TOXODONTIA OF SALLA, BOLIVIA (LATE OLIGOCENE): TAXONOMY, SYSTEMATICS, AND FUNCTIONAL MORPHOLOGY

By

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TOXODONTIA OF SALLA, BOLIVIA (LATE OLIGOCENE): TAXONOMY, SYSTEMATICS, AND FUNCTIONAL MORPHOLOGY

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The Salla Beds of Bolivia preserve a diverse sample of mammals that lived during the "Splendid Isolation" of South America. The fossil-bearing beds of Salla are known to be late Oligocene (ranging from about 27 to 24 million years ago), a time when the endemic mammals evolved advanced characters, such as high-crowned teeth and specialized locomotor adaptations, and when primates first appeared and rodents first diversified in South America.

Though this fauna has received much attention in the literature, the most common order at Salla, Notoungulata, has been largely neglected. This work provides the first description of Toxodontia notoungulates from Salla, as well as a study of their ontogenetic development, functional anatomy, and phylogeny.

The results of the alpha taxonomy indicate that the Toxodontia of Salla are different species from those of the classical Patagonian Deseadan localities. This difference is judged to be a result of the geographic differences rather than temporal ones since the lower (older) regions of Salla are contemporaneous with the younger Patagonian Deseadan localities. Most of the Toxodontia of Salla represent new species. Two, however, are known from other low-latitude Deseadan localities, but not from the high-latitude localities of Patagonia (*Eurygenium* sp. is known from the Pataca Formation of Southern Bolivia and the Tremembré Formation of Brasil is the type locality for *Rhychippus brasiliensis*).

Four new species are described (two notohippids and two leontiniids) and a novel method of determining feeding ecology of extinct herbivores by use of a multivariate analysis of morphological features associated with feeding in extant ungulates is employed. Other discoveries in this work include the first descriptions of a notohippid skeleton, of the deciduous teeth of a notohippid and a mesotheriid, and the first description of the postcranial elements of the macraucheniid ?*Coniopternium primitivum*. This litoptern is shown to have the oldest "knee-lock" known, similar in principle to, but distinct from, that seen in horses.

The Salla Beds provide a snapshot of life in Bolivia during the initiation of the building of the Andes. This fauna is shown to be more diverse, both in terms of species richness and morphological adaptations, than previously known.

CHAPTER 1
INTRODUCTION

Overview

The Salla Beds are a late Oligocene mammal-bearing unit located in the Eastern Cordillera of the Andes of Bolivia (Hoffstetter, 1968; MacFadden et al. 1985). These beds lie in a mountane basin adjacent to the Aymaran village of Salla (pronounced "sál-ya" by its residents). It is universally accepted as being of the Deseadan South American Land Mammal Age (SALMA) and is generally considered to be late Oligocene (MacFadden et al., 1985; Kay et al., 1995; Flynn and Swisher, 1995), though some workers (Sempere et al., 1990; McRae, 1990) interpret its age as early Miocene.

Salla had a diverse mammalian fauna and a number of works have been published regarding most of the orders of mammals present. Mammalian orders previously studied include the marsupials (Patterson and Marshall, 1978; Villarroel and Marshall, 1982; Hoffstetter and Petter, 1983; Wolff, 1984a), rodents (Hoffstetter and Lavocat, 1970; Lavocat, 1976; Patterson and Wood, 1982), primates (Hoffstetter, 1969; Wolff, 1984b; Rosenberger et al., 1991), litopterns (Cifelli and Soria, 1983a and 1983b) and the pyrothere (MacFadden and Frailey, 1984). The most common order of mammals at Salla, the Notoungulata, however, has been generally neglected in the literature. The only two works regarding Salla notoungulates are a description of the skeleton of <u>Trachytherus</u> <u>spegazzinianus</u> in an unpublished masters thesis (Sydow, 1988) and an abstract regarding the skeleton of a notohippid referred to Eurygenium (Shockey, 1995).

This study describes and discusses notoungulates of the suborder Toxodontia Owen 1853 in terms of their phylogeny, functional morphology, and ecology. It relies heavily upon the excellent collection of fossil mammals that have been acquired during UF-Bolivian expeditions to Salla which began in 1981.

Currently, other investigators are studying the notoungulates from Salla. Ralph Hitz of the University of California, Santa Barbara, is describing the interatheriids; and Marcelo Reguelo of the Museo de la Plata is describing the archaeohyracids, with Richard Cifelli of the University of Oklahoma, and the hegetotheriids, with Richard Madden of Duke University.

The Deseadan SALMA is regarded as being a critical time in South American paleomammalogy since it is an age that records the first appearance of advanced ungulates (Pascual and Ortiz Jaureguizar, 1990), primates in South America (Hoffstetter, 1969), and the early diversification of South American rodents (until recently [Wyss et al., 1993] the Deseadan had recorded the oldest South American rodents).

Increasing our knowledge of the most common mammalian order of this time may facilitate our understanding of the environments in which these ungulates lived and into which rodents and primates immigrated. This time period is also of interest, particularly in Bolivia, since it is a time when the Andes began their considerable uplift (see Sempere et al., 1990). These mountain building events likely had continental, as well as regional, effects on the flora and fauna of the late Oligocene.

The continental endemism, or "Splendid Isolation (Simpson, 1980)", of South American's extinct ungulates also provides an opportunity to examine the universality of principles of ecomorphology based upon our knowledge from extant ungulates. One might wonder if the ungulates of this "lost continent" adapted to the challenges of acquiring nutrition from vegetation in similar ways as modern ungulates (See Chapter 5).

The general format of this work includes an overview of relevant history and geologic context (Chapter 1, below); a general materials and methods section (Chapter 2); a systematic paleontology section (Chapter 3); a study of juvenile specimens (Chapter 4); functional morphology section sections, one regarding morphological features associated with feeding (Chapter 5) and another (Chapter 6) regarding locomotion; a phylogenetic analysis (Chapter 7), a review and revision of the fauna of Salla (Chapter 8), and a general summary (Chapter 9).

The introduction gives an overview of South American paleomammalogy, particularly in regard to the Deseadan South American Land Mammal Age. This is followed by an account of the history, geography, and geology of Salla.

The methods section presents the general principles, procedures, and definition of terms used throughout the dissertation. Specific details that apply only to particular sections are covered in the appropriate chapters.

The systematic paleontology section is in the format used by vertebrate paleontologists (see Simpson, 1945). This section includes the systematics and descriptions of taxa in the three families of Toxodontia represented at Salla, the Leontiniidae, Notohippidae, and Toxodontidae.

Our recent discovery of juvenile notoungulate specimens presents an opportunity to note tooth homologies in taxa in which this is usually difficult to determine due to the simplicity of these teeth and because crown patterns wear away easily. In one case, this study illustrates the development and origin of a novel structure that is diagnostic for a distinct lineage of notoungulates, the mesotheriids (see Chapter 4).

Chapter 5 examines the feeding ecology of the Toxodontia. Principles derived from extant ungulates are applied to the extinct ungulates of Salla in order to generate hypotheses regarding their biology. Hypsodonty and muzzle morphology were examined to help understand the feeding ecology of these taxa, which can aid in our understanding of their environment.

Locomotory adaptations were examined in Chapter 6. Postcranial elements of the notohippid Eurygenium sp. were compared with those of two other ungulates of Salla, the typothere notoungulate Trachytherus spegazzinianus and a litoptern cf. Coniopternium primitivum. These are described and discussed in an attempt to infer modes of locomotion in these animals.

The phylogenetic analysis relies heavily on techniques of cladistics in order to attempt to understand the phylogenetic relationships of the Salla taxa. Although cladistic methods are employed, the nomenclature is conventional (see discussion Chapter 7).

A revised faunal list for Salla is also presented with the justification for the revisions (Chapter 8).

Major findings of the alpha-taxonomy, systematics, and functional morphology are reviewed in the Summary and Conclusions (Chapter 9).

History of South American Paleomammalogy

Early History

Paleomammalogy in South America has rather august origins. Her first two students were Georges Cuvier and Charles Darwin.

Cuvier's initial involvement was somewhat clandestine; even unethical by our modern conventions. He described the "giant sloth" Megatherium Cuvier, though he had never seen the specimen. He based his description on a poor copy of figures that that had been prepared for Juan Bautista Brú y Ramón of the Real Gabinete de Historia Natural, who had intended to publish the initial description (see Simpson, 1984). Cuvier thus described the first fossil mammal from South America, using Brú's figures. Cuvier also described South American proboscidian specimens that he obtained (directly and honestly) from Alexander Humboldt, who had explored much of South America (see de Terra, 1955).

