7.1. (continued)

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<i>Branisella boliviana</i> Hoffstetter, 1969
(= <i>Szalatavus attricuspis</i> Rosenberger et al., 1991)
Order Rodentia Bowdich, 1821
Family Agoutidae Gray, 1821
<i>Incamys bolivianus</i> Hoffstetter and Lavocat, 1970
<i>Branisamys luribayensis</i> Hoffstetter and Lavocat, 1970
<i>Cephalomys bolivianus</i> Lavocat, 1976
Family Octodontidae Waterhouse, 1839
<i>Migraveramus beatus</i> Patterson and Wood, 1982
<i>Sallamys pascuali</i> Hoffstetter and Lavocat, 1970
Order Pyrotheria
Family Pyrotheriidae
<i>Pyrotherium macfaddeni</i> Shockey and Anaya, 2004
<i>P. romeroi</i> Ameghino, 1889
unnamed gen. and sp.
Order Astrapotheria
genus indeterminate
Order Litopterna Ameghino, 1889
Family Proterotheriidae Ameghino, 1887
Genus and species indeterminate
<i>Salladolodus deuterotherioides</i> Sora and Hoffstetter, 1983
(regarded as a didolodontid by some students)
Family Macraucheniidae Gervais, 1855
<i>Coniopternium primitivum</i> Cifelli and Soria, 1983a
Family Adianthidae Ameghino, 1891
<i>Thadanius hoffstetteri</i> Cifelli and Soria, 1983b
<i>Tricoelodus boliviensis</i> Cifelli and Soria, 1983b
Order Notoungulata Roth, 1903
Interatheriidae Ameghino, 1887
Two unnamed species (See Hitz, 1997)
Suborder Typotheria Zittel, 1892
Archaeohyracidae Ameghino, 1897
<i>Archaeohyrax</i> Ameghino, 1897
<i>Protarchaeohyrax</i> Reguero et al., 2003
Mesotheriidae Alston, 1876
<i>Trachytherus alloxus</i> Billet et al., 2008
Hegetotheriidae Ameghino, 1894
<i>Prohegetotherium schiaffinoi</i> (Kraglievich, 1932)
<i>Sallatherium altiplanense</i> Reguero and Cerdeño, 2005
Suborder Toxodonta Owen, 1853
Family Leontiniidae Ameghino, 1895
<i>Anayatherium ekecoa</i> Shockey, 2005
<i>Anayatherium fortis</i> Shockey, 2005
Family Notohippidae Ameghino, 1894
<i>Eurygenium pacegnum</i> Shockey, 1997
<i>Pascualihippus boliviensis</i> Shockey, 1997
<i>Rhynchippus</i> cf. <i>R. brasiliensis</i> Soria and Alvarenga, 1989
Family Toxodontidae Owen, 1845
<i>Proadinothierium saltoni</i> sp. nov.

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Hoffstetter of Paris (Hoffstetter, 1968) accomplished further fieldwork that provided material for numerous publications regarding the geological setting and the fauna. The discovery of the primate *Branisella boliviana* Hoffstetter, 1969 sparked interest in Salla that was followed up with works on other faunal members such as the rodents (Hoffstetter and Lavocat, 1970; Hoffstetter, 1976; Lavocat, 1976; Patterson and Wood, 1982), marsupials (Patterson and Marshall, 1978; Villarroel and Marshall, 1982; Hoffstetter and Petter, 1983; Wolff, 1984b; Sanchez-Villagra and Kay, 1997), a suspected “condylarth” and the

litopterns (Soria and Hoffstetter, 1983; Cifelli and Soria, 1983a,b). More recently, one or both of us have described some of the other ungulates, including notohippid, leontiniid, and mesotheriid notoungulates (Shockey, 1997; Shockey, 2005; and Shockey et al., 2007, respectively), the postcranials of the litopterns (Shockey, 1999), and the common pyrothere of Salla (Shockey and Anaya, 2004). Reguero and Cerdeño (2005) have described the hegetotheriid notoungulates. As the oldest known primate of South America, *Branisella* continues to be a subject of intensive study (e.g., Wolff, 1984a; Rosenberger et al., 1991; Takai and Anaya, 1996; Kay et al., 2002).

### 7.1.3 Goals of Paper

The purpose of this present work is to summarize and update the state of knowledge regarding the fauna of Salla, especially in regard to postcranial skeletal form and function. This will be accomplished by general descriptions of selected taxa with summaries of their comparative and functional anatomy. For both practical and principled reasons, special attention is given to tarsal elements. On the practical side, tarsals elements are less fragile than other elements and are thus often preserved. But also, as complex working elements of the hind limb, they provide both functional and phylogenetic information (Szalay, 1985). That is, hind limbs are more exclusively devoted to locomotion than the forelimbs, which may be involved in (and adapted for) other functions, such as gathering food, modifying the environment for housing, or for grooming (Szalay, 1985, 1994). Thus, tarsal elements are more likely to provide pure information regarding locomotion than elements of the manus or other components of the forelimb. Also, since the tarsals function as integrated parts of the hind limb they are not especially phenotypically plastic since alteration of one element may change its role in relation to the remaining members of the functional complex.

A secondary goal is to document, in a single work, a summary of the fauna, including an updated faunal list (Table 7.1) and figures of some instructive specimens. This will be accomplished by a general description of selected specimens, followed by discussions regarding their comparative and functional anatomy. Phylogenetic implications will also be noted.

## 7.2 Materials and Methods

### 7.2.1 Fossil Material and Abbreviations

Fossils of Salla examined for our studies are housed at the following institutions (with abbreviations used in the text): Vertebrate Paleontology Division of the Florida Museum of Natural History, University of Florida (FLMNH, with UF indicating FLMNH specimens); the Princeton University

collection in the Yale Peabody Museum, Yale University (PU); the Muséum National d'Histoire Naturelle, Paris (MNHN-Paris); Museo Nacional de Historia Natural, La Paz, Bolivia (MNHN-Bol); and in the developing collection of the Facultad de Ingeniería Geológica, Universidad Autónoma "Tomás Frías," Potosí, Bolivia (UATF).

Other abbreviations include SALMA, South American Land Mammal "age"; Ma, millions of years before present; I, C, P, M represent upper incisors, canines, premolars, and molars (lower case letters for the respective lower teeth); to emphasize the lack of understanding of tooth homologies of xenarthrans compared to other mammals, we designate Cf for upper caniniformes and Mf for upper molariformes (lower case letters for the respective lower teeth); Mt, metatarsal; Mc, metacarpal.

### 7.2.2 Categories of Locomotion and Confidence in Functional Interpretations

To summarize general functions of taxa examined, we use a modified version of the locomotor categories of Argot (2003) and define general feeding categories (Table 7.2).

We infer function via one or (preferably) more of the following independent methods:

- (1) Morphology is consistent with paradigm (sensu Rudwick, 1964) for hypothetical function
- (2) Morphology is consistent with that of extant modern analogs of known function
- (3) Taxon is bracketed by taxa of known function (sensu Witmer, 1995)
- (4) External (non-morphological) physical evidence for function (e.g., diet known via stomach content or associated coprolites; putative digger found in fossil burrow)

As usual for faunal overviews, we will provide the best functional hypothesis for the taxa discussed (see Section 7.4.1). However, since the quality of evidence varies, we wish to provide information regarding the confidence one may have in the hypotheses. For example, functional interpretations based upon complete skeletons will likely be closer to the true function than those based upon fragmentary material. Also, interpretations based upon two converging lines of evidence will be superior to those derived from a single principle or observation (or pseudo-replicates, like multiple observations of interdependent phenomena). The following means will be used to communicate our level of confidence in the hypotheses, from low levels of confidence ( $\alpha$ ) to high confidence in robust hypotheses ( $\delta$ ):

*Alpha ( $\alpha$ ) level hypothesis:* Hypothesis *plausible* from only one line of evidence or the hypothesis has a higher level of confidence ( $>\beta$ ), but it is in conflict with plausible and competing hypothesis.

*Beta ( $\beta$ ) level hypothesis:* Hypothesis *probable* from one line of evidence or,  $\alpha$ -level hypothesis that is compatible

TABLE 7.2. Locomotor and feeding categories (locomotor categories adapted from Argot, 2003).

Locomotor type	
Arboreal	Rarely on ground; typically forages and shelters in trees; usually exhibits particular specializations for climbing.
Scansorial	Adept climber that also forages on the ground during a considerable proportion of its time.
Subcursorial	May never climb, displays incipient adaptations for running.
Cursorial	Never climbs, displays marked adaptations for running.
Fossorial	Adept digger, forages and/or shelters below ground, shows marked adaptations for digging.
Graviportal	Massive, never climbs, may move rapidly for brief periods, but typically moves slowly.
Feeding categories	
Carnivory	Meat is most significant source of calories, dental adaptations (or other oral adaptations [e.g., shearing beak]) for shearing meat
Omnivory	Meat an important source of calories, but also relies largely upon arthropods, plants or fungi for nutrition. Usually has unspecialized dentition, but may display incipient adaptations for shearing meat.
Herbivore, unspecialized	General classification for animal that gets nearly all of its nutrition from plant material. Adaptations to crush and/or slice plant material, such as lophos on occlusal surfaces of cheek teeth. Mandibular condyle usually high above tooth row in order to facilitate simultaneous occlusion of all grinding teeth.
Browser	Herbivore that consumes a variety of nutrient rich foods, such as new leafy growth, buds, fruits, and seeds. Adaptations for selective feeding may include narrow muzzle, proboscis, or dexterous manus.
Grazer	Herbivore that receives nearly all of its calories from grasses. Adaptations for grazing include high crowned cheek teeth, broad muzzle.

with a second, independently derived  $\alpha$ -level hypothesis or, internal independent confirmation via evidence of same general function in two systems (e.g., grazing deduced via hypsodonty *and* broad muzzle; digging via specialized forelimb and specialized pelvis).

*Gamma* ( $\gamma$ ) *level hypothesis*:  $\beta$ -level hypothesis consistent with another independently derived and congruent  $\beta$ -level hypothesis.

*Delta* ( $\delta$ ) *level hypothesis*: Unusually compelling evidence, which may include direct physical evidence of function (e.g., method d, above), or morphological feature is a direct result of function (see macraucheniid example in text), or three compatible and independent  $\beta$ -level hypotheses.

## 7.3 Mammal Fauna of Salla

### 7.3.1 General Mammalian Fauna

A revised faunal list is provided in Table 7.1. It conservatively records 47 species of mammals, including many of the natives of Simpson's Stratum I: marsupials (six sparassodont and three paucituberculata species), xenarthrans (five species of cingulates and five species of sloths) and four orders of extinct, endemic, South American ungulates: Pyrotheria (three species), Astrapotheria (one indeterminate species), Litopterna (five species), and Notoungulata (13 species). Immigrant (Stratum II) taxa include rodents (five species) and the primate *Branisella boliviana* (= *Szalavus attricuspis*).

For the sake of convenience and for stability of nomenclature, we generally follow the higher level classifications of McKenna and Bell, 1997. Such may not reflect the actual phylogenies of taxa, but the systematics of most of the above

family level groups discussed are not so confidently known that they may be regarded as dogma.

### 7.3.2 Systematic Paleontology

SUPERCOHORT THERIA PARKER  
AND HASWELL, 1897  
COHORT MARSUPIALIA ILLIGER, 1811  
MAGNORDER AMERIDELPHIA  
SZALAY, 1982  
ORDER SPARASSODONTA  
AMEGHINO, 1894a  
FAMILY BORHYAENIDAE  
AMEGHINO, 1894a  
*FREDSZALAYA* GEN. NOV.

*Material* – UF 172501 (Holotype), partial skull with partial upper dentition (right P3-M1, roots of right C – P2, and left M2-4) and associated vertebral and costal fragments and the left calcaneum.

*Locality* – The holotype (Figures 7.1, 7.2 and Appendix) was collected 15m below the El Planimiento by Roger Portell, Gary Morgan, and Bruce J. MacFadden in 1986.

*Type species* – *Fredszalaya hunteri* sp. nov.

*Etymology* – To honor Fred Szalay, especially for his contributions to our understanding of marsupial evolution.

*Diagnosis* – Same as for species.

*FREDSZALAYA HUNTERI* sp. nov.

*Etymology* – In reference to Dr. Szalay's longtime affiliation with Hunter College, City University of New York, and to suggest the predacious nature of the animal.