Darwin's involvement in South American paleontology began during his tenure as naturalist (1831 - 1836) aboard the H.M.S. Beagle (see Darwin, 1845). Among the many natural history specimens he collected, Darwin discovered some unique fossil mammals. These were later described by Richard Owen (1840) in a series of works that Darwin edited.

Of particular relevance to this overview was Darwin's discovery of fossils in the banks of the Rio Tercero, Argentina, near Santa Fe in early October 1833. The fossils included a horse tooth, some xenarthran remains and a strongly curved tooth unknown to Darwin. A month later and some 180 miles to the northeast in what is now Uruguay, he visited a ranch where the skull of a hippo-size fossil mammal had been placed upon a fence, presumably as a decorative curio. It also served as a target for stone throwing youths who had destroyed the teeth by the time Darwin arrived. He purchased the skull and sent it to England.

The rescued skull had strongly curved alveoli for the molars. The strange tooth that Darwin had found in the banks of the Rio Tercero some weeks before and 180 miles away fit perfectly into the socket for the M2 (see Owen, 1840: Pl 1). Owen gave the descriptive generic name Toxodon (=bowed tooth) to this animal, which serves as the genotype for the family Toxodontidae and suborder Toxodontia Owen 1853 (see Mones, 1988 and 1993 for review of nomenclature). He found it quite an odd beast, referred it to the "Pachydermata" (now regarded as a polyphyletic group which included elephants, rhinos, and hippos) but noted "affinities" with rodents, xenarthrans, and the manatee.

Owen later received fossil mammals from a British naval officer, Bartholomew James Sulivan. Sulivan had collected these while on expedition near Santa Cruz, Argentina. Though smaller, having more complicated teeth, and lacking a diastema, Owen noted that the fossils were similar to Toxodon. He named this genus Nesodon Owen 1846. This animal came from Tertiary beds of Patagonia, and, unlike Toxodon, was never found in association with "conventional" animals like Equus.

After the work of Darwin and Owen, a hiatus occurred in the paleomammalogy of South America. The clues that the Tertiary of South America was very odd did not provoke serious investigations for several decades. The nineteenth century, however, would not end quietly for the paleontology of South America. The findings of the Ameghino brothers would stimulate investigators from North America and Europe to explore desolate regions of Patagonia in search of fossil mammals.

The Classical Deseadan of Patagonia

The Ameghino brothers, Florentino, Carlos, and the less-well known Juan, grew up in fossil-rich Luján, Argentina (see Simpson, 1984). Florentino and Carlos amassed a huge collection of Pampean fossils (Neogene) and were destined to make a life-study of fossils of Argentina. Juan supported the work by running the family stationery business.

In 1885, Florentino Ameghino received some fossils from an Argentinean army captain, don Antonio Romero. These, some dinosaur bones and a couple of mammal teeth, had been discovered in Neuquén province in northwestern Patagonia. Quite naturally (and erroneously) Ameghino assumed that the mammal teeth, a molar and "defensa" (defensive tooth, or tusk), were the same age as the accompanying dinosaur bones. Ameghino described and named them (honoring the generous officer) Pyrotherium romeroi Ameghino, 1888. He later received more pyrothere material from Neuquén along with fossils of astrapotheres and a mesotheriid that Ameghino would make the holotype of Trachytherus spegazzinianus (Ameghino, 1889).

Carlos Ameghino began exploring Patagonia in 1887 and soon collected more pyrothere specimens from Chubut and Santa Cruz provinces. By his seventh expedition to Patagonia, Carlos had demonstrated unequivocally that the beds from which the pyrotheres came underlay the extensive, marine

"Patagonian Formation," whereas pyrotheres were never found above this formation. He thus proved that the fauna associated with pyrotheres were significantly older than the Santacrucian faunas, which overlay the "Patagonian Formation".

Unfortunately, the elder Ameghino overestimated the age of both the "Patagonian Formation" and the "couches a Pyrotherium", or the Pyrotherium Beds (=Deseadan). Ameghino believed that the "Patagonian Formation" was Eocene (later regarded as Miocene, but now considered a series of transgressions of various ages [see Flynn and Swisher, 1995]). Though he was correct regarding the sequence, he incorrectly assumed that the underlying "Pyrotherium Beds" were Cretaceous because dinosaurs were found near (but not among) the mammalian fossils. The overestimate of the ages of these strata influenced his thinking regarding the relationships of the Patagonian fossils mammals with those of the rest of the world.

Because of the supposed great antiquity of the mammals of the Pyrotherium Beds and their superficial similarity to modern mammals, Ameghino believed that these animals were ancestral to many extant taxa. He noted similarities of Pyrotherium to elephants (Ameghino, 1895), notohippids to equids (Ameghino, 1897), and archaeohyracids to hyracoids (Ameghino, 1897) and argued for group after group that the fossil taxa from Patagonia gave rise to the extant animals. A later student of South American paleontology would write regarding these differences and similarities, "On one hand, they are remarkably exotic in comparison with the fossil or recent mammals of any other continent, and on the other they parallel these mammals in many features, now considered largely adaptive or secondary, in a way often amazing (Simpson, 1934c: p. 1)".

Florentino Ameghino's major works concerning the Pyrothere Beds (=Deseadan) were published in 1895 and 1897. Ameghino's first contribution (1895) gave descriptions of Deseadan forms found by Carlos mostly from near the Rio Deseado, whereas the specimens of the second contribution (Ameghino, 1897) came largely from Carlos' work at Cabeza Blanca. Some taxa (e.g., Pleurostylodon) first described as having come from the Pyrothere Beds were later recognized by Carlos to represent a distinctive and much older fauna (See Simpson, 1934c). Carlos suggested "Notostylopeén" (=Casamayoran) as the name for the older fauna.

Ameghino (1906: fig. 24) ultimately published a map showing the range of the Pyrothere Beds and the known exposures. These localities and their inferred "connections" includes Carlos' localities which are now known as Cabeza Blanca, La Flecha, and the Gran Barranca. Romero's locality was indicated as a point near the town of Neuquén. Several of Ameghino's Pyrotherium localities have been explored by other teams (see below); however, the Romero site, if it indeed was in Neuquén (see Chaffee, 1952), has not been rediscovered.

Tournouër and Gaudry. In 1898, André Tournouër went to Patagonia to collect fossils (see Simpson, 1984). He fortuitously met Carlos Ameghino in Patagonia who directed him to some of his Pyrotherium localities. Tournouër worked several years in Patagonia, at times side-by-side with Carlos and even with the elder Florentino during his unique visit to Patagonia. Tournouër sent many specimens to Paris where they were studied

Table 1.1. Biochronology of Gaudry (1906):

Age	Stage	Guide Fossils or Diagnostic Taxa
Quaternary	Étage du Pampéen	Macrauchenia
Pliocene	Étage Tehuelche	Galets, Lits d'Hu
Miocene	Étage Santacruzien	Nesodon, Diadiaphorus
Oligocene	Étage Patagonian	Fish, whales, and mollusks
	Deseado:Gisement du Coli-Huapi	Colpodon, Astrapotherium
Upper Eocene	Étage du Deseado	Pyrotherium, astrapothere
Lower Eocene	Étage de Casamayor	Notostylops, Protogonia, etc
----------	Étage Magellanien	oysters Pyrotheriorum
Cretaceous	Étage Guaranien	dinosaurs

Table 1.2. Synonomy of names applied by early twentieth century workers to the early Tertiary land mammal faunas of South America. (Adapted from Simpson, 1933.)

Ameghino, 1906	**Gaudry, 1906**	**Feruglio, 1929**	**Simpson, 1933**
Colpodonéen	du Deseado	Capas con *Colpodon*	Colhué-Huapí
Pyrotheréen		Capas con *Pyrotherium*	Deseado
Astraponotéen	[not distinguished]	Capas con *Astraponotus*	Musters
Notostylopéen	de Casamayor	Capas con *Notostylops*	Casamayor
Notostylopéen Basal	[not distinguished]	Pehuenche	Río Chico

and described by Albert Gaudry (see below). The specimens had been collected along the Rio Deseado, the Gran Barranca, and probably what is now know as Cabeza Blanca.

Gaudry (1906) described much of the Pyrotherium fauna, giving it the locality-based name "Étage du Deseado" after localities located along the Rio Deseado in Santa Cruz province. His Deseado Stage, however, was not equivalent to Ameghino's Pyrotherium beds (contra Loomis, 1914), but a combination of it and the Colpodon faunas of Ameghino (Gaudry, 1906; see Table 1.1).

Gaudry also studied other fossil faunas from Patagonia, both terrestrial and marine. He was impressed at how different the fossil land-mammals were from those of Europe, writing that "Patagonia ... perturbs our belief in the similarity of the course of evolution in the world as a whole (Gaudry, 1906: 101 [English translation from the French in Simpson, 1984: 102])." Evolution in South America appeared to have followed a different course.

Although the unique mammals of Patagonia could not be compared to European fossils for relative dating, the marine fossils were comparable to those of the Old World. Gaudry regarded the "Patagonian Formation" as Oligocene which had major consequences for the ages of the mammalian faunas. If the "Patagonian" marine formation was indeed Oligocene, then the overlying Santacrucian could not be Eocene, as Ameghino had maintained. Gaudry regarded this marine formation as Miocene and considered the Deseado and Casamayoran (=Notostylops Beds) as being in the Upper and Lower Eocene, respectively (Ameghino had believed these later two to be Cretaceous).

Gaudry had standardized the nomenclature of the land mammal ages, upwardly revised their relative ages, and emphasized the unique nature of the mammals of Patagonia. The differences of the mammals of Patagonia could no longer be attributed to their great antiquity, but it was becoming apparent that they had followed a different "course of evolution."

Hatcher and the Princeton expeditions. Support for Gaudry's biochronology came via expeditions of the North American John Bell Hatcher (see Hatcher, 1903, and Simpson, 1984). Hatcher was exceedingly skeptical of Ameghino's theories, particularly in regard to the antiquity of the Deseadan. He led three expeditions to Patagonia and, although he recovered a fabulous Santacrucian (mid-Miocene) fauna, he failed to find Deseadan fossils.

Although Hatcher never found any Deseadan exposures, his work ultimately supported his belief that the Deseadan was Tertiary rather than Cretaceous in a way unexpected by him. Hatcher had collected many invertebrate specimens of the "Patagonian Formation". These marine fossils, along with their excellent field information, permitted a detailed and what appeared to have been the definitive work on the "Patagonian Formation" (Ortmann, 1902). Ortmann concluded that it was Miocene. (The "Patagonian" has come to be regarded as several distinct transgressions of various ages ranging from the Eocene through the Miocene [see Flynn and Swisher [1995] and references therein.)

Loomis and the Amherst College expedition. The Amherst College expedition of 1911 had better luck than Hatcher in finding Deseadan fossils (Loomis, 1913 and 1914). Frederic B. Loomis, along with two Amherst students (Phillis L. Turner and Waldo Shumway) and an experienced field collector from Wyoming (William Stein), went to Patagonia and made a large collection of fossil mammals from Cabeza Blanca, in Chubut.

Loomis indicated that he called upon Florentino Ameghino on his way to Patagonia, but that elder Ameghino was "sick unto death" (Loomis, 1913: 27) (within days, on 6 August 1911, Florentino Ameghino died). Loomis makes no mention of trying to contact Carlos Ameghino and apparently did not meet him, as implied by his uncertainty as to whether the Deseadan locality that he worked was one that Carlos had previously explored (this was, as confirmed by Carlos [Ameghino, 1915]).

Loomis (1914) published a monograph regarding the entire Deseadan which was largely based upon the specimens the Amherst crew collected. He followed Gaudry in calling the "formation" the "Deseado"; however, he equated the Deseado with only the Pyrotherium Beds of Ameghino, whereas Gaudry's concept of the Deseado included both the Pyrotherium and Colpodon Beds.

Loomis (1914) was the first to place the Deseadan in the Oligocene. He believed that the "Patagonian" marine transgression occurred soon after the Deseadan since he had found fossil mammal bones in the lowest part of the Patagonian Formation which had been bored into by marine invertebrates (Cabeza Blanca is topped by the marine "Patagonian"). He was confident that these fossils had originated in the Deseadan beds but were later bored into during the earliest part of the Patagonian transgression. Based on the work of Ortmann (1902), he assumed an early Miocene age for the "Patagonian" Formation and thus deduced that the Deseadan was Oligocene.

Although Loomis seemed to follow the developing consensus that South America was isolated during much of the Cenozoic, he did not support Gaudry's assertion that Pyrotherium was of a uniquely South American order. Instead, he (Loomis, 1914) followed Ameghino and referred Pyrotherium to Proboscidea. He did not, however support Ameghino's notion that notohippids were ancestral to equids.

Riggs and the Marshall Field Paleontological Expedition to Patagonia. Deseadan exposures were next explored by Elmer S. Riggs, who led the "Marshall Field Paleontological Expedition to Patagonia" from 1922 to 1924 (see Marshall, 1978) (Subsequently, Riggs led a second expedition to Bolivia). Riggs and his crew collected Deseadan specimens at La Flecha, Pico Truncado, the Gran Barranca, and Cabeza Blanca. Many of the Deseadan specimens were later described by Bryan Patterson.

Patterson's works regarding Deseadan mammals include descriptions of upper cheek-teeth of notoungulates (Patterson, 1934a), a description of specimens of Trachytherus spegazzinianus from Cabeza Blanca (Patterson 1934b), the description and naming of a new notohippid (Argyrohippus praecox) from La Flecha (Patterson, 1935), descriptions of internal ear structures of some notoungulates, including those of a Deseadan notohippid and leontiniid (Patterson, 1936), descriptions of a Deseadan notohippid brain cast (Patterson, 1937), and a description of an adianthid (Litopterna) from Cabeza Blanca (Patterson, 1940). In addition to the Deseadan material of the Marshall Field expedition, his studies were aided by fossils found during the Scarritt Patagonian Expeditions of the American Museum of Natural History.

Simpson and the Scarritt Patagonian Expedition. The stated purpose of the Scarritt Patagonian Expedition was to explore pre-Deseadan horizons in Patagonia and do a "similar service" (Simpson, 1932: 1) for the Mustersan and Casamayoran as Loomis and Riggs had for the Deseadan. For stratigraphic purposes, the Scarritt team made collections at Deseadan and Colhuehuapian localities with the agreement that the American Museum of Natural History staff would revise the earlier faunas and leave the revision of the Deseadan and Colhuehuapian to the Field Museum. Although it took him over 30 years, Simpson completed the "Beginnings of the Age of Mammals", which was published in two parts (Simpson, 1948 and 1967). In preparation for the major revision of the Deseadan, Patterson visited the MACN in 1951 where he studied and cataloged many Deseadan specimens. Patterson's work regarding the Deseadan remained unfinished at his death in 1979.

The Scarritt team was led by G. G. Simpson, and consisted of C. S. Williams and a number of various local assistants (see Simpson, 1934b). The first expedition occurred in 1930-31 and the second in 1933-34. During this second expedition, a new Deseadan fauna was discovered at Rinconada de los Lopez and has come to be know as "Scarritt Pocket", named for the expedition's patron (H. S. Scarritt). The most conspicuous member of this fauna was a large-bodied leontiniid which Simpson named as a new genus, Scarrittia (Simpson, 1934a) (incredibly, Simpson designated the type as a specimen left in the field, despite the fact that many other fine specimens had been collected).

Simpson (1933) revised the nomenclature of the early Tertiary, providing a "Rosetta Stone" for the "stages" of early workers (Table 1.2). His

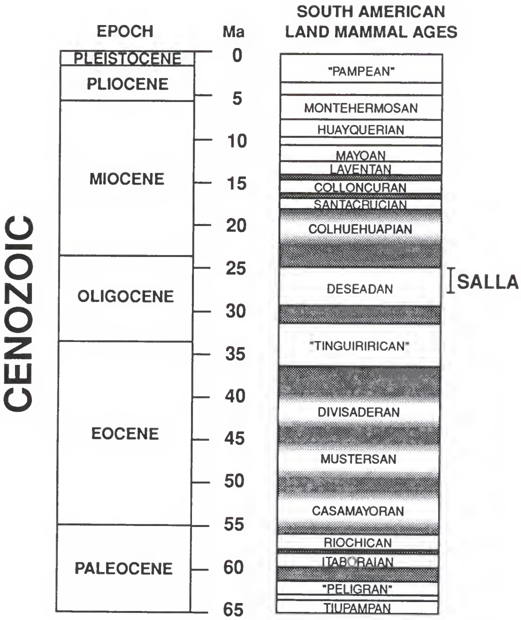

Figure 1.1. South American Land Mammal Ages (SALMAs) as currently conceived. (Modified from Flynn and Swisher, 1995.)

attempt to stabilize the nomenclature was successful as evidenced by the fact that his terminology is still in use (See Figure 1.1).