*Diagnosis* – Medium size borhyaenid with short muzzle and broad posterior palate, short but distinctive molar protocones, weak parastyle, but well developed stylar cusp B, with stylar shelf, especially on M1-2, well developed carnassial postmet-

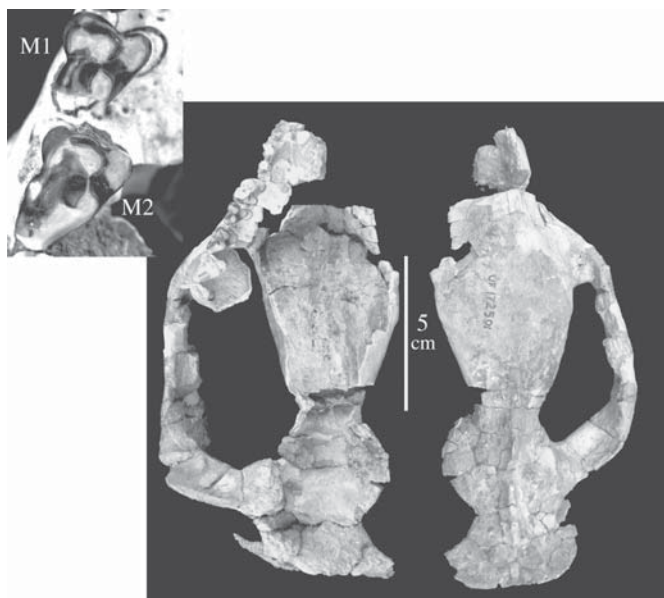


FIGURE 7.1. Holotype of *Fredszalaya hunteri* gen. et sp. nov. (UF 172501). Views of the skull are ventral (left) and dorsal (right). The insert at upper left is occlusal view of the right M1–2.

acrista, M4 short, lacking metacone, but nearly as wide as M3 with well developed, elongated, blade-like preparacrista. Foramen ovale absent.

Smaller than species of *Pharsophorus* with relatively wider posterior palate, upper molars with smaller styler cusp A and larger styler cusp B, more conspicuous styler shelf; M4 wider with greater development of protocone and with carnassial preparacrista.

Larger than *Notogale mitis* with greater development of upper molar protocones, especially that of M4.

Larger than *Sallacyon hoffstetteri* Villarroel and Marshall, 1982, also differing by the presence of well-developed styler cusp B of M1-2, better developed protocone of M4, M4 relatively and absolutely wider, zygomatic arch more rectangular.

Differs from *Prothylacynus patagonicus* by its smaller size, shorter muzzle with crowded premolars, better developed molar protocones, protocone retained in a larger M4 and absence of foramen ovale.

Similar to *Borhyaena* spp. by the absence of the foramen ovale on the alisphenoid, but differs by its smaller size, relatively and absolutely shorter muzzle, relatively larger protocones and styler shelves of upper molars.

**Description** – The skull is grossly similar to that of the Santacrucian *Prothylacynus patagonicus* Ameghino, 1891 (see Sinclair, 1906; Marshall, 1979). The cranial vault is quite flat and the zygomatic arches are exceedingly wide, suggestive of massive jaw muscles. The incisors are not preserved and only parts of the roots of the canines remain. These indicate that the canines were fairly robust.

The P1 is broken, but both roots remain and indicate that the tooth was set obliquely to the tooth row, with the anterior

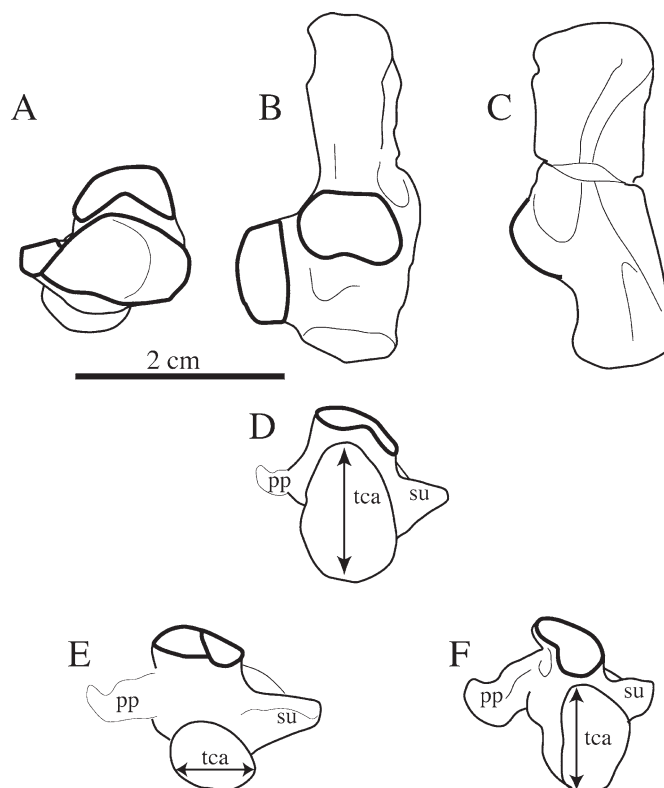


FIGURE 7.2. Calcaneum (left) of the holotype of *Fredszalaya hunteri* gen. et sp. nov. (A–D) compared to the posterior view of the morphotype of a terrestrial marsupial calcaneum (E) and that of the grasping morphotype (F). Views of the calcaneum of *Fredszalaya hunteri* (UF 172501) are A, distal; B, dorsal; C, lateral; and D, posterior. E and F are adapted from Szalay, 1994: Figure 6.16. Abbreviations are pp, peroneal process; su, sustentacular process; and tca, tuber calcani.

root being more labial than the posterior. Crowns are missing from P2-3, but enough of these teeth are present to indicate that the P2 is larger than P1 and that P3 is the largest premolar, having a slightly larger anteroposterior dimension than the M1.

The protocone of M1 is basined and sits low on the crown. The paracone is much higher and it is slightly worn such that it grades into a styler cusp (styler cusp B of many workers) that lies adjacent to its labial surface. A small styler shelf is present. The metacone is conspicuously higher and more robust than the paracone. The post metacrista is broken on the M1, but is preserved on M2 and the left M3. This forms the distinctive, oblique shearing blade of the upper molars. The protocones, styler cusps, and styler shelves are progressively smaller on M2-3. M4 is smaller than the preceding molars, lacking a metacone, but the protocone is retained and better developed than that of the M3. A well-developed crista connects the paracone to the parastyle, forming a shearing blade.

The zygomatic arches and glenoid fossae are preserved. The glenoid is oval and deep, being buttressed posteriorly by

bony ridge nearly the entire width of the fossa and anteriorly by the terminal end of the jugal. Unlike *Prothylacynus*, but like *Borhyaena* (see Sinclair, 1906), there is no foramen ovale.

Given its distinctive morphology and close association to the skull in the field, there is no reasonable doubt that the associated calcaneum (Figure 7.2) is that of the *Fredszalaya*. It is similar to that of *Borhyaena* (see Argot, 2003), differing by its more transverse (rather than strongly oblique) distal border (as seen in dorsal view) and its shorter sustentaculum, resulting in a narrower lower ankle articulation. It has no fibular facet, which appeared also to be lacking in *Borhyaena*, but damage made its absence uncertain (Argot, 2003). The calcaneal tuber of *Fredszalaya* is narrow and deep. The cuboid facet is concave and circular, suggesting the socket of a ball-and-socket calcaneocuboid articulation that would have allowed significant rotation of the foot. There is no proximal component of the cuboid facet as seen in didelphids, but the cuboid facet is somewhat medially placed such that nearly half of the facet is sculpted into the body of the short sustentacular process. The lateral portion of the distal calcaneal surface is not excavated, but has a slight convexity that suggests that the cuboidal surface of the calcaneocuboid joint was not just a simple “ball”. The distolateral area where the peroneal process would have been (if present) is broken.

The narrow transverse ankle joint and narrow but deep tuber calci are typical of grasping metatheres (Figure 7.2; Szalay, 1994 text and Figure 6.16) and unlike that expected of most borhyaenids, which are typically regarded as being terrestrial animals (Sinclair, 1906; Marshall, 1978; Szalay, 1994). A relevant exception is provided by Argot (2003), who documented a variety of skeletal features of *Prothylacynus* that are likely related to adaptations for climbing (see her discussion and, especially, her Figure 21).

*Biology of Fredszalaya hunteri* – The shearing nature of the elongated metacristae of M1-M3 and elongated blade-like preparacrista of the M4 predicts meat-eating habits for *Fredszalaya*. This prediction, derived from the principle of shearing as a means of cutting meat, is supported by the observation of carnivorous habits in extant marsupials having similar shearing crests, as well as historical observations of the recently extinct carnivorous *Thylacinus* (Tasmanian “wolf”). Carnivory has even been confirmed in an extinct, Tertiary borhyaenid (*Lycopsis logirostrus* of the middle Miocene, La Venta) by the presence of rodent remains within the body cavity of the borhyaenid (Marshall, 1977:p. 641). *Fredszalaya*, however, is less extreme in its meat cutting adaptations than some other borhyaenids. For example, the styler shelves and protocones are retained, whereas these are significantly reduced in *Borhyaena*. Thus, it is likely that *Fredszalaya* was not a meat specialist, but foraged on other food items, much like the morphologically similar *Prothylacynus* (Marshall, 1978; Argot, 2003).

As noted above, climbing abilities are suggested by the morphology of the calcaneum. Such a hypothesis, based upon a single element, must be regarded as tentative.

*Phylogeny of Fredszalaya hunteri* – Although the skull of *Fredszalaya* is superficially more similar to that of *Prothylacynus* than that of *Borhyaena*, we regard the absence (loss) of the foramen ovale to represent a synapomorphy uniting *Fredszalaya* with *Borhyaena*. Similarities of form between *Fredszalaya* and *Prothylacynus* would represent the plesiomorphic condition for the lineage leading to *Borhyaena*.

PROBORHYAENIDAE AMEGHINO, 1897  
 PARABORHYAENA BOLIVIANA HOFFSTETTER AND  
 PETTER, 1983

*Comments* – Proborhyaenids were large to huge carnivorous marsupials, with the skull of *Proborhyaena gigantea* reaching two feet in length (Marshall, 1978). The last records of these giant terrestrial carnivores were in the Deseadan, with two named genera: *Proborhyaena* and *Paraborhyaena*, the later described from Salla (Hoffstetter and Petter, 1983).

In their summary of the Salla fauna, MacFadden et al. (1985) noted that all proborhyaenids remains lacked precise stratigraphic data. The discovery of a jaw (UATF-V-000129) during our recent expedition to Salla by colleagues Darin Croft and Rodolfo Salas at the base of Unit 3 at Pasto Grande provides the first stratigraphic control for this huge carnivorous taxon.

Work is in progress on this specimen, but for now we document its stratigraphic position at the very base of Unit 3. This places it in a normal paleomagnetic horizon that, according to the “best fit” hypothesis of Kay et al. (1998), would be Chron 10n.2n. This would indicate an age of about 28.6Ma. We also provide the observation that the animal had but one pair of large, blunt lower incisors. This was previously unknown for *Paraborhyaena* (Hoffstetter and Petter, 1983; Babot et al., 2002) and it represents the most derived condition of incisors known for proborhyaenids (*Proborhyaena* has two pairs and the romantically named *Callistoe* Babot et al., 2002 has three pairs).

No postcranials are known from *Paraborhyaena*. Aside from various fragments tentatively referred to *Proborhyaena* (see Marshall, 1978), the only postcranial remains of any proborhyaenid recovered are those of *Callistoe vincei*, currently under study by Judith Babot (see Babot et al., 2002). So, for now little can be deduced regarding locomotion for proborhyaenids in general, but in regards to *Paraborhyaena* we may be content with commenting that it was one of the largest carnivorous marsupials.

ORDER PAUCITUBURCULATA AMEGHINO, 1894  
 ARGYROLAGIDAE AMEGHINO, 1904

PROARGYROLAGUS BOLIVIANA WOLFF, 1984

*Comments* – Postcranials of *Proargyrolagus* are yet to be known. However, Sanchez-Villagra and Kay (1997) methodically considered cranial characters to establish a general hypothesis regarding its feeding habits. Based on its small size (~100g, which made folivory most unlikely), unrooted lower incisors, and the unusually high crowned cheek teeth, they regarded *Proargyrolagus* as being an herbivore that gathered food items, like seeds, at ground level. They also

noted the well-developed nasal region (similar to that seen in water-conserving rodents of arid regions) that suggests that *Proargyrolagus* could have tolerated dry environments.

Based upon the remarkable convergence between the postcranial skeletons of Plio-Pleistocene argyrolagids (*Argyrolagus* and *Microtragulus*) with those of desert dwelling heteromyid kangaroo rats and dipodid jerboas, Simpson (1970) proposed that argyrolagids were also specialized for bipedal, ricocheted locomotion. Applying such a hypothesis to *Proargyrolagus*, however, would represent an extrapolation from the data, not an interpolation, since none of the proposed phylogenies of argyrolagids implies that *Proargyrolagus* is bracketed by *Argyrolagus* and *Microtragulus* (see Sánchez-Villagra and Kay, 1997).