Recent studies. Regarding the Deseadan SALMA, Simpson (1940) regarded it as early Oligocene. Later radiometric studies of Deseadan localities in Patagonia initially supported this assignment. Several workers (Marshall, et al., 1977; Marshall and Pascual, 1978), based on radiometric data, placed the upper temporal limit of the Deseadan of Argentina at about 34 Ma.

Spalletti and Mazzoni (1978) found and obtained a radiometric date from a basalt within the Deseadan level of the Gran Barranca. The oldest date they obtained was 28.8 ± 0.9 Ma, suggesting that the Deseadan ranged up into the middle Oligocene. Andreis (1977) likewise had reported younger ages from a Deseadan locality (Cañadón Hondo), but listed three different ages on three different pages of his work (24 ± 3, 28 ± 3, and 29 ± 3 Ma). Marshall (1982) concluded that the Deseadan of Patagonia ranged from earliest to middle Oligocene, or from about 36 to 27 Ma. Work at the Deseadan locality of Salla, Bolivia would soon stimulate more refinements in the age of the Deseadan.

Exploration of Salla (1962 to present)

In 1962, G. Bejarano discovered fossils in the Salla-Luribay Basin which is located in the Departamento de La Paz, about 90 km southeast of La Paz, Bolivia (Hoffstetter, 1968). These, the Salla Beds, were prospected from 1964 to 1966 by Leonardo Branisa, who collected fossils for Princeton University. His discovery of the Deseadan Pyrotherium in Bolivia was first announced by Baird et al. (1966). Robert Hoffstetter went with Branisa to Salla in 1965 and soon after published the first reasonably complete faunal list (Hoffstetter, 1968). Noting genera that were otherwise known only from the Deseadan of Patagonia, he concluded that the Bolivian fauna establishes "le synchronisme des Couches de Salla avec le Déséadien de Patagonie (1968: 1)". Following the convention of the time, he assigned this Deseadan fauna to the lower Oligocene.

Hoffstetter and colleges described some of the taxa in further detail, including rodents (Hoffstetter and Lavocat, 1970), marsupials (Hoffstetter and Petter, 1983), and the then, and still, oldest primate known from South America, Branisella (Hoffstetter, 1969). Hoffstetter et al. (1971) also reported other Deseadan localities in the vicinity of Salla and another, Lacayani, 50 km to the northwest.

Hartenberger and Villarroel also worked at Salla with Hartenberger (1975) describing more of the rodent fauna. In his visits to Salla, Villarroel began recording locality and stratigraphic information of the fossil bearing units (Villarroel and Marshall, 1982). He noted a conspicuous ash that was exposed throughout much of the region and thus served as a stratigraphic marker horizon. This he named the "Nivel Guia" (Villarroel and Marshall, 1982).

The University of Florida's involvement at Salla began in the late seventies, when Ron Wolff of the Department of Zoology and a recent graduate, Ken Campbell, planned paleontological field work in Bolivia. To determine the feasibility of the project, Wolff and Campbell mounted a self-financed expedition to Bolivia in 1978. They, along with Carl David Frailey, then a student at the University of Kansas, explored the Quaternary localities Tarija and Ñuapua. They also briefly visited Salla.

They returned to Salla was in 1981. Bruce MacFadden joined the team and since Campbell had moved on to the Los Angles County Museum the work had become a joint UF-LACM project with funding from the National Science Foundation. Carlos Villarroel, then of GEOBOL, joined MacFadden, Wolff, and Campbell for the 1981 field season and showed them some of the localities that he had previously worked. Felix Vargas, of Salla, who had served as an assistant to Branisa, also worked that field season.

Their second day in the field MacFadden found a maxilla containing M1-3 of "Branisella" (this specimen would later become the holotype of Szalatavus attricuspis Rosenberger et al. 1991), thus the horizon from which it came was named the "Branisella Level". MacFadden also began collecting paleomagnetic samples.

MacFadden and Campbell returned to Salla in 1984 (crew members included Gary Morgan and Roger Portell of UF, Gonzalo Barriga and Armando of GEOBOL, Richard Cifelli of the University of Oklahoma, and Felix Vargas of Salla).

Meanwhile, a Japanese team had obtained ash samples from Salla and reported fission-track (zircon) ages of 51.8 ± 2.6 and 54.0 ± 2.4 Ma (Hayashida et al., 1984), 15 - 20 million years older than expected.

MacFadden soon had the paleomagnetic samples analyzed for the pending 1985 manuscript and Cifelli summarized the fauna. Peter K. Zeitler performed ^{40}K-^{40}Ar analysis and Naeser examined the zircons from the ash to determine the fission track ages. Given that it seemed established that the

Deseadan was early Oligocene, the investigators expected fission track and ^{40}K-^{40}Ar ages of about 35 Ma. In anticipation of this, MacFadden had been tentatively correlating the Salla paleomagnetics with early Oligocene chrons. He was surprised when Noye Johnson called to report fission tracks ages of about 22 Ma. Assuming that these were in error, MacFadden awaited the ^{40}K-^{40}Ar results. These too conflicted with an early Oligocene age. The ^{40}K-^{40}Ar age was about 26 Ma (see Table 1.3 for summary of radiometric ages of Salla).

Their report of a late, rather than early, Oligocene age for the Deseadan was initially and informally greeted with considerable skepticism, but direct and indirect support soon followed. Hayashida and Danhara (1985) reanalyzed the ash samples of Hayashida et al. (1984) using the external detector method (Naeser, 1979) rather than the re-etch method originally used. This resulted in age determinations ranging from 27.2 - 24.0 Ma, rather than the Eocene ages. Naeser et al. (1987) confirmed the early Oligocene age by way of ^{40}K-^{40}Ar ages of 28.0 - 25.1 Ma and fission track ages of 34.5 Ma from the base of the section to 23.5 form the upper regions. Indirect support for the late Oligocene interpretation came from Marshall et al. (1985), who reported even younger radiometric ages (23.4 -21.0 Ma) for Scarritt Pocket.

UF expeditions continued, with field crews working in 1986 (crew included MacFadden, Morgan, Portell, and Heidi Sydow of UF, Federico Anaya Daza then of GEOBOL, and Noye Johnson and Lee McRae of Dartmouth College) and in 1987 (MacFadden, Morgan, Portell, McRae, William Wall of Georgia College, Michale Whitelaw, and Jeffery Walker of the University of Pennsylvania). In 1989, severe altitude sickness prevented a graduate student from accomplishing a proposed study of the paleosols of

Table 1.3. Summary of the radiometric ages derived from ash samples of Salla are given below. The radimetric techiques used include isotopic techniques (^{40}K-^{40}Ar and ^{40}Ar-^{39}Ar) and fission track analysis of zircons.

Horizon (Unit)	**Method**	**Source**	**Age (Ma)**
Unit 8	fission track	MacFadden et al., 1985	22.0 ± 2.0
Unit 7	fission track	MacFadden et al., 1985	22.2 ± 1.9
Unit 6-7	^{40}Ar-^{39}Ar	Kay et al., 1995	24.8 ± 0.3
Principal Guide	^{40}K-^{40}Ar	Naeser et al., 1987	25.1 ± 0.7
Principal Guide	^{40}K-^{40}Ar	MacFadden et al. 1985	26.4 ± 1.0
Principal Guide	^{40}Ar-^{39}Ar	Kay et al.,1995	24.9 ± 0.5
Unit 2	^{40}Ar-^{39}Ar	Kay et al., 1995	27.8 ± 2.7
Unit 1	^{40}K-^{40}Ar	Naeser et al., 1987	28.0 ± 0.9
Unit 1	^{40}K-^{40}Ar	Naeser et al., 1987	27.2 ± 3.6
Unit 1	^{40}K-^{40}Ar	Naeser et al., 1987	27.9 ± 0.9
Unit 1	fission track	Naeser et al., 1987	24.2 ± 3.6
Unit 1	fission track	Naeser et al., 1987	23.5 ± 2.2
Unit 1	fission track	Naeser et al., 1987	34.5 ± 4.0

Salla. MacFadden, Anaya, along with Thure Cerling of the University of Utah, visited the site in 1990 to collect soil samples for stable isotope studies.

MacFadden, Anaya, and I visited Salla briefly in March of 1992. I returned later in the year (May-June) with Morgan and Portell of UF, Anaya, then (and now) with MNHN-Bol, and Bolivian students Rafael "Burro" Flores Alba and Juan Carlos Butron. During this season, we found several juvenile specimens of Trachytherus and a juvenile notohippid (see Chapter 5). Portell found a notohippid skeleton (Chapter 3 and 5).