COHORT PLACENTALIA OWEN, 1837

MAGNORDER XENARTHRA COPE, 1889

ORDER CINGULATA ILLIGER, 1881

PELTEPHILIDAE AMEGHINO, 1894

CF. *PELTEPHILUS* SP.

*Comments* – For their dermal horns, cranial shield, and slicing anterior teeth, peltephilid armadillos have inspired much curiosity. This family of armored Xenarthrans is best known from the early middle Miocene Santacrucian SALMA, however, until now, little more than isolated osteoderms had been known from the Deseadan.

The few peltephilid specimens of Salla are variable in terms of size, tooth number, robustness of mandible, and fusion or absence thereof of the mandibular symphysis. This variation suggests that more than one species is present at Salla, but we are unable to rule out within species variables such as ontogenetic changes or sexual dimorphism at this time. Further study is indicated and is being undertaken.

The peltephilid specimens of Salla (Figure 7.3) are grossly similar to the well-known Santacrucian *Peltephilus* Ameghino, 1887 (see Scott, 1903). Similarities include seven teeth of the mandible (though two specimens of Salla have eight), hoof-like ungual phalanges of the pes, and the presence of horn-like cranial osteoderms, including an anterior pair (preserved in a MNHN-Paris specimen), as predicted by Ameghino (1894). Some differences between the Salla and Santacrucian animals are significant, with the Salla peltephilids having generally plesiomorphic characters. For example, whereas other known peltephilids have fused mandibular symphyses, both peltephilid mandibular specimens in the UF collection have unfused symphyses. These may represent immature individuals, as a larger specimen in the PU collection (PU 21143) does have a fused symphysis. Also, whereas other known peltephilids have but seven teeth in the mandible, two of the specimens of Salla (UF 93587 and PU 21143) have an additional small tooth anterior to the seven that appear to be homologous to the seven of UF 93586 (this anterior tooth is designated as “mf 0” in the Appendix).

Much of the pes is preserved in UF 93515 (Figure 7.3). Mt II, III, and IV are subequal in size, suggesting a similar form to that of *Peltephilus strepens* which was functionally tridac-

tyl having much reduced Mt I and V (Mt I and V are missing on the Salla specimen). Like *P. strepens*, the Salla peltephilid has concavities of the distal metatarsals, though not as pronounced as in the Santacrucian example. Also, the peltephilid of Salla has hoof-like ungual phalanges, even blunter than those of the Santacrucian animal (compare the hoof in our Figure 7.3 with that of Scott, 1903: plate 16.14).

Ameghino’s interpretation of the biology of peltephilids was sensational. He wrote of them as, “ferocious and meat eating, like a tiger and armed with horns like a rhinoceros – one’s imagination could not conjure anything more lively (Ameghino, 1934:317: translated from Spanish by BJS).” Modern interpretations are less imaginative. Vizcaíno and Fariña (1997) dispute this traditional “killer armadillo” reconstruction. Citing evidence from the skull and forelimbs of the Santacrucian *P. ferox*, they interpret it as being fossorial and herbivorous.

Although there is insufficient postcranial material of the Salla peltephilid to obtain any metatarsal index, we note that the metatarsals are not long, but proportionally similar to those reported for Santacrucian peltephilids (Scott, 1903) and to those of our comparative sample of Florida “road kill” *Dasyopus* specimens. Neither the Santacrucian taxa nor the Salla peltephilid show any specializations for which they could be regarded as cursorial.

Based upon the cranial morphology of *Peltephilus*, Vizcaíno and Fariña (1997) argued against meat eating in peltephilids; they noted that the teeth were too slender to resist struggling prey and that the apparent location of the main bite force was at the anterior jaw rather than half way between the tempromandibular joint and anterior grasping teeth (as predicted from mechanical models [e.g., Greaves, 1995] and observed in extant carnivores). Their arguments for herbivory included the wide zygomatic arch, which strongly suggests lateral jaw movements, and their high crowned teeth (though the relevance of the later for xenarthrans may be questioned). Their favored hypothesis was that *Peltephilus* ate subterranean plant material.

Though the mandibular symphysis is unfused in most of our sample of peltephilids of Salla, there is still evidence that significant forces were applied at the anterior region of the jaw. That is, the anterior region is the deepest and thickest part of the mandible. So, the greatest forces (and the equal opposing forces) associated with the bite appear to have occurred at that anterior region, just as in *Peltephilus* (Vizcaíno and Fariña, 1997). Whether these forces involved vegetable matter or animal, we offer no opinion, but subterranean feeding seems well-suited for an animal with a specialized anterior bite, since, at initial contact, the anterior snout would usually be the only part of the animal in contact with the food item in an underground environment (the rest of the animal would be separated from its food by soil).

SUPERFAMILY GLYPTODONTOIDEA GRAY, 1869

*Comments* – Glyptodonts are not common at Salla, but some osteoderms are in the various collections of Salla. These are

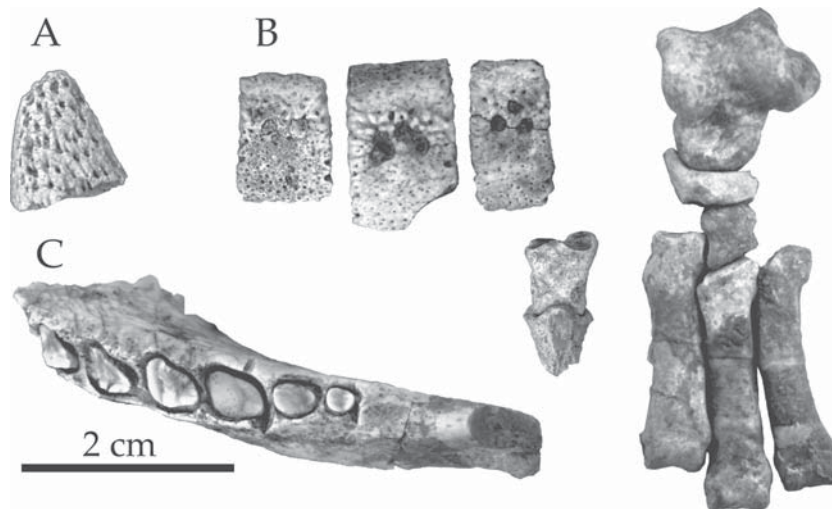


FIGURE 7.3. Peltephilidae. A, UF 93551, nasal horn; B, UF 93515, associated osteoderms, partial pes with medial and distal phalanges; C, UF 93586, left mandibular ramus.

largely unstudied, but Freddie Carlini (personal communication) identified two species from two families (Glyptodontidae and Palaeopeltidae) during visits to the UF collection.

Shockey (2001) described an isolated distal femur that he referred to the Glyptodontoidea. It was quite distinctive, having exceedingly asymmetric trochlear ridges, with the medial being much higher and nearly conical in shape, and a patellar trochlea having a sinuous path such that the patella must have rotated transversely during knee flexion-extension. This rotation of the patella likely resulted in differential tension on the crus, which in turn would have caused rotary movement of the crus in addition to the flexion-extension.

Evidence of this complex knee extension is also implied by the complex ball-and-socket medial knee articulation coupled with the sliding lateral articulation of various glyptodonts and sloths. The biomechanical consequences of this joint are poorly understood, but the near ubiquity of the ball-n-socket/sliding knee joint among sloths and glyptodonts is curious.

#### ORDER PILOSA FLOWER, 1883

#### SUBORDER FOLIVORA DELSUC ET AL., 2001

#### MYLODONTIDAE GILL, 1872

#### UNNAMED GENUS (Shockey and Anaya, in preparation)

*Comments* – Along with UATF geology student, Luis Lopez, we recovered a fairly complete skull (UATF-V-000127, Figure 7.4) of an unnamed genus of mylodontid sloth during our visit to Salla in January of 2003. It came from Unit 4 (the “Principle Guide Zone”) at Calabozza Pata, Salla.

It is distinguished by its broad muzzle, large external nares, oval to sub-figure-eight molariform occlusal surfaces, and teeth composed of relatively equal amounts of vasodentin, orthodentin, and cement. It differs from other Deseadan sloths by being smaller than species of *Octodontotherium* and *Orophodon*, and its distinctive tooth histology of nearly equal proportions of the three tissues. The orthodentine does

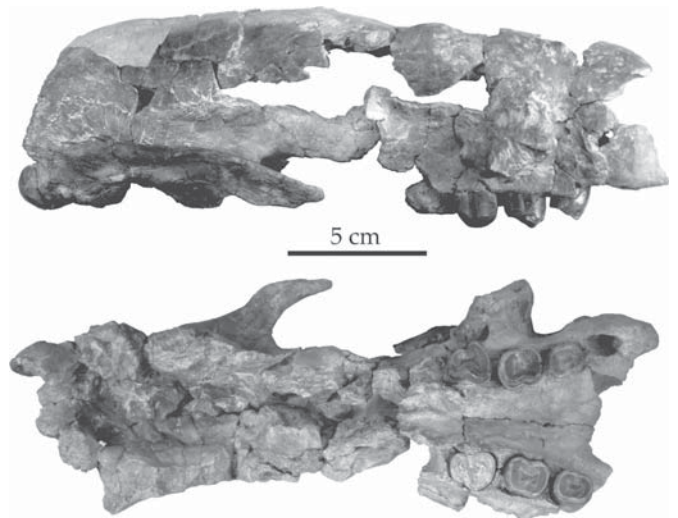


FIGURE 7.4. Mylodontidae. Lateral and ventral views of cranium, UATF-V-000127.

not appear to have been much harder than the other tissues, since the teeth wore quite smoothly, without the orthodentine forming a palpable ridge, as is typical for sloths.

The broad muzzle of UATF-V-000127 suggests that the animal ate grass, since many modern grazers have broad muzzles that help them acquire much grass (a poor quality food) with a single bite (Gwynne and Bell, 1968; Solounias et al., 1993). Mylodontids have frequently been interpreted as being grazers (McDonald, 1997 and references therein), an interpretation confirmed in *Myodon darwini* via the contents of its coprolites (Moore, 1978).

Based upon the broad muzzle, we suspect that this mylodont of Salla also was a grazer. The only caveat at this time is that we are curious in regard to the functional significance of



the enlarged external nares and the consequences of its development. Did the large nose have some critical function that had selective value (with the broad muzzle being merely a consequence of developing the tall and broad external nares)? Of course, the two could have a complementary adaptive-functional history: e.g., the nose as an adaptation for water conservation in arid environments and the broad muzzle for eating about the only commonly found vegetation available in such environments (grass).

ORDER PYROTHERIA AMEGHINO, 1895  
 FAMILY PYROTHERIIDAE AMEGHINO, 1889  
*PYROTHERIUM* AMEGHINO, 1888  
*PYROTHERIUM MACFADDENI* SHOCKEY  
 AND ANAYA, 2004

*Comments* – Various postcranial remains of *Pyrotherium macfaddeni* are in the collections of MNHN-Paris, MNHN-Bol, PU, and UF. These illustrate the extreme graviportal nature of the beast. These collections also contain various tarsal elements that illustrate the curious foot of the animal (see Shockey and Anaya, 2004). *Pyrotherium* is plantigrade and almost uniquely has a reversed form of the calcaneo-astragalar articulation (i.e., the ectal facet of the calcaneum is concave and sustentacular facet is convex). It also has well-developed fibular-calcaneal and cubo-astragalar articulation. As far as we know, this form is only seen in the embrithropod *Arsinoitherium* and is quite unlike the tarsus of any other known South American native ungulate.

We are confident that this graviportal beast was a slow, terrestrial herbivore. The huge surface area of its teeth indicates that mechanical digestion was important for the animal and may suggest that chemical digestion was not as efficient as that of other ungulates.

ORDER LITOPTERNA AMEGHINO, 1889  
 FAMILY PROTEROTHEIIDAE AMEGHINO, 1887  
 SUBFAMILY PROTEROTHEIINAE AMEGHINO, 1885  
 GENUS INDETERMINATE

*Comments* – The presence of proterotheriids at Salla was confirmed with the discovery of a functionally monodactyl partial pes referable to the group (Shockey, 1999; see also Figure 7.5). The enlarged Mt III was broken such that it was not possible to estimate the length of this element. The length of the Mt III of the Salla proterotheriid remains unknown, but a left Mt III, bulk cataloged (AMNH 14153) with several Loomis notoungulate specimens from Cabeza Blanca, is complete (see Figure 7.5b). AMNH 14153 is 81.5 mm long and has a proximal width of 16.9 mm. Since this Patagonian specimen has a distinctive dorsal component of the distal keel, a feature absent in the Salla specimen, it is probably a species distinct from that of Salla and apparently is more derived towards cursorial habits. Neither specimen was associated with dental remains, so they can only be noted as proterotheriine proterotheriids.