A much larger crew returned in 1994. This joint MNHN-Bol/UF/Duke University was composed of up to 15 people with the three institutional leaders being Anaya, MacFadden, and Richard Kay. During this expedition, several more specimens of Branisella were found and are currently being studied by Kay. On the evening of 8 June we received a reminder of the tectonic forces that shaped the region. Our camp was shaken by a rather conspicuous earthquake. We later learned that it had a magnitude of 8.3.

Geography and Geology of Salla

The Salla Beds are located at the interface of the Altiplano and the Eastern Cordillera of the Andes, 90 km southeast of La Paz, in the Departamento de La Paz. The exposures are just to the west of the Aymaran community of Salla which has an elevation of 4000 m at about 17°10′20″ South latitude and 67°36′42″ West longitude. The Salla Beds erode to a "badlands" topography, being cut by numerous "quebradas" (arroyas) that only flow during the rainy season (the austral summer). These drain to the north, into the Río Mullakha Jahuira, which flows year-round. The Río Mullakha Jahuira in turn flows northeast to the Río Luribay and, ultimately, into the Amazon.

Tertiary sediments, known collectively as the Salla-Luribay Basin (e.g., Villarroel and Marshall, 1982), lie nonconformably within the Devonian basin. These are oriented in a NNW to SSE direction, with a present-day altitude ranging from about 3300 to 4000 m.

The Luribay Conglomerates forms the base of the Tertiary sediments (Ahlfeld and Branisa, 1960; Fig. 1.2). These are exposed as vertical walls along the Río Mullakha Jahuira, where they may be up to 150 m thick. These are formed by pebble to large cobble-size stones (a few to 500 mm diameter) stones. Hoffstetter (1976) had considered these conglomerates to be of Eocene age. This age assessment was based on an unvouchered specimen of unknown taxonomic designation, other than the anecdotal report that it was a notoungulate. Hoffstetter was also likely influenced by the assumption that the Deseadan was early Oligocene in estimating the age of the Luribay Conglomerates. In 1995, Ruben Andrade and I prospected the Luribay Conglomerates where they are exposed the Rio Mukalah Jahuiria. We failed to find any fossils, so this formation still lacks biostratigraphic as well as radiometric data to aid in an age determination.

The gradational contact between the upper Luribay Conglomerates and lower tuffs of the Salla Beds suggests a gradual change from the deposition of large clasts to the fine-grained sediments characteristic of Salla. This intermittent, gradational change implies that the Luribay Conglomerates is not of much greater antiquity than the Salla Beds.

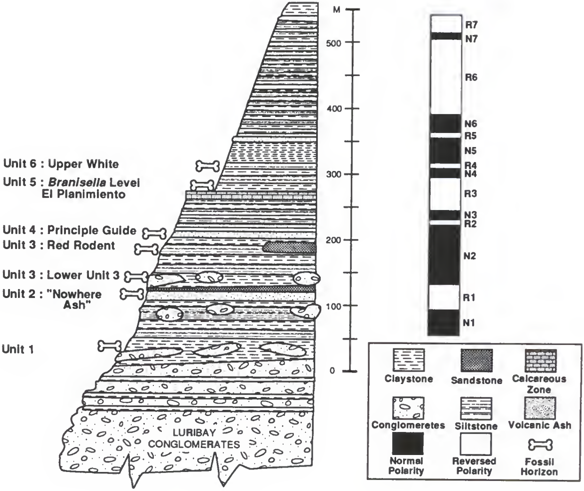

Figure 1.2. Composite stratigraphic section of the Salla Beds of Bolivia. (Adapted from MacFadden et al., 1985.)

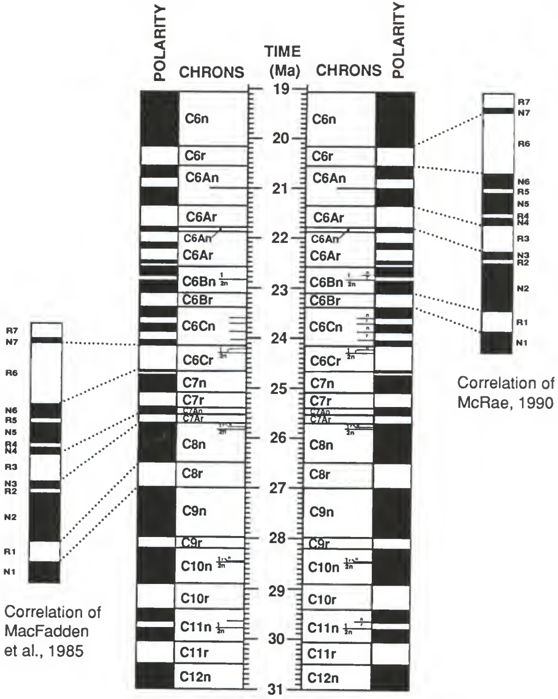

Figure 1.3. Paleomagnetic reversals of MacFadden et al. (1985) from Salla. The interpretation of MacFadden et al. is shown at left, correlatated with the revised global paleomagnetic time scale of Berggren et al. (1995). The interpretation of McRae (1990) is given in the upper right.

The fossiliferous Salla Beds overly the Luribay Conglomerates, with some conglomerates being deposited after its initiation. The predominant sediments of the Salla Beds are claystones and siltstones, but horizons of sandstone, limestone, and ash are also present (see Hoffstetter, 1976; Villarroel and Marshall, 1982; MacFadden et al., 1985; and Fig 1.2). A conspicuous carbonate exposed at Tapial Pampa and just below Cero Poco Poconi is called the "El Planimiento". It is a relatively durable stratum that formed some of the few flat surfaces at Salla. The El Planimiento immediately underlies the Branisella Level. Ashes occur at several levels throughout the beds. These occur at the lower sections, up through the Principal Guide, and again at the Upper White and in the upper, fossil-poor regions. Several of these ashes have yielded isotopic or fission track ages (see Table 1.3).

MacFadden et al. (1985) noted the conflict between the isotopic and fission track ages, with the fission track ages generally being somewhat younger than the isotopic ages of the same ashes. They elected to use the older isotopic date to correlate the paleomagnetics, in part, because their sixth magnetic reversal (R6) occupied a large range (presumably a long period of time), as did the upper Oligocene Chron C6 (C6Cr of Berggren et al., 1995) (Fig. 1.3).

McRae (1990) restudied the paleomagnetics of Salla, collecting at the same localities that MacFadden had in 1981 and reported in MacFadden et al. (1985). Her correlation of the the Salla samples with the magnetic time scale relied on the fission track ages rather than the ^{40}K-^{40}Ar dates. This resulted in an interpretation in which the entire sequence was correlated within

Chron 6, giving the Salla Beds an age about 4 million years younger than that proposed by MacFadden et al. (1985) (see Fig. 1.3).

Sempere et al. (1990) hypothesized that the deposition of the Tertiary sediments over the Paleozoic bedrock at the Salla-Luribay Basin was related to the "tectonic crisis" that occurred in the region during the late Oligocene and early Miocene. McBride et al. (1983) had described two nearby batholiths (Illimani and Quimsa Cruz) that had become emplaced during the late Oligocene-early Miocene. The Illimani batholith lies to the north of Salla and the Quimsa Cruz to the northeast. Both had granodioritic magma emplaced around 26.9 to 27.5 Ma with a similar event repeating itself at Quimsa Cruz at about 23.6 to 23.9 Ma.

Sempere et al. (1990) argued that the deposition of the Salla Beds occurred during the second pulse (the Quimsa Cruz event at 23.6 - 23.9 Ma), implying that the Luribay Conglomerates would have been deposited during the time of the first pulse (the Illimani-Quimsa Cruz event). The scenario may be summarized as mountain-building at Illimani and Quimsa Cruz promoted run-off that flowed into the Salla-Luribay Basin, depositing moderately large stones during the first pulse. The second phase came from northeast of Salla (Quimsa Cruz), with mud and silt flowing into the basin. In both phases, drainage from the Salla Luribay Basin went to the south (Sempere et al., 1990).

Sempere favored the McRae (1990) magnetic correlation, whereas other workers (Flynn and Swisher, 1995) regard the fission track age as inaccurate and support the late Oligocene age assignment. Recent ^{40}Ar-^{39}Ar ages reported by Kay et al. (1995) also support a late Oligocene interpretation.