Although not as advanced in regard to running abilities as the Loomis specimen, the Salla proterotheriid can confidently be classified in the general category of a cursor. The more

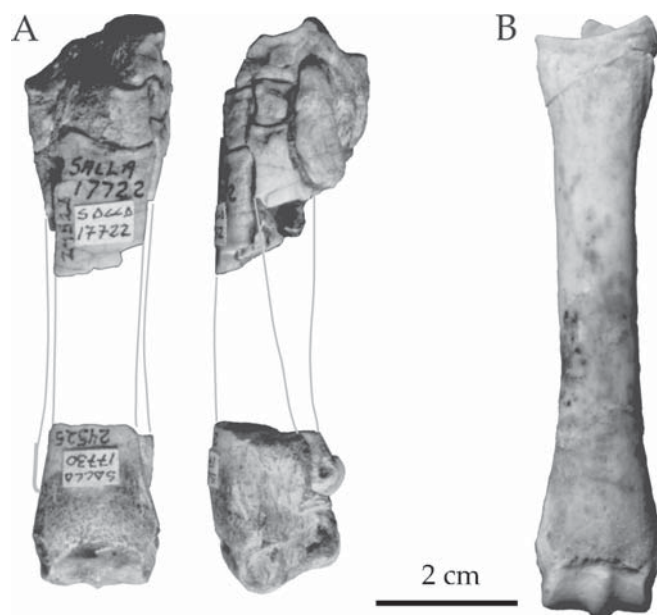


FIGURE 7.5. Proterotheriid pes. A, partial right pes of the proterotheriid of Salla, composite of the distal tarsals and proximal Mt II-IV (PU 24528) and distal metapodials (PU 24525). (Reconstructed as if from a single individual.) B, left Mt III from Cabeza Blanca (AMNH 14153).

specific reconstruction as it being a forest dwelling running animal similar to dasyproctid rodents and Old World, Recent forest ungulates, like duikers (Shockey, 1999 and references within), should be regarded as tentative.

FAMILY MACRAUCHENIIDAE GERVAIS, 1855  
*CONIOPTERNIUM* AMEGHINO, 1895

*Comments* – With a little doubt, Cifelli and Soria (1983a) referred the Salla macraucheniid (?*Coniopternium primitivum*) to *Coniopternium* Ameghino, 1895. We are content to drop the query and suggest that the slight angle of the calcaneal tuber of the Salla macraucheniid(s) (Figure 7.6) and that of *Coniopternium andium* is a homologous, derived character that can be regarded as a synapomorphy for *Coniopternium* spp.

Due to various skeletal modifications restricting movement to the parasagittal plane (deep trochlea of astragalus and humerus and transversely elongated astragalonavicular joint), the non-supinating antebrachium, and elongated metatarsals, Shockey (1999) inferred that the macraucheniids of Salla were adapted for a cursorial mode of locomotion (Figures 7.5 and 7.6). Additionally, he proposed that the deep suprapatellar fossa (“patellar pit”) of the femur served as a pit “into which the patella *could* have slid (Shockey, 1999:p. 385, emphasis not in original),” thus serving as a passive stay: a knee lock structurally different from that of modern horses (see Hermanson and MacFadden, 1996; Shockey, 2001). At that time, no macraucheniid patella had been recovered from Salla, so Shockey constructed a model patella that indeed “locked” and resisted movement when cloth “ligaments” attached to it were pulled.

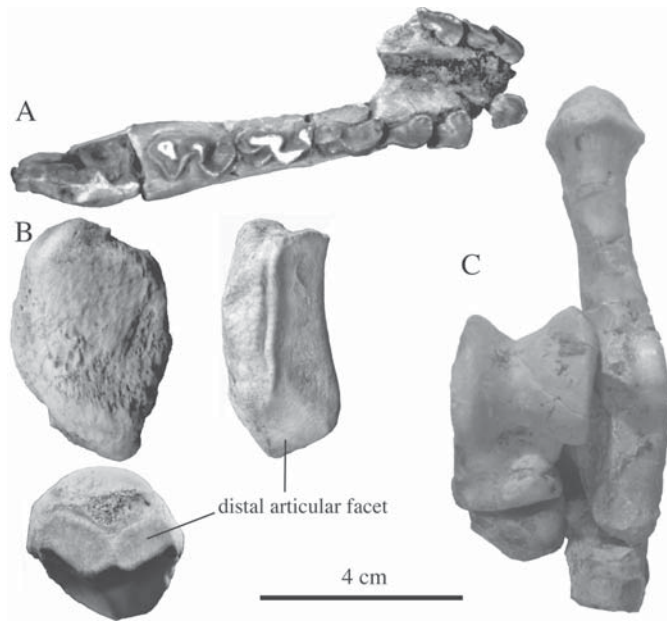


FIGURE 7.6. *Coniopternium* cf. *C. primitivum*. A, UF 172122, mandible of juvenile with left di2-dc and right di2, di3-dp4, with m1 still in crypt; B, UATF-V-000133, patella (views clockwise from upper left: dorsal, lateral, distal); C, UF 172426, left calcaneum, astragalus, navicular, and cuboid.

As originally proposed, the suggestion of a macraucheniid knee lock was as an untested hypothesis. The model patella merely illustrated what *could* have occurred, but said nothing as to what the animal actually did in life. Fortunately, during our expedition to Salla in January 2004, we recovered patellae associated with two partial skeletons of macraucheniiids. These patellae unambiguously show distal articular surfaces (Figure 7.6), in addition to the typical facet for articulation with the patellar groove during knee flexion-extension. The only plausible explanation for the distal articulation of the patella is that it contacted the distal surface of the patellar pit of the femur into which its shape conforms (reconstructed in Figure 7.7).

In response to the incorrect and over-used dogma of “form follows function”, investigators are now quick to note non-functional explanations for morphology (e.g., exaptations, phylogenetic inertia, multiple functions for a single form; see Ross et al., 2002 for summary). Articular facets, however, do provide information regarding the relative position of bones. Indeed, in the case of the *Coniopternium* patella, the form (presence of distal articular facets) is a direct result of function (patellar “locking” in the suprapatellar fossa). Thus, we can say with considerable confidence that the knee of *Coniopternium* did indeed hyperextend during the life of the animal such that the patella locked into the patellar pit. Such an adaptation would have allowed the animal to stand for considerable amounts of time without expending much energy.

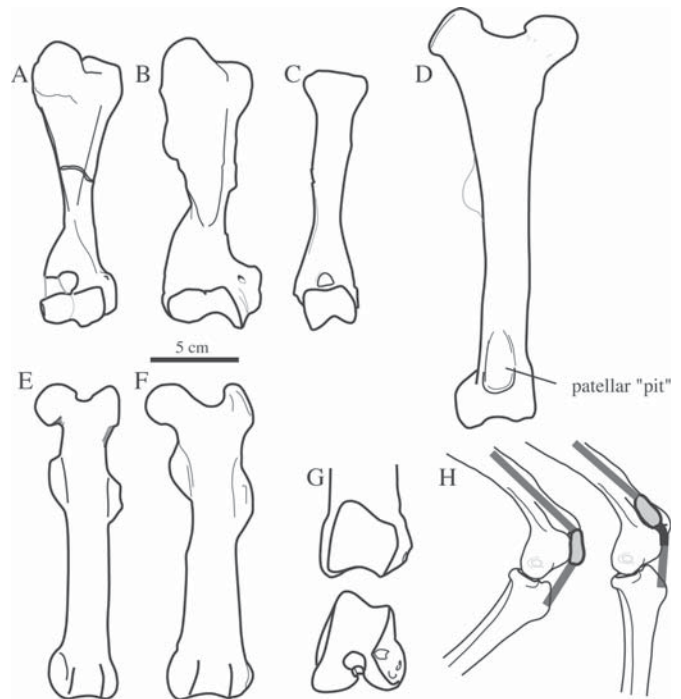


FIGURE 7.7. Ungulate limb bones. Cranial views of humeri (A, *Eurygenium pacegnum* Bol-V-00364; B, *Trachytherus alloxus*, UF 91933; C, *Coniopternium* sp., UF 149207) and femora (D, *Coniopternium* sp. MNHN-Bol-V-004502; E, *Eurygenium pacegnum pacegnum* Bol-V-00364; F, *Trachytherus alloxus*, UF 90960; and G, *Proadinothierium*, cf. *P. saltoni* sp. nov. (anterior view also provided) MNHN-Paris [uncataloged]), and H, a functional reconstruction of the knee lock of *Coniopternium* sp. show as flexed (left) and hyper-extended and locked (right). (H modified from Shockey, 1999.)

ORDER NOTOUNGUALTA ROTH, 1903  
SUBORDER TYPOTHERIA ZITTEL, 1892  
FAMILY MESOTHERIIDAE ALSTON, 1876  
*TRACHYTHERUS ALLOXUS* BILLET ET AL., 2008

*Comments* – *Trachytherus* is a sheep sized notoungulate with distinctive gliriform incisors and a robust postcranial skeleton (see Figures 7.7 and 7.8). Individuals vary considerably, but there is no discontinuity in the size or other characters to suggest the presence of either two species at Salla or even sexual dimorphism of the one present.

In an unpublished master’s thesis, Heidi Sydow (1988) described two partial skeletons of *Trachytherus* and concluded that this Deseadan mesothere was a “scratch digger”, sensu Hildebrand, 1985. Her hypothesis was supported by our functional analysis (with D. Croft) of mesotheres, which included *Trachytherus*, as well as the mesotheriines, *Plesiotypotherium* and *Mesotherium* (Shockey et al., 2007). In terms of limb proportions and development of specializations associated with strength of the forelimb, *Trachytherus*, *Plesiotypotherium* and *Mesotherium* compared most favorably to extant scratch diggers, like wombats

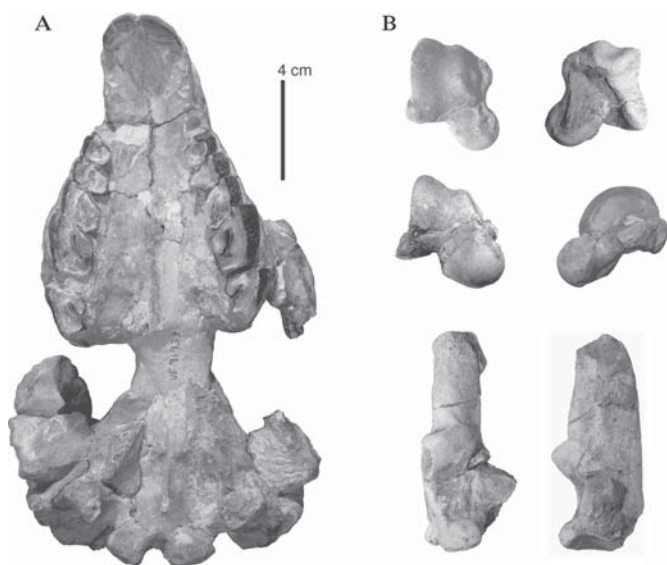


FIGURE 7.8. *Trachytherus alloxus*. A, UF 91933 skull (palatal view); B, UF 172437, astragalus (views clockwise upper left, dorsal, plantar, medial, distal); and UF 172514, calcaneum in dorsal view (left) and lateral view (right).

(*Vombatus*, *Lasiorhinus*), badgers (*Taxidea*), and, especially, armadillos (*Orycteropus*).

Adaptations for digging of the forelimb of *Trachytherus* include the well developed and distally placed crests for the deltoid and pectoralis muscles, enlarged medial epicondylar process of the humerus (Figure 7.7b), enlarged and medially curved olecranon, enlarged pisiform, and fissured ungual phalanges. The manus is pentadactyl, with just modest reduction of the first digit, a condition nearly identical to the Pleistocene *Mesotherium* (see Shockey et al., 2007).

The lower limb is similar to that described for *Eurygenium* (Figure 7.7), except that there is less calcaneofibular contact in *Trachytherus*.

The astragalus is remarkable for the conspicuous asymmetry of the trochlear ridges (lateral being much higher than the medial crest), a constricted neck, which is fairly long in some specimens, but always longer than those of the notohippids of Salla. The head is subspherical, forming the ball of a ball-and-socket joint with the navicular. The lateral and medial walls of the astragalus are oblique with distinctive lateral and medial processes such that the plantar surface is broader than the dorsal trochlea. A well-developed groove for the digital flexor is separate from the trochlea.