Since the absolute age of the Colhuehuapian SALMA is so poorly known (Flynn and Swisher, 1995; and Fig. 1.1) it can not help constrain the age of Salla. It is unlikely that the Salla Beds are contemporaneous with the Colhuehuapian since there is only one genus (Proadinotherium) common to both (compare revised Salla faunal list [Table 8.1] with that of the Colhuehuapian [Marshall et al. 1983: table 8]), whereas numerous genera from the classical Deseadan localities are know from Salla. The upper limit of the Colhuehuapian is no younger than mid-Miocene since it is overlain by an unnamed marine unit that contains the mid-Miocene mollusk Nodipecten sp. (Smith and Zinsmeister, 1982; Marshall et al., 1986). This presents the possibility that the Colhuehuapian is as young as 16-18 Ma, which should provoke skepticism since this is the approximate age for Santacrucian SALMA (Flynn and Swisher, 1995; see Fig. 1.1) a more derived fauna than that of the Colhuehuapian. The point here, however, is that the Colhuehuapian, as presently known, does preclude the Deseadan from the early-Miocene upper limit as suggested by some workers (MacCrae, 1990; Sempere, 1990).

Defining the upper limit of Salla would aid in constraining the lower limit of the Colhuehuapian SALMA since it is underlain by Deseadan beds at the Gran Barranca and because Salla appears to be somewhat younger than Deseadan localities of Patagonia. Although Marshall et al. (1985) had reported a radiometric age of about 21 Ma for Scarritt Pocket, this is regarded as being in error. Flynn and Swisher (1995) reported that Swisher has redated Scarritt Pocket and Pico Truncado and found these to be in the 29-27 Ma range. They indicated that no Patagonian Deseadan locality was younger than 27 Ma, making Salla the youngest Deseadan locality known, even assuming the older interpretation of MacFadden et al. (1985).

In addition to the radiometric data, some biostratigraphic evidence suggest a younger age for Salla than Scarritt Pocket. Archaeohyracids make their last appearance in the Deseadan, are quite abundant at the Branisella Level of Salla, but are nonexistent in the adjacent Upper White (see Chapter 7). Scarritt Pocket lacks the stratigraphic depth of Salla, but does contain archaeohyracids (see Chaffee, 1952), suggesting that it is as old or older than the mid-section of Salla. (Of course the disappearance of archaeohyracids from Salla may represent a local extinction, but it is noteworthy that a continental extinction of this family appears to have occurred before the Colhuehuapian.)

Although the Sempere et al. (1990) model is attractive for its explanation of both the timing and process of deposition of the Salla-Luribay Basin, this work will follow the interpretation that Salla is late Oligocene (MacFadden et al., 1985; Kay et al., 1995; Flynn and Swisher, 1995). This is based upon not just a mere bias for isotopic dating over fission track, but that two methods of isotopic dating (^{40}K-^{40}Ar and ^{40}Ar-^{39}Ar) yield similar ages. Incidentally, the isotopic and paleomagnetic data are in better agreement with the recent revision of the standard paleomagnetic time scale of Berggren et al. (1995). For example, the assignment of the lower section of Salla to C10r implied an upper limit age of about 30 Ma on the Berggren (1985) scale, whereas the ^{40}K-^{40}Ar age at this section is 27.2 ± 0.9 Ma. The paleomagnetic age of C10n1r of the revised scale is about 28.5 Ma, close to the margin of error for the ^{40}K-^{40}Ar age calculated from that horizon.

One minor point to be made for the interpretation of the late Oligocene age for Salla is that it provides more time for the evolutionary changes seen between the Deseadan and the Colhuehuapian. An early Miocene Deseadan would seem to "squeeze" the Colhuehuapian between the Deseadan and Santacrucian.

The late Oligocene age hypothesis for Salla implies that the Illimani-Quimsa Cruz pulse (27.5-26.9 Ma) occurred during the deposition of the lower section of Salla, about the time that the "Nowhere" ash was deposited; probably no later than the deposition of the Principal Guide and not much earlier than the time of deposition of the lowest ashes of Unit 1 (see Table 1.3). An apparent disadvantage of the late Oligocene age hypothesis for Salla is that it would fail to explain the deposition of the Luribay Conglomerates, an event that must have been conspicuous given the size of the rocks deposited and the thickness of the section (up to 150 m). This deposition, however, could have been fairly rapid, occurring just prior to the deposition of the lowest horizons of the Salla Beds.

The late Oligocene hypothesis for Salla implies that the second tectonic pulse (the Quimsa Cruz event of 23.6 - 23.9 Ma) occurred after the deposition of the Salla Beds, since the uppermost horizons appear to be older than the this tectonic event. McRae (1990) speculated that the deposition at Salla ceased because the region had been uplifted. If so, this uplift would have occurred around the time of the second pulse, suggesting that they may be related. That is, the initial uplift of Salla may be a result of the same tectonic forces that gave rise to Quimsa Cruz (the second pulse). For sure, the Salla-Luribay Basin has been uplifted to its present and considerable altitude.

A hypothetical scenario of the late Oligocene of the Salla-Luribay Basin, based on a synthesis of Sempere (1990), McBride (1987), McCrae (1990), but with the ages of MacFadden et al. (1985), is as follows:

1) (27.5 Ma) A major mountain building event occurred in the region of Illimani and Quimsa Cruz beginning around 27.5 Ma. These regions to the north and east of Salla were uplifted, sending run-off down a montane river which flowed through the Salla-Luribay Basin. The larger sediments (cobbles) settle in the Salla-Luribay Basin with water and lighter sediments flowing south to the newly forming mid-Andean Basin, the precursor to the Altiplano. The Luribay cobbles accumulated rapidly.

2) (27.5 - 25 Ma) Following initial and rapid deposition of cobbles and boulders in the Salla-Luribay Basin, lighter sediments accumulate as the rate of mountain-building to the north and east diminishes. Intermittent volcanic activity continues such that the region is occasionally covered in ash.

3) (≈25 Ma) Once the basin fills to the El planimiento level, deposition slows such that carbonates begin to form. This is a temporary condition, possibly due to a blockage of sediment flow from the nearby newly formed heights.

4) (25 - 24 Ma) Sediment flow into the basin resumes.

5) (23.9 Ma) A second mountain building phase begins around 23.9 Ma. The Salla Basin itself is uplifted to such an extent that deposition of sediments within the basin ceases.

Stratigraphic Nomenclature

The nomenclature used for the stratigraphic horizons at Salla is based on the field observations of MacFadden (field notes), which were loosely based on the work of Villarroel (summarized in Villarroel and Marshall, 1982). The complete section is numbered from bottom to top with conspicuous horizons serving as boundaries (see Fig. 1.2). See Table 1.4 for complete list of UF localities.

Unit 1: The lowest exposures, just above the Luribay Conglomerates up to the "Nowhere Ash" form Unit 1. The lower boundary of Unit 1 is somewhat ambiguous due to the interbedding of the conglomerates with the base of the finer grain sediments that are characteristic of the Salla Beds. The upper boundary of Unit 1 ends just below the "Nowhere Ash".

Unit 2: Horizons among the "Nowhere Ash" form Unit 2.

Unit 3: Unit 3 begins above the "Nowhere Ash" and extends to the Principal Guide Level. Much of the upper horizons of Unit 3 is composed of red sediments that produce many rodents. This is informally referred to as the "Red Rodent Zone".

Unit 4: The ash layers of the Principal Guide and the interbedded sediments form Unit 4.

Unit 5 begins above the Principal Guide and terminates just below the Upper White Level. The El planimiento carbonate is exposed in many regions of Unit 5. Just above the El planimiento is the horizon from which all the specimens of Branisella for which there is stratigraphic data came. This horizon is call the Branisella Level.

Table 1.4. Localities of Salla, Bolivia listed in the UF “site” file.