The calcaneum has a small fibular facet that is obliquely oriented on the dorsal prominence. The ectal facet is convex and broad. The lateral calcaneal border has a groove for the tendon of the peroneus longus and one specimen (UF 172514) preserves a small peroneal process this is not directly adjacent to the distal region of the peroneal groove. The apex of the tuber is rugose and lacks a distinctive groove for the Achilles tendon. The cuboid facet is teardrop shaped, slightly concave,

and obliquely oriented and appeared to have allowed a sliding articulation with the cuboid; thus, along with the ball-and-socket articulation of the astragalonavicular joint, would have permitted some rotation of the pes.

Although no articulated pes of *Trachytherus* of Salla is available for study, much of the pes is preserved in a specimen of *T. spegazzinianus* recently collected from the Deseadan of Moquegua, Peru (Shockey et al., in preparation). This illustrates that the pes of *Trachytherus* was pentadactyl. Other than its larger size and retention of the hallux, the form and relative position of the elements are similar to those of the hegetothere pes described below.

We regard the scratch digging hypothesis for *Trachytherus* as being robust, since the postcranial morphology of the animal is consistent with a digging paradigm and with the morphology of known, extant scratch diggers as noted above (see also Shockey et al., 2007). Also, other mesotheres (*Plesiotypotherium* and *Mesotherium*) have fossorial adaptations. Indeed, the mesotheriine mesotheres were more derived in this respect as they evolved ossified reinforcement of their pelvis, like that seen in some extant diggers (Hildebrand, 1985; Shockey et al., 2007).

#### FAMILY HEGETOTHERIIDAE AMEGHINO, 1894

*Comments* – Reguero and Cerdeño (2005) demonstrate the presence of two species of hegetotheres at Salla, *Prohegetotherium schiaffinoi* (Kraglievich, 1932) and *Sallatherium altiplanense* Reguero and Cerdeño, 2005. They noted, but did not describe, the femur and a partial pes (Reguero and Cerdeño, 2005: Figure 7.5d) associated with cranial material of *P. schiaffinoi*. We provide here brief descriptions of these elements.

UF 172445 is a damaged skull of *Prohegetotherium schiaffinoi* associated with fragmentary postcrania and a nearly complete left femur (missing the greater trochanter) and a distal right femur. These distal femora have long, narrow, but deep, petallar grooves, suggestive of running animals (Rose, 1999).

The partial pes (UF 172502, Figure 7.9 and Appendix) was found in close association with cranial material of two individuals of *Prohegetotherium* (UF 91661 and 91662), but it is unknown to which, if either, it pertains. This pes is very similar to that of the Santacrucian *Hegetotherium mirabile*, described and figured by Sinclair (1909: Figure 7.4a and plate 6.19). Like that of *Hegetotherium*, the *Prohegetotherium* pes is tetradactyl and has a small fibular facet of the calcaneum. A distal tibia-fibula, into which the astragalus perfectly fits, is solidly fused, indicating that the *Prohegetotherium* also had a fused distal crus. Also, as in *Hegetotherium*, the Mt II is shorter than the Mts III and IV, having a more proximal articulation with the tarsals, overlapping part of the ectocuneiform. The Mt V was not preserved, but an impression in the matrix on the lateral side of Mt IV unambiguously indicates that it was present and smaller than the Mt IV.

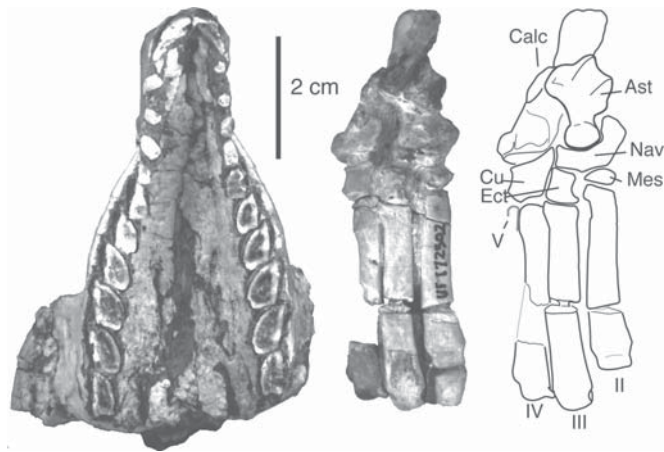


FIGURE 7.9. Hegetotheriids of Salla. *Sallatherium altiplanense* (Reguero and Cerdeño, 2005), Holotype, UF 91621, partial skull (palatal view); *Prohegetotherium schiaffinoi* (Kraglievich, 1932), UF 172502, partial pes in dorsal view (left) and dorsal view in outline (right). (See also Reguero and Cerdeño, 2005.)

The pes of *Prohegetotherium* is similar to that of *Trachytherus* (noted above), but differs by its smaller size, lack of the first digit, fused distal tibia-fibula, lesser asymmetry of the astragalar trochlea, and its relatively and absolutely smaller fibular facet. Otherwise, the hind feet of these animals are remarkably similar in their general appearance, the relative lengths of the their metatarsals to one another, and the form by which Mt II overlaps the ectocuneiform and Mt III, and Mt III slightly overlapping Mt II. The pes of *Prohegetotherium* is quite distinct from that of the interatheriid as indicated in the description and comments below.

#### ARCHAEOHYRACIIDAE AMEGHINO, 1897

*Comments* – The archaeohyracids of Salla are under study by Marcelo Reguero and his colleagues. They recognize two genera at Salla, *Archaeohyrax* and *Protarchaeohyrax*, which are represented by numerous teeth, jaws, and cranial material in all noted collections of Salla. Postcrania, however, have never been reported.

We note the presence of two astragali (UF 17069 [left] and UF 17089 [right]), possibly of the same individual, found in close association with fragmentary dental remains of adult and juvenile archaeohyracids. The astragali are very similar to those known for *Prohegetotherium*, but are larger (see Appendix) and have a greater asymmetry of trochlear ridges. Also the groove for the digital flexor is further removed from the astragalar trochlea, sitting upon a distinctive process. Such would have provided greater leverage for digital flexion, offering a modest clue regarding archaeohyracid locomotion compared to that of the hegetothere.

#### SUBORDER INCERTAE SEDIS

#### FAMILY INTERATHERIIDAE AMEGHINO, 1887

#### UNNAMED TAXA, HITZ, 1997

*Comments* – We deviate from McKenna and Bell (1997) and nearly all authorities, by not classifying interatheriids within

the Typotheria. We leave their higher ordered classification unresolved (see Section 7.4.3).

Hitz (1997) described (but did not name) two distinct and otherwise unknown interatheriid taxa of Salla in his doctoral dissertation (formal naming is a work in progress). He also described a nearly complete skeleton of the smaller taxon. This skeleton, however, lacked foot bones, so the pes has been unknown for any Deseadan interatheriid. However, several UF and MNHN-Bol tarsal specimens have been found in association with interatheriid teeth. These are so similar to the tarsal form seen in Santacrucian interatheriids (*Interatherium*, *Protypotherium*) that there can be little doubt that they are from interatheres. The description below is based upon UATF-V-000132, a partial left pes, and UF 173247, a right proximal tarsus (calcaneal tuber missing) found articulated and fused by matrix (see Figure 7.10 and Appendix).

The proximal tarsus of the interatheres of Salla is so distinct that it cannot be confused with that of similar sized typotheres of Salla. The most conspicuous feature of the calcaneum is its well-developed, rabbit-like fibular facet. This appears as a semicircular, dorsal process in lateral view. The articular surface is proximodistally straight, covering the strongly convex surface of the protuberance that supports it. This is quite distinct from the obliquely oriented and weaker fibular facets of the calcani of *Trachytherus* and *Prohegetotherium* (Figures 7.7–7.10). The ectal facet is also distinguished by its inclined, more vertical orientation, such that the calcaneoastragular contact may be characterized as side-to-side rather than overlapping.

The astragalus has a well-defined, fairly deep trochlea. The lateral and medial sides are vertical and parallel to one another, rather than oblique as seen in *Trachytherus*, *Prohegetotherium* and the archaeohyracid (below). It lacks the astragalar peroneal process that inserts between the distal fibula and the calcaneum in *Trachytherus* and *Prohegetotherium*. The neck is relatively longer and much more conspicuous than that of the nototheriids noted below, and the head is subspherical, forming the ball of the ball-and-socket joint with the navicular. The ectal facet is convex and has a nearly vertical orientation to meet the steeply inclined ectal facet of the calcaneum. The fibular facet is vertical and lacks the peroneal process that is present in typotheres (e.g., *Trachytherus*, see Figure 7.8b) and basal notoungulates, such as *Colbertia* (see Cifelli, 1983).

The pes of the Salla interatheriid appears to be tetradactyl, but functionally tridactyl, with Mt I being absent and Mt V being reduced in size compared to Mt II–IV. The articulation of the Mt III and IV with the distal tarsals lies in about the same plane, similar to that of the Santacrucian *Protypotherium australe* and *Interatherium robustum*, but unlike that of *P. attenuatum* in which the articulation between the cuboid and Mt IV and V appear more distal than the navicular/Mt III joint.

Elements of the pes of UATF-V-000132 are about the size as the homologous elements reported for the Santacrucian interatheriid *Protypotherium attenuatum* (Sinclair, 1909: p. 46), but smaller than *P. australe* (p. 39), and quite a bit

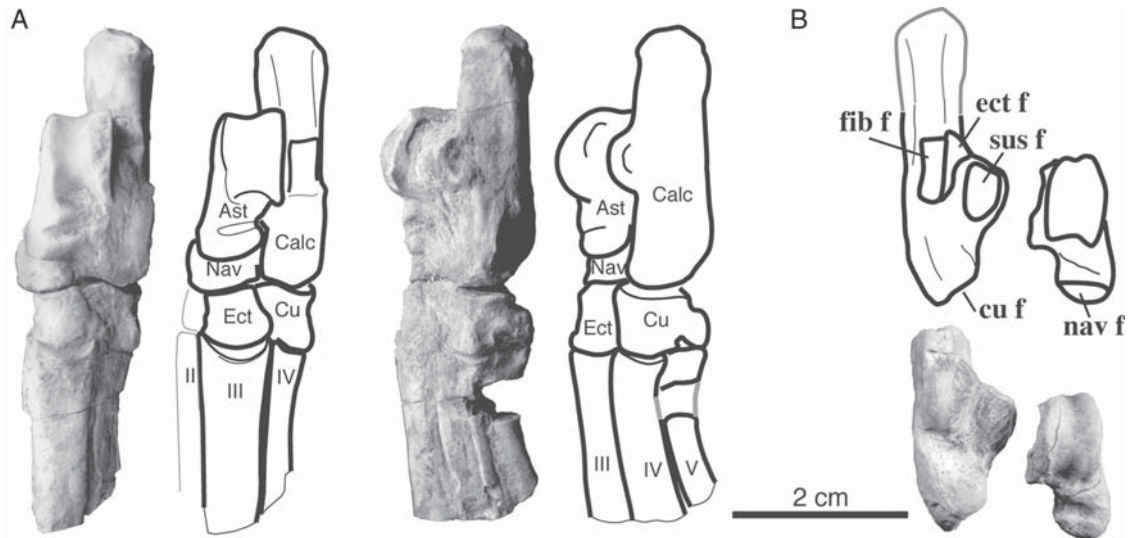


FIGURE 7.10. Intertheriidae. **A**, UATF-V-000132, partial left pes, in frontal and lateral views; **B**, UF 173247, proximal tarsus: calcaneum (left) and astragalus (right) (Shown as photos and in outline).

larger than *Interatherium robustum* (p. 63). The foot of the Salla interatheriid differs from those of *Protypotherium* spp. by having a narrower cuboid and by the compact manner in which Mt III and IV of the Salla specimen interface with one another.

The form of the proximal tarsus of the Salla interatheriid and the Santacrucean interatheres is distinct from those of known typotheres. These differences include parallel sides of the astragalus, lacking the astragal peroneal process, the robust, dorso-ventrally oriented fibular articulation of the calcaneum, and the more transverse articulation between the two proximal tarsal elements (strongly inclined ectal facets). This form is more similar to that of the notohippid tarsals described below (see Figure 7.11), that noted by Chaffee (1952) for *Rhynchippus pumilus*, and of the tarsus of the early toxodontids *Adinotherium* and *Nesodon* (Scott, 1912).