UF Nº	Locality Name	Stratigraphic Level	GPS data
YB 028	Alpha Pata North	“highest strat. level”	
YB 093	Aramani	Level 3	
YB 094	Calaboza Pata	Principal Guide Level	
YB 055	CalabozaPata, South	Branisella Level	
YB 054	Calaboza Pata, South	Principal Guide Level	
YB 081	Calaboza Pata West	Red Rodent Level	
YB 001	Calaboza Pata (east of cul de sac)	Red Rodent Level	
YB 080	Calaboza Pata	Red Rodent Level	17°10.22’ S 67°37.68’ W
YB 056	Calaboza Pata (south of cul de sac)	Red Rodent Level	
YB 082	Calboza Pata East	Red Rodent Level	
YB 090	Ciudad de los Cranios	Branisella Level	17°11.17’ S 67°37.50’ W
YB 095	Ciudad de los Cranios	Upper White	
YB 103	Poco Pocoi, far north	----------------	
YB 096	Huichinca	Branisella Level	17°10.87’S 67°37.65 W
YB 053	Huichinca	Upper White	
YB 097	Irupata Loma	Branisella Level	
YB 098	Irupata Loma	Upper White Level	
YB 047	Chaccha Tapial Chuchu	Branisella Level	17°11.46’S 67°37.37 W
YB 052	Jacha Huay Kallumi	Upper White	
YB 087	Jacha Huay Kallumi	Branisella Level	
YB 026	Jiska Tapial Chuchu	Upper White level	
YB 083	Kara Tranca Pata	----------------	
YB 050	Kara Tranca Pata	Principal Guide Level	
YB 051	Kara Tranca Pata	Red Rodent Level	
YB 024	Pasto Grande	(unspecified)	
		“camp” GPS	17°10.17’S 67°38.72 W
YB 068	Pasto Grande	Principal Guide Level	
YB 048	Pasto Grande	Unit 1	
YB 085	Pasto Grande	Unit 2	
YB 049	Pasto Grande	Units 4-5	
YB 045	Poco Poconi	Principal Guide Level	17°09.74’S 67°37.98 W
YB 032	Poco Poconi	Branisella Level	
YB 100	Poco Poconi, North	Upper White Level	
YB 099	Poco Poconi, East	Unit 3	
YB 046	Poco Poconi, West	Branisella Level	
YB 031	Poco Poconi, West	Red Rodent Level	
YB 084	Poco Poconi	Branisella Level	
YB 002	Quebrada Chala Jahuira	Buff Rubbly (Unit 1)	
YB 039	Salla (unspecified)	(unspecified)	

Table 1.4. Continued.

UF Nº	Locality Name	Stratigraphic Level	GPS data
YB 030	Sebada Chura Pata	Upper White	
YB 027	Sici Lomo Cayo, east	Red Rodent Zone (base)	
YB 025	Sici Lomo Cayo, west ("Japanese 'primate' locality")	50 m below Principal Guide Level	
YB 076	Sici Lomo, west	Red Rodent Level	
YB 040	Tapial Pampa	(unspecified)	
YB 041	Tapial Pampa East	Branisella Level	
YB 021	Tapial Pampa East	Upper White Level	
YB 101	Tapial Pampa East	Unit 7	
YB 042	Tapial Pampa West	Branisella Level	17°11.18'S 67°37.35 W
YB 022	Tapial Pampa South	Upper White Level	
YB 023	Tapial Pampa West	Upper White Level	
YB 044	Tapial Pampa	Branisella Level	
YB 043	Tapial Pampa	Upper White Level	
YB 102	Toloma	(uncorrelated; highest level of Villarroel)	
YB 029	Willa Kkollu	Unit 1 (base)	17°10.39'S 67°39.16 W

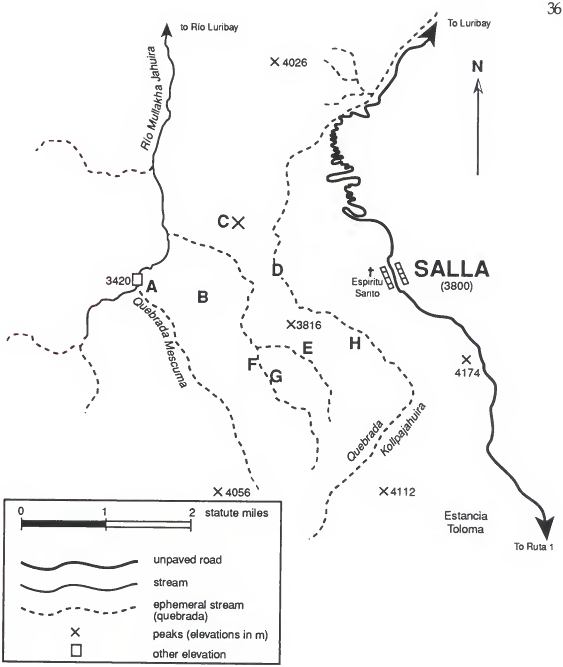

Figure 1.4. Map of the Salla Beds showing the drainage and UF localities discussed in the text: A) Willa Kkollu, B) Pasto Grande, C) Cerro Poco Poconi, D) Caloboza Pata, E) Tapial Pampa, F) "Ciudad de los Cranios", G) Chaccha Tapial Chuchu, H) Iru Pata Loma

Unit 6: The layers of "pop corn" (bentonitic) ash about 15 m above the El Planimiento compose Unit 6.

Horizons above Unit 6 have produced very fossils. None are referred to in this work.

Fossil Localities

In addition to the general Salla designation, nineteen localities are named in the UF site files, most of which expose more than one horizon and thus have separated designations (see Table 1.4). These localities are not of equal areas nor are they evenly represented by specimens in the UF and MNHN-Bol collections. Most of the specimens have come from relatively few localities, several of which have been extensively collected. Summary statements are given for these fossiliferous sites. Their general positions are indicated on the map (Fig. 1.4).

The base of the Salla Beds are exposed at Willa Kkollu (Fig. 1.4A). These may be seen overlying the Luribay Conglomerates which are exposed along the nearby Rio Mullakha Jahuira. These sediments show prominent folding where Quebrada Miscuma meets the Río Mullakha Jahuira.

Pasto Grande (Fig. 1.4B) covers a broad area to the east of Willa Kkollu. Much of the lower horizons, Units 1, 2, and 3, are exposed in this region.

The Principal Guide, Unit 5, including "El Planimiento and the Branisella level are exposed at Cero Poco Poconi (Fig. 1.4C). (Local names of geographic features are followed. The Poco Poconi referred to here is not the Poco Poconi of the U. S. Army Topographic Command map (copied from

Instituto Geográfica Militar sheet 6042 II), which is the elevation point (3816 m) near Tapial Pampa (Fig. 1.4E). Our Poco Poconi is located at 17° 09.83′ S and 67° 37.94″ W.

A large section of the "Red Rodent Zone" of Unit III is exposed at Caloboza Pata (Fig. 1.4D). The Principal Guide is also exposed in this area.

The most extensively collected area is the Tapial Pampa region (Fig. 1.4E) (the area from which the "El Planimiento" section of MacFadden et al. [1985] was taken). It contains long exposures of the El Planimiento, Branisella, and Upper White levels. The flats atop the El Planimiento often serve as the area for base camp. Tapial Pampa is bisected by a deep quebrada that seasonally flows to the northwest to the Rio Mullakha Jahuira. The area on the northeast side is referred to as Tapial Pampa East, whereas the southwestern region is named Tapial Pampa West.

Important localities in the region of Tapial Pampa include "Ciudad de los Cranios"(Fig. 1.4F), Chaccha Tapial Chuchu (Fig. 1.4G), and Irupata Loma (Fig. 1.4H). These sites have exposures of the Branisella and Upper White levels, with portions of Unit 5 below the "El Planimiento" being exposed in the quebradas.

CHAPTER 2
MATERIALS, METHODS, AND DEFINITIONS

Materials

The notoungulates described in this work were collected at Salla between 1981 and 1994 and are housed and curated at the Museo Nacional de Historia Natural (MNHN-Bol) in La Paz, Bolivia, and the Vertebrate Paleontology collection of the Florida Museum of Natural History (UF), Gainesville, Florida. Additional Salla specimens studied are from the Princeton University Collection at the Yale Peabody Museum, New Haven, Connecticut. Data were also obtained from specimens from localities of Argentina, these being curated in several museums in South and North America. These institutions with their abbreviations are given in Table 2.1.

Several of the taxa described in this work represent new, unnamed species. Although proposed holotypes are designated, the formal naming of these taxa is deferred for publication in a format more accessible to paleomammalogists. The naming of two of the notohippid species described in this work will be published in the Journal of Vertebrate Paleontology (Shockey, in press). The two new leontiniids are being named in a work in progress.

Cumbersome designations such as "leontiniid species A" will be used to discriminate among the taxa. The disadvantage of this clumsiness is judged to be outweighed by the advantage of formally naming these taxa in a readily accessible medium.

Table 2.1. Institutional Abbreviations

ACM, Pratt Museum at Amherst College, Amherst, Massachusetts
AMNH, American Museum of Natural History, New York
FMNH, Field Museum of Natural History, Chicago, Illinois
GEOBOL, Servicio Geológico de Bolivia, La Paz, Bolivia.
MACN, División Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina;
MLP, División Paleontología Vertebrados, Museo de La Plata, Argentina;
MNHN-Bol, Museo Nacional de Historia Natural, La Paz, Bolivia;
PVL, Coleción de Paleontología de Vertebrados Instituto Miguel Lillo, Universidad Nacional de Tucumán, Argentina;
UF, Vertebrate Paleontology Collection, Florida Museum of Natural History, University of Florida, Gainesville, Florida.
YPFB, Yacimientos Petroliferos Fiscales Bolivianos collection in Santa Cruz, Bolivia.