#### SUBORDER TOXODONTIA OWEN, 1853

##### FAMILY NOTOHIPPIDAE AMEGHINO, 1894

cf., *PASCUALIHIPPUS BOLIVIENSIS* SHOCKEY, 1997

*Comments* – The partial pes described below (Figure 7.12) was found at the type locality of *Pascualihippus boliviensis* (Unit II of Pasto Grande) in association with lower molar fragments of a notohippid. These teeth are of a size similar to teeth of *Pascualihippus* and *Eurygenium pacegnum*, but are not referable to the latter taxon due to the presence of an entolophid fossetid, a feature lacking in *E. pacegnum*. The tarsus described below is similar to those of early toxodontids (e.g., *Adinotherium*), so it is possible that it may be that of the toxodont, *Proadinotherium*, and the association with the notohippid teeth is merely a coincidence. However, we note the phylogenetic analysis of Toxodontia by Shockey (1997) in which *Pascualihippus* was shown as being the sister taxon to toxodontids;

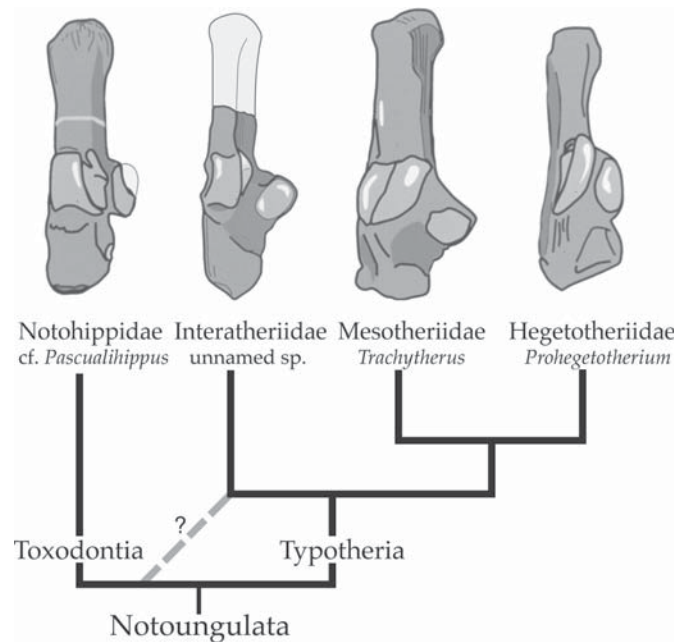


FIGURE 7.11. Comparative calcani in phylogenetic context. Bold lines indicate hypothesis from phylogenetic analysis of Cifelli (1993) and dashed line ambiguously placed to suggest alternative hypotheses as intertheriids, Typotheria and Toxodontia as unresolved tritomy, or intertheriids sister taxa to Toxodontia.

thus such a similar tarsus is a reasonable probability for *Pascualihippus*.

The calcaneum of UF 172410 has a fairly robust tuber, and is rectangular in dorsal view. The fibular facet is large and has proximodistal orientation, like that of the interthere noted above, but unlike that of *Trachytherus* and *Prohegetotherium*,

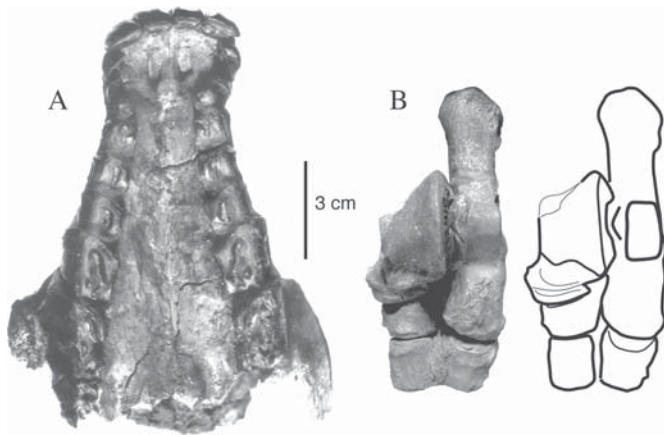


FIGURE 7.12. *Pascualhippus boliviensis*. A, Holotype MNHN-Bol-V-003642, ventral view of palate; B, referred left tarsus (UF 172410), calcaneum, astragalus, navicular, cuboid, and ectocuneiform, dorsal views (photo and in outline).

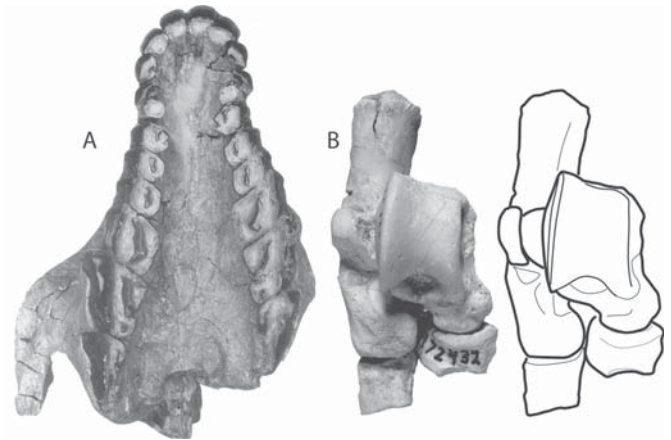


FIGURE 7.13. *Eurygenium pacegnum*. A, palatal view of holotype (MNHN-Bol-V-003643); and B, dorsal view of tarsus (UF 172432) shown as photo and in outline.

both of which have obliquely oriented fibular facets. Also, the ectal facet is vertically oriented. A small, but well-developed oval facet is present on the medial side of the calcaneum, which articulates with a similar facet of the navicular, clearly indicating the “reverse alternating tarsus” of Cifelli (1993) where tarsal alternation occurs by way of robust calcaneonavicular contact, rather than the more familiar cuboastragalus alternating tarsus. On the navicular, just distal to the facet for calcaneal articulation, is a smaller facet for cuboid articulation.

The astragalus has a short neck and a modestly well-developed, somewhat asymmetric trochlea. The astragalus neck is much shorter than those of *Trachytherus*, *Prohegetotherium*, and the interatheriids noted above. The head is broader than deep, much less spherical than the notoungulate specimens described previously, indicating limited mobility, except in the parasagittal plane.

#### *EURYGENIUM PACEGNUM* SHOCKEY, 1997

*Comments* – *Eurygenium pacegnum* is the most completely known notohippid, being represented by a nearly complete skeleton (Shockey, 1997). One of us (Shockey, 1997) provided a brief description of this skeleton, including a limited account of the poorly preserved pes. The strength of the forelimb and relatively low Mt/femur ratio was noted, suggesting that the animal was not adapted for speed as originally suggested for notohippids (e.g., Loomis, 1914).

Since the tarsus of the skeleton of *Eurygenium* (MNHN-Bol-V-003643) was poorly preserved (thus not figured in Shockey, 1997), we provide a figure of another specimen (UF 172432: Figure 7.13), a partial pes, similar to that of cf. *Pascualhippus*, but smaller and lacking the distinctive navicular facet on the calcaneum. A faint facet is seen on the navicular for cuboid articulation, suggesting that *Eurygenium* had some, perhaps transient, articulation with the calcaneum, but not the strong “reverse alternating tarsus” of *Pascualhippus*.

Data from the *Eurygenium* skeleton was recently included in a multivariate analysis that included extant species of known function (Shockey et al., 2007). Like *Trachytherus*, *Eurygenium* shared morphometric space among the larger bodied fossorial taxa. But it also tracked closely with the semi aquatic capybara (*Hydrochoerus*). This was a consequence of similar body size and limb proportions with capybara and suggests the hypothesis that *Eurygenium* was a competent swimmer. The discriminant function analysis of this study classified *Eurygenium* with the extant “generalists”.

Caution should be used regarding the swimming hypothesis, since it was only empirically derived, not generated from any *a priori* principles. Thus, a semiaquatic hypothesis should be considered as being unsupported, though there may not be any particular evidence against it. So, we continue to regard *Eurygenium* as having general terrestrial adaptations and suggest that it was capable of digging and swimming. Support for the digging hypothesis, independent of the aforementioned multivariate analysis, is found in the cleft ungual phalanges. Such digits are frequently found in extant diggers (see Hildebrand, 1985; Shockey et al., 2007).

#### FAMILY TOXODONTIDAE OWEN, 1845

##### *PROADINOTHERIUM* AMEGHINO, 1895

##### *PROADINOTHERIUM SALTONI*, SP. NOV.

*Holotype* – UF 149222 (Figure 7.14) damaged, but reasonably complete mandible containing the complete dentition.

*Locality* – The holotype comes from Unit 3 of Pasto Grande of the Salla Beds.

*Diagnosis* – Relatively small toxodontid having rooted incisors, no diastema between c and p1, lower premolars without fossettids, molar entolophid transverse with fossetid. Differs from *Proadinothierium leptognathum* by its smaller size (linear dimension about 80% those of *P. leptognathum*), the lack of diastema, and presence of enamel on both the external and internal surfaces of the incisors (internal enamel absent in adults of *P. leptognathum*).

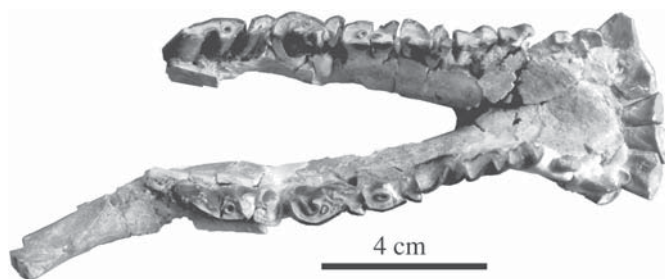


FIGURE 7.14. *Proadinothierium saltoni* sp. nov. Mandible (holotype, UF 149222) in occlusal view.

*Etymology* – In memory of Justine Salton, with special regard to the field season that she worked with us at Salla.

*Description* – Plant roots grew through the holotype, breaking it to bits, but these fragments have been reconstructed to give a reasonably good indication of the jaw morphology (Figure 7.14, dental metrics given in Appendix). The lower incisive battery is similar to that of *Adinothierium* (see Scott, 1912: Plate XVII: Figure 7.10), but the incisors of *P. saltoni* have shorter crowns. These incisors are enlarged, spatulate, and have long, but closed roots; those of the i3s extend posteriorly to the level below the p2. The lower canine is much smaller than the incisors and may be described as “incisiform”, with the qualification that it looks nothing like the incisors of this animal.

No diastema occurs between the c and p1 as in the *P. leptognathum* specimen figured by Loomis (1914: Figure 81). The p1 is smaller than the canine and is little more than a peg-like structure, ovoid in occlusal view with a tiny fossettid in the middle.

The p2 is shaped like a double crescent and lacks a fossettid. None of the lower premolars of the holotype, or those of the more heavily worn referred specimen, UF 149223, has any fossettids, which is indicative of the deep, broad ectoflexid (premolars of other known nesodontine toxodontids form fossettids early in wear [see Scott, 1912: plate XVIII, Figures 7.4 and 7.5]).

The m1 is moderately worn, having formed a trigonid-talonid fossettid. It and the other lower molars have an entolophid fossettid. The m2 is less worn and demonstrates the generalized form of advanced toxodontids (sensu Cifelli, 1993) a 7/9 morphology (sensu Shockey et al., 2004), where the trigonid has the form of the number seven and the talonid a number nine, the entolophid representing the upper part of the nine, pierced by the entolophid fossettid.

No postcranials have been found associated with *P. saltoni* teeth at Salla, but we refer a distal femur of the MNHN-Paris collection to this taxon (Figure 7.7). This referral is based upon the distinctive, enlarged medial trochlear ridge, similar to that of other toxodontids and unlike the femora of similar-sized taxa of Salla (e.g., *Eurygenium*, *Trachytherus*; the femur of *Pascualihippus* is unknown).

The medial trochlear ridge of the Salla toxodontid is considerably higher than the lateral ridge of the patellar trochlea, but is not bulbous, as in *Toxodon* or *Hoffstetterius*, which have been shown to function just like knee locks of horses (Shockey, 2001). The functional significance of the less modified, but enlarged MTR of *Proadinothierium* is unknown, but it may have served to prevent medial dislocation of the patella or to prevent lateral movements of the lower leg (Shockey, 2001). Whatever the function, it has been shown that having an enlarged MTR, at least in bovids, is correlated with living in open habitats (Kappelman, 1988). This morphology likely, and incidentally, served as a “preadaptation” for the knee locks seen in later toxodontids. These have been documented to the late Miocene (Shockey, 2001), but our observations of the distal femur of cf. *Pericotoxodon* from the La Venta Beds in the MNHN-Paris collection extends the toxodontid knee lock back to middle Miocene (about 13 Ma). This is roughly the same time that knee locks evolved in horses (Hermanson and MacFadden, 1996).

## 7.4 Discussion

### 7.4.1 Biology of Form

The species richness of the Salla fauna is mirrored by the diversity of morphological adaptations; some mammals show specializations for running, digging, and climbing (uncommon), whereas others were less specialized and perhaps more versatile in their locomotor abilities.

#### 7.4.1.1 Marsupials

Given the great diversity of primary consumers at Salla, it not surprising to see a fair diversity of carnivorous marsupials. With our description of *Fredszalaya hunteri* and the work in progress on a small dog-like marsupial, the species richness of sparassodonts now includes six taxa. The huge *Paraborhyaena*, was presumably terrestrial ( $\alpha$ -level hypothesis), but the calcaneum of *Fredszalaya* suggests some climbing abilities ( $\alpha$ -level hypothesis), perhaps like the morphologically similar *Prothylacynus* (Argot, 2002).

#### 7.4.1.2 Xenarthrans

Though instructive postcranials of dasypodids are lacking (e.g., complete ulnae, metatarsals), one might presume typical dasypodid digging and insectivorous habits for these animals ( $\alpha$ -level hypotheses) until there is evidence to the contrary. Likewise, we presume fossorial locomotion ( $\alpha$ -level hypothesis) for the peltephilid based upon the indirect (extrapolated) link of phylogenetic relationship to *Peltephilus* and the more fully developed hypothesis of digging for that taxon offered by Vizcaíno and Fariña (1997). The postcranial evidence presented here, though incomplete, is at least consistent with a digging hypothesis. Like *Peltephilus*, the Salla peltephilid

appears have focused forces for biting at the anterior region of its jaw, though its mandibular symphysis was not fused in most known specimens. A strong anterior bite is unusual for carnivorous or herbivorous mammals, or any kind of mammal for that matter. The closest analog among mammals we think of is the anterior cutting teeth of fruit eating and blood drinking bats. For now, we are content to continue wondering about the strange peltephilids.

Like most of the notoungulates summarized below, the mylodontid sloth of Salla has high crowned (indeed, ever-growing) teeth. Additionally, it had a broad muzzle. The hypselodonty and broad muzzle each is suggestive of grazing in this most ancient of mylodontids ( $\beta$ -level hypothesis).

#### 7.4.1.3 *Pyrotheria*

The relatively huge head and grossly robust postcranial skeleton of *Pyrotherium macfaddeni* leaves no real doubt about its unspecialized, terrestrial locomotion ( $\gamma$ -level hypothesis). The tusks and probable proboscis provided the animal a means to probe around and manipulate its environment to find and obtain food items. Its relatively low crowned teeth makes it unlikely that it was a grazer, but in absolute terms the crowns were fairly high, so it probably could have consumed some grasses. Despite that caveat, it is probably best classified as a browser ( $\beta$ -level hypothesis).

#### 7.4.1.4 *Litopterna*

The proterotheriid and macraucheniid litopterns show marked adaptations for cursorial habits ( $\beta$ -level hypotheses). The macraucheniiids are regarded as open habitat cursors ( $\alpha$ -level hypothesis) and the small proterotheriid has been compared to forest dwelling cursorial rodents (e.g., dasyproctids) and artiodactyls (e.g., duikers and tragulids) (Shockey, 1999) ( $\alpha$ -level hypothesis). (No postcranials are known for the adiantid litopterns.) The narrow muzzles (known in the macraucheniid and assumed for the proterotheriid) and low crowned dentition suggest browsing ( $\beta$ -level hypothesis).

#### 7.4.1.5 *Notoungulata*

The smaller notoungulates (interatheriids, hegetotheriids, and archaeohyracids) appear to show modest developments associated with quick locomotion, such that they may be regarded as cursorial ( $\gamma$ -level hypothesis for interatheres and hegetotheres, but only  $\alpha$ -level hypothesis for the poorly known archaeohyracids). There is no compelling evidence at Salla for saltatory habits in these small notoungulates, but given their size and general cursorial adaptations such should be considered ( $\alpha$ -level hypothesis). Suggestive evidence for saltatory activity includes the fused tibia-fibula at the upper ankle joint in the interatheriid (Hitz, 1997) and *Prohegetotherium*. This is unknown for the archaeohyracid, but we note the greater mechanical advantage at the astragalus for the digital flexors.

The body of evidence strongly supports the hypothesis of fossorial habits ( $\delta$ -level hypothesis) for the mesotheres

*Trachytherus* (for details see Shockey et al., 2007). Modern wombats, with their digging abilities, high crowned cheek teeth, and gliriform incisors, serve as a model for *Trachytherus* biology, though due to the extreme convergence of the postcranial skeletons of mesotheres with those of aardvarks (*Orycteropus*) the precise method of digging in *Trachytherus* is probably more similar to that of *Orycteropus* (see Shockey et al., 2007).

The notohippid *Eurygenium* is regarded as subcursorial generalist ( $\beta$ -level hypothesis) as we note only modest adaptations for speed in its skeleton. Weaker evidence suggests that this generalist was capable of swimming and digging ( $\alpha$ -level hypotheses). Postcranial elements of *Pascualihippus* and the toxodontid *Proadinothierium* are poorly known and thus are only suggestive of terrestrial, subcursorial habits ( $\alpha$ -level hypothesis). No postcranials of the leontiniid *Anayatherium* are known, so we defer any comments on its locomotion, but we note that its narrow muzzle and mesodont cheek teeth imply browsing ( $\beta$ -level hypothesis).

Deseadan faunas typically contain numerous high crowned notoungulates. Remarkably for the late Oligocene, the notoungulate taxa almost exclusively have high crown, or hypsodont, dentitions (11/13 species). The only notoungulates at Salla lacking hypsodont teeth are the leontiniids. Leontiniids at Salla are exceedingly rare, but even they have moderately high crowned, mesodont teeth (Shockey, 2005).

Compared to contemporaneous faunas throughout the world, Deseadan faunas have a remarkably large number of herbivores having high crowned teeth (Patterson and Pascual, 1972; Flynn and Wyss, 1998; MacFadden, 2000). The phenomenon of this "precocious hypsodonty" began in South America around 35–30 Ma, about 15 million years earlier than in North America (MacFadden, 2000). For some, this precocious hypsodonty has implied the early spreading of grasslands in South America (Stebbins, 1981; MacFadden, 2000). Pascual and Ortiz Jaureguizar (1990) provided an alternative explanation for this precocious hypsodonty, suggesting that it was a response to tooth wear caused by volcanic grit that dusted the plants during that time. In more general terms, Janis (1995 and references therein) demonstrated that any dust or grit covering low lying plants in open country may contribute to the evolution of high crowned teeth.

The robust evidenced for *Trachytherus* being a digging specialist (Sydow, 1988; Shockey et al., 2007), along with suggestive evidence of fossorial habits in other Tertiary notoungulates (e.g., homalodotheres [Scott, 1930], *Scarrittia* [Chaffee, 1952], toxodontids [Hildebrand, 1985]), adds another dimension to the problem of precocious hypsodont of notoungulates. Did hypsodonty evolve in response to eating subterranean foods covered with abrasive grit?

To have confidence in the grazing hypothesis, there must be some independent evidence for grazing in notoungulates. Stable isotopic studies have no utility in this context, since the global carbon shift did not occur until much later (MacFadden, 2000). That is, prior to the global carbon shift,



C4 photosynthesis was insignificant; so even grasses would have been predominantly C3.

Microwear or other dental abrasion analyses are wanting, but they have the potential to be illuminating. A major challenge for investigators beginning this work will be to develop techniques that can discriminate between wear caused by phytoliths of grass versus non-biogenic abrasives, such as volcanic grit, dust, or dirt.

Meanwhile, we must use morphological characters independent of hypsodonty to test grazing hypotheses for these hypsodont herbivores. One such morphological feature that appears to be independent of hypsodonty, but associated with grazing is muzzle width (Gwynne and Bell, 1968; Solounias et al., 1993). Shockey (1997) noted the broad muzzle of *Pascualihippus* and argued that it, in the context of the animal's hypsodont dentition, indicated that grass was a significant portion of the animal's diet (indeed, the generic name, in addition to honoring Rosendo Pascual, means "grazing horse") ( $\gamma$ -level hypothesis). The toxodontid *Proadinotherium saltoni* also had a broad cropping dentition and hypsodont teeth, providing two lines of evidence suggestive of grazing ( $\gamma$ -level hypothesis).

The smaller notoungulates (interatheres, archaeohyracids, hegetotheres) have hypsodont-to-hypsodont dentitions, suggestive of grazing, but they have narrow muzzles, suggestive of more selective feeding. Also, due to their small body size with the implied high mass specific metabolic rate, it is unlikely that they could have obtained the quality of nutrients they would have required from grasses alone. Thus, we tentatively characterize them as being selective feeders, foraging upon richer food items (seeds, fruits, tubers and protein and calorie-rich new-growth, leafy material) at ground level ( $\alpha$ -level hypothesis).

#### 7.4.1.6 Immigrant Taxa

Rodents of Salla are numerous and diverse but nothing is known of their postcranial skeletons, other than that we have referred a couple of proximal tarsals to the order, but not to any particular genus. We offer no hypotheses regarding their locomotion or feeding ecology at this time.

The impulse to assume that the monkey *Branisella* was arboreal is tempered by the evidence provided by Kay et al. (2002). Based upon the relatively high crowned teeth and the low primate diversity at Salla, they interpret *Branisella* as being more terrestrial than other platyrrhines. This evidence, along with some details of the sediments, were used to suggest that Salla was dry and not forested, an interpretation consistent with the interpretation of MacFadden, 1990, but at odds with the results of the body size distribution analysis of Croft (2001; discussion below).

#### 7.4.2 Paleoecology of Salla

There is a near consensus that the habitat of Salla was fairly open and dry, with much grass and scattered patches of brush

and trees. Such would explain the numerous hypsodont taxa, which include nearly all of the numerous notoungulates, as well as the marsupial *Proargyrolagus*, and (relative to other primates) *Branisella*. However, we note the small body size of most of the hypsodont notoungulates, animals that may have had difficulty getting enough nutrients to fuel their presumably high mass specific metabolic rates if they were feeding on grass. Of the larger hypsodont notoungulates, *Trachytherus* had a narrow muzzle, suggestive of specialized feeding, and it was almost certainly a digger. Their high crowned teeth may have just served to protect the animal against the rapid tooth wear caused by eating dirt-covered vegetation, rather than phytolith-filled grasses. Of the larger notoungulates, only *Pascualihippus* and *Proadinotherium* show independent evidence of grazing – their broad muzzle, a character also seen in the hypsodont/hypsodont mylodontid sloth.

Croft (2001) showed that the distribution of body size of the herbivores of Salla was similar to body size distributions seen in extant, forested habitats but distinct from the patterns of modern arid regions. He was conscious that his findings were in conflict with the prevailing hypotheses and suggested that the slope of his cenogram could have been artificially flattened since it included taxa from all horizons. That is, there was not a single Salla fauna, but a dynamic fauna that changed over time.

Given that the Salla Beds contain up to 600 m of sediments, deposited over a time span of about 3 million years (MacFadden et al., 1985), it is probably inappropriate to discuss the paleoecology of Salla as if it were a single phenomenon. Clearly, the depositional environment changed over time and work in progress suggests that there were some changes in the fauna, though many taxa are found at all horizons. In the mean time, caveats must accompany any comments about the environment of Salla.

#### 7.4.3 Phylogenetic Considerations

##### 7.4.3.1 Xenarthrans

The occurrence of the complex (medial ball-and-socket/lateral sliding) knee joint in Tertiary glyptodonts and sloths (Shockey, 1999; Salas et al., 2005) presents an interesting problem. This morphology is absent in armadillos and pampatheres. The current and essentially universally accepted dichotomous model of xenarthran phylogeny (armored cingulates vs. hairy pilosans) is incompatible with any suggestion that the complex knee articulation of cingulated glyptodonts and pilosan sloths is homologous. Thus, one might assume that the complex, rotary knee joint of sloths and glyptodonts evolved independently. With much curiosity and some discomfort, we include the complex knee joint as a homoplasy among sloths and glyptodonts; along with other such similar distinctive structures, including their fused mandibular symphyses with mandibular spout, deep mandibles, short and wide nasals, descending process of the jugal, and the tri-lobe ("carved tooth") nature of glyptodonts and the most primitive sloths known, *Pseudoglyptodon*

*sallaensis* of Salla and *P. chilensis*, from the early Oligocene Tinguirirican fauna (McKenna et al., 2006).

#### 7.4.3.2 *Notoungulata*

The intertheriid tarsus reveals problems for systematists. Although the intertheriids had been almost universally considered to be nested within the Typotheria (e.g., Simpson, 1945; Cifelli, 1993; but see Reguero, 1999 for another interpretation), they have several derived tarsal traits that occur in the “advanced Toxodontia” (sensu Cifelli, 1993; = leontiniids, notohippids, and toxodontids), but not Typotheria. These tarsal characters include the well-developed calcaneofibular articulation, which is dorsoventrally oriented (rather than oblique), absence of the astragalar peroneal process, nearly vertical lateral and medial walls of the astragalar body, and the steeply inclined orientation of the articulation of the calcaneum and astragalus at their ectal (lateral) contact. Characters of the tarsus were not included in the phylogenetic analysis of Reguero (1999), thus, our finding here provide independent support for the exclusion of the Intertheriidae from Typotheria.

These shared characteristics of the intertheriid and “advanced Toxodontia” tarsus is significant. If they are indeed homologous, it will have a profound effect on our interpretations of the inter-familial relationships of notoungulates. It would suggest that intertheriids are more closely related to the “advanced Toxodontia”, which would have even broader implications, since this Toxodontia-intertheriid form is quite similar to the tarsus of the Arctostylopida (Cifelli et al., 1989; Missiaen et al., 2006; and discussion below). If, instead, this suite of characters represents a homoplasy, then it evolved independently evolved at least three times (Arctostylopida, “advanced Toxodontia”, and intertheriids [and similar to the lagomorph morphology]), and it likely suggests a tarsal form required when near equal forces are transmitted through the fibula-calcaneum and the tibia-astragalus.

The similarities of the Toxodontia-intertheriid form to that of the Arctostylopida are of interest. The Arctostylopida are a small group of ungulates, mostly from Asia but represented in North America by *Artostylops* (see Cifelli and Schaff, 1999 for a review of the Arctostylopida). Initially, arctostylopids were regarded as being notoungulates (e.g., Matthew, 1915; Simpson, 1945), but later students of the groups generally regarded the dental similarities between Arctostylopida and notoungulates to represent homoplasies (Cifelli et al., 1989; Cifelli and Schaff, 1999; Missiaen et al., 2006), largely based upon differences in the tarsi of notoungulates and arctostylopids.

Previous comparisons of the arctostyloid tarsus to that of notoungulates have noted significant differences (Cifelli et al., 1989; Missiaen et al., 2006). However, these authors used the putative primitive notoungulate form (e.g., *Colbertia*) to compare notoungulates with the actostyloid, *Paleostylops* (= *Gashatostylops* of Cifelli et al., 1989). Cifelli et al. (1989) at least noted the presence of the arctostyloid-like

calcaneofibular joint of “advanced Toxodontia”, but reasoned that this would have evolved too late (perhaps not until the Oligocene) to have any relevance on the arctostyloid-notoungulate question. However, they were not aware of the same form occurring in intertheriids. This form is unknown prior the Oligocene, but if it is homologous with that of the “advanced Toxodontia”, then its origins must have occurred much earlier. Even if the intertheriid form is not homologous with that of the Toxodontia, the record of the intertheriids goes back to the Riochican (Cifelli, 1993; generally regarded as Paleocene). If these early Tertiary notopithicine intertheriids had a similar form, then it would be most relevant in regard to the arctostyloid-notoungulate problem. Unfortunately, however the tarsus of these Paleocene-Eocene notopithicine intertheriids remains unknown. Indeed, prior to this report, the oldest record of any intertheriid tarsus was Santacrucian, early-middle Miocene [Sinclair, 1909]).

Bloch (1999) reported on the discovery of a partial skeleton of the North American arctostyloid, *Arctostylops*. He noted several tarsal characters that he regarded as putative synapomorphies to unite arctostylopids with notoungulates. These included astragalus with tibial protuberance and elongated, constricted neck with oblique dorsal ridge, and calcaneum with proximally positioned sustentaculum). Since he had compared the tarsus of *Arctostylops* with the primitive notoungulate morphotype, he listed the “steeply inclined ectal facet” of arctostylopids as being different from the form of notoungulates. The steeply inclined ectal facet of the Toxodontia-intertheriid morphotype negates that difference and strengthens Bloch’s argument for arctostyloid-notoungulate affinities. We also add the well-developed, anteroposteriorly oriented fibular facet of the calcaneum, the lack of astragalar peroneal process, and the nearly vertical medial and lateral walls of the astragalar body to Block’s list of putative synapomorphies. Further study of the skeleton of *Arctostylops* and the postcrania of notoungulates should help resolve this interesting notoungulate-arctostyloid problem.

#### 7.4.4 Concluding Remarks

Regarding Salla, Simpson (1984:p. 214) wrote: “A needed monograph, including all the species present in the various collections, has not yet been published.” Such a work is still wanting, but we hope that our efforts here will serve in the interim to better document the varied and curious fauna of Salla.

This overview of the Salla fauna includes a review of previous works of Salla and a report of some of our new findings. The new includes *Fredszalaya hunteri* gen. et. sp. nov.; stratigraphic context for one of the last surviving proborhyaenines (*Paraborhyaena*) with the observation that it had a single pair of incisors; the first description of the peltephilid of Salla (with the documentation of the unfused mandibular symphysis); the documentation of one of the oldest mylodontid skulls; the significant elongation of Mt

III of a Deseadan proterotheriid; the macraucheniid patella that provides an example of form resulting from function (essentially proving that Deseadan macraucheniids had knee locks); the analysis of interatheriid tarsals (casting doubt upon its classification as a typtothere and suggesting a closer relationship with Toxodontia and raising the problematic possibility of a notoungulate-arctostylopid relationship); the first descriptions of the tarsals of *Pascualihippus*, *Eurygenium*, *Prohegetotherium*, and the unnamed interatheriids of Salla; as well as the distal femur of *Proadinothierium* along with the description of the new species of toxodontid, *P. saltoni*.

In addition to being a review and to documenting new data, we like to think of this work as being a preview of works to come. We have noted some of our works in progress and those of some of our colleagues. Perhaps most importantly, we should note work in the Tinguirirican faunas (early Oligocene), which has great potential for resolving some of the current conflicts regarding some of the phylogenetic hypotheses.

We are conscious of the fact that we have raised more questions than illuminated answers (e.g., the complexities regarding peltephilid biology, phylogenies of interatheres and arctostylopid, and the function of notoungulate hypsodonty) and hope to see continued works regarding these varied and interesting problems. We have deferred (i.e., avoided) paleoecological conclusions and note work in progress by D. Croft and ourselves.

A saying in Bolivia goes, “*Chanchito limpio nunca engorda* (the clean pig never fattens).” The relevance here is that some answers still lie in the field, at Salla and at other Tertiary localities of South America, and that we and other investigators need to continue to soil ourselves with Tertiary sediments in order to resolve some of these little mysteries of life on that ancient, “lost” continent.

**Acknowledgments.** Recent fieldwork at Salla has been sponsored by the National Geographic Society (7507–03 to BJS). Previous field seasons have been sponsored by various NSF grants to B. J. MacFadden, BJS, and to Kay, Madden, and MacFadden. We thank the many people who assisted us in our museum studies. These include Mary Ann Turner, Lyndon Murray, and Daniel Brinkman of the Yale Peabody Museum; Christian de Muizon of the Muséum National d’Histoire Naturelle, Paris; Denny Dively and Jin Meng of the American Museum of Natural History; and Bruce J. MacFadden and Richard Hulbert of the Florida Museum of Natural History. Alfredo Carlini provided identifications for most of the cingulate specimens. Darin Croft, Jay O’ Sullivan, and Eric Sargis provided critical reviews of this manuscript for which we are thankful. We are especially grateful to the administration of the Universidad Autónoma “Tomás Frías,” Potosí, Bolivia, especially Pedro Lopez, for helping revive our studies in Bolivia.

## Appendix

Metric data (mm) of proximal tarsals and other elements of taxa discussed in text

### Proximal tarsals

Taxon	Specimen ID	Astragalus Length	Trochlear Width	Calcaneum Length
Marsupialia				
<i>Fredszalaya hunteri</i>	UF 172501	–	–	33.2
Xenarthra				
cf. <i>Peltephilus</i> sp.	UF 93515	15.3	12.7	–
Pyrotheria				
<i>Pyrotherium macfaddeni</i>	UF 172765	–	–	150
Litopterna				
<i>Coniopternium</i> sp.	UF 172426	38.4	25.5	88.5
Notoungulata				
<i>Trachytherus alloxus</i>	UF 172437	35	15.4	–
<i>Trachytherus alloxus</i>	MNHN-Bol-F-94-k	37.5	14.7	–
<i>Trachytherus alloxus</i>	UF 90960	34.6	14.8	58.8
<i>Trachytherus alloxus</i>	UF 172514	–	–	66.7
<i>Prohegetotherium schiaffinoi</i>	UF 172502	15.1	7.1	67.3
<i>Prohegetotherium schiaffinoi</i>	UF 172445	15.9	7.2	–
Archaeohyracid	UF 176069	20.0	8.5	–
Archaeohyracid	UF 176089	19.8	8.6	–
Interatheriid, large sp.	UATF-V-000132	17.5	7.8	29.2
Interatheriid, large sp.	UF 173247	17.7	7.5	–
Interatheriid, small sp.	UF 172970	–	–	20.8

(continued)

## Appendix (continued)

Taxon	Specimen ID	Astragalus Length	Trochlear Width	Calcaneum Length
<i>Eurygenium pacegnum</i>	UF 172432	32.7	16.0	59.6
<i>Eurygenium pacegnum</i>	Bol-V-003644	–	–	54.0
<i>Eurygenium pacegnum</i>	Bol-V-004077	26.3	15.0	–
cf <i>Pascualihippus boliviensis</i>	UF 172410	39.6		17.9 74.5
<b>Other elements</b>				
Taxon	Specimen ID	Element	L	W
<b>Marsupialia</b>				
<i>Fredszalaya hunteri</i> <sup>a</sup>	UF 172501	C-nuchal crest	162	–
		C – M4	34	–
		P3	8.8	6.4
		M1	(7.5)	6.5
		M2	9.5	7.6
		M3	10.3	9.1
		M4	4.8	8.8
		<b>Xenarthra</b>		
Peltephilid (unnamed taxon)	UF 93586 UF 93587 PU 21143 UF 93515	mf1–mf7	32.5	
		mf “0” – mf7	34.0	
		mf “0” – mf7	40.5	
		Mt II	23.7	6.3 (proximal)
		Mt III	25.1	6.1 (prox.)
Mylodontid (unnamed genus)	UATF-V-127	Mt IV	24.0	6.0 (prox.)
		Cf-Mf4	67.1	–
		Mf1	13.2	10.1
		Mf2	14.0	11.6
		Mf3	19.3	13.0
		Mf4	(≈10)	(≈10)
<b>Litopterna</b>				
<i>Coniopternium</i> spp.	UF 149207 MNHN-Bol- V-004502 MNHN-Bol- (no #) UF 172425	Humerus	158	40 (condyles)
		Femur	238	48 (condyles)
		Fémur	265	–
		Mt III	118	–
<b>Notoungulata</b>				
<i>Trachytherus alloxus</i>	UF 91933 UF 90960	Humerus	185	66
		Humerus	146	55
<i>Prohegetotherium schiaffinoi</i>	UF 172502	Mt III	60	–
		Femur	179	–
		Mt II	28.8	6.0
		Mt III	32.9	6.1
		Mt IV	(32)	5.5
Interatheriid, large sp.	UF 172445 UATF-V-132	Femur	91.3	20.2
		Mt III	–	7.5 (proximal)
		Mt IV	–	7.0 (prox.)
<i>Eurygenium pacegnum</i>	MNHN-Bol- V-3644	Mt V	–	3.5 (prox.)
		Humerus	156	–
		radius	126	–
		Mc II	52.1	–
		Mc III	52.1	–
		Mc IV	48.5	–
		Mc V	(30)	–
		Femur	175	–
		Tibia	164	–
		Mt III	44.5	–
		Mt IV	44.3	–
Mt V	42.5	–		

(continued)

## Appendix (continued)

Taxon	Specimen ID	Element	L	W
<i>Proadinothereum saltoni</i> <sup>a</sup>	UF 149222	i1	8.4	4.8
		i2	11.8	4.8
		i3	(13)	4.6
		c	6.9	2.5
		p1	5.5	3.5
		p2	8.5	4.3
		p3	9.5	5.5
		p4	10.8	6.5
		m1	12.6	6.9
		m2	16.9	6.8
		m3	23.0	6.9

<sup>a</sup>Holotype

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