Dental Measures and Terminology

As is usual in paleomammalogy, teeth were important structures for determining taxonomy, phylogeny, and function. These organs provided both qualitative and quantitative information.

The terminology used to describe notoungulate dental characters is topographically based, but is intended to demonstrate homologous structures with the presumed isotemnid outgroup (Simpson, 1967; Cifelli, 1993) and with other notoungulates. This terminology is most influence by the mid-century students of South American paleomammalogy Simpson (e.g., 1932) and Patterson (1934a). Their system is fundamentally trituberuculate, though the phylogenetic distance from other eutherians reduces the confidence that even these basic cusps are homologous with similar structures in other mammalian orders (see below).

The comparison of notoungulate teeth is frustrated by the extreme changes in occlusal patterns that occur with development and wear (see Chapter 5) and the trend for teeth to become less complex in several notoungulate lineages. Some become simplified to such an extent that the occlusal surfaces of their teeth are little more than featureless ovoids (e.g., hegetotheriids). Simplified dentitions occur in notohippids (e.g., Eurygenium), mesotheriids, archaeohyracids, interatheriids, and hegetotheriids, almost all of the notoungulates of Salla. The tooth crowns of Proadinotherium (see Chapter 3) retain identifiable features with wear; however, geologically younger, more advanced toxodontids ultimately develop simplified crown patterns (e.g., Toxodon). The general trend toward loss of crown features in various notoungulates is best illustrated by Cifelli (1993: fig. 15.6).

The dentition of the isotemnid Pleurostylodon is used as the sister-taxon to the Toxodontia in this study. These teeth are also used as a model to identify homologies among the taxa studied (see Fig 2.1). This choice is appropriate since isotemnids are believed to be ancestral to the Toxodontia and possibly Typotheria (see Cifelli, 1993). Also, I had available for study a cast of AMNH 28636, a specimen of Pleurostylodon sp. in which the dentition was completely unworn.

The disadvantage of using the isotemnid as a model is that it is phylogenetically and temporally distant (Casamayoran) from the taxa under study. This is particularly problematic with the isotemnid lower molars which lack a paraconid and have a trigonid cuspule (metaconulid) unknown in the Deseadan taxa. A closer model for an outgroup for the advanced Toxodontia of Salla is not available, largely due to the depositional hiatus that occurred before the Deseadan.

The upper premolars and molars (for convenience and readability, the informal terms "cheek-teeth" will be used for generic discussions of postcanine teeth) of Pleurostylodon show the major cusps and lophs that will be discussed. Though these cusps may not represent the homologous structures of other eutherian mammals, particularly the hypocone (Patterson, 1934a and references therein), the terms are used as topographic indicators. They are intended, however, to indicate homologous structures within the Notoungulata. See Table 2.2 for the list of dental terms and their abbreviations.

The molars develop a "hypocone," which Patterson (1934a) believed represented a posterior division of the protocone. Regardless of its genesis, the posterolingual molar cusp will be denoted as the hypocone since this topographic designation is unambiguous, parsimonious, and consistent with the interpretation of homologies given in Chapter 4.

Figure 2.1 illustrates the major cusps and lophs in the upper molar of an isotemnid (2.1A) and a slightly worn notohippid molar (2.1B). The major lophs are the ectoloph, protoloph, and metaloph. A crochet arises from the metaloph anterolabially such that it meets the internal wall of the ectoloph or a cristae (small crest) which arises from the ectoloph. The molars have a hypocone which is often distinct from the protocone until advanced wear. In unworn molars, the separated proto-hypocones appear as lingual infoldings

Table 2.2. Dental Abbreviations

ant; anterior
B/ b; "breadth" or transverse dimension of incisors and incisiform canines.
Cg/cg; upper/lower cingulum
Cr; cristae
Crch; crochet
D/d; "depth" or anteroposterior dimension of upper/lower incisors and incisiform canines
Eclh; ectoloph
entlph *f*; entolophid fossettid
L/l; anterior posterior length of upper/lower post-canine teeth
lbl; labial
lng; lingual
HI; hypsodonty index of upper molars
hi; hypsodonty index of lower molars
HC; hypocone
hypolph; hypolophid
I,C,P,M; upper incisors, canines, premolars and molars respectively
i,c,p,m; for the appropriate lower teeth
Mc; metacone
Mtlh; metaloph
mc; metaconid
mm; millimeter
PC; paracone
pc; paraconid
PCR; paracone ridge
PCRH; paracone ridge height
PCL; protoconule
PMW; premaxilla width
PMW$_{max}$; max. premaxilla width
post; posterior
Post. Cg; posterior cingulum
Post *f*; posterior fossette (upper)
post *f*; posterior fossettid (lower)
PrC; protocone
PRLH; protoloph
Ps; parastyle
PW; palatal width
tal; talonid
tri; trigonid
tri-tal *f*; trigonid-talonid fossettid
W/w; transverse width of upper/lower postcanine teeth.

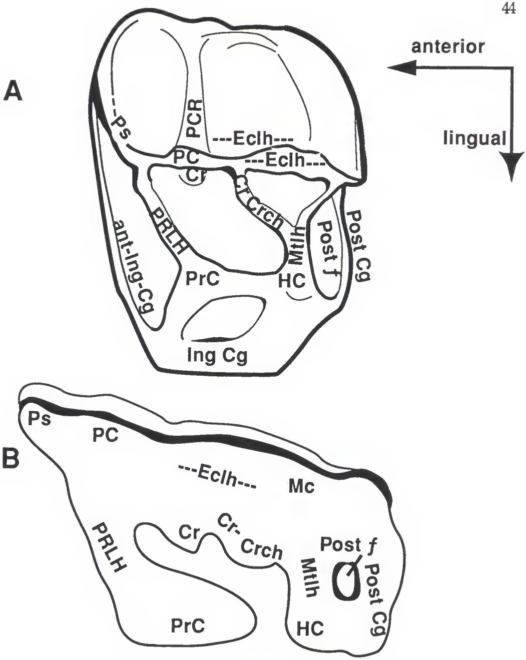

Figure 2.1. Terminology to describe upper post canine teeth. Molar A is based upon the isotemnid out-group (Pleurostylodon) and molar B is a somewhat worn notohippid molar (Rhynchippus sp., cf. R. brasiliensis). ant., anterior; Cg, cingulum; Cr, cristae; Crch, crochet; Eclh, ectoloph; *f*, fossette; HC, hypocone; lbl, labial; lng, lingual; Mc, metacone; Mtlh, metaloph; PC, paracone; PCR, paracone ridge; PrC, protocone; post, posterior; PRLH, protoloph.

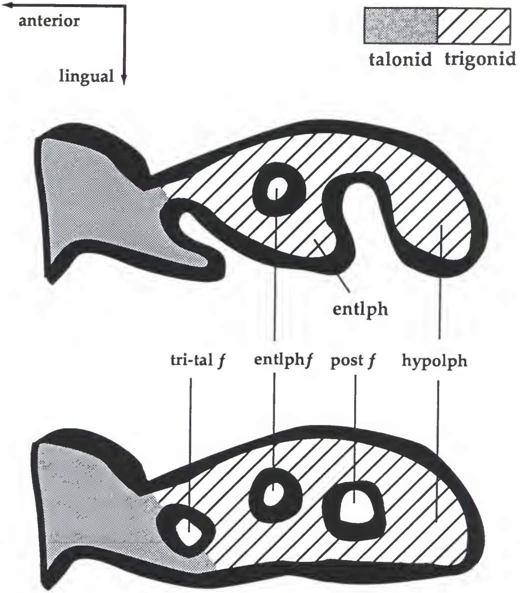

Figure 2.2. Terminology indicating topographical regions of lower post-canine teeth based upon a little-worn (A) and heavilly worn (B) toxodontid lower molar. entlph, entolophid; entlph *f*, entolophid fossettid; hypolph, hypolophid; post *f*, posterior fossettid; tri-tal *f*, trigonid-talonid fossettid.

of enamel which follow the contour of the internal edge of the protoloph and the lingual wall of the crochet-cristae loph. Ameghino (e.g., 1897) referred to this infolding of enamel as a "l'échancrure" (plunging neck line), while Simpson (1932) gave it the prosaic name "anterior valley". In many taxa, this valley is bifurcated by an anterior (first) crista. Taxa in which the first and second cristae unite early lack the bifurcated appearance of the central valley.

The cheek teeth are often ringed by a cingulum which is typically some distance from the occlusal surface until advanced wear. In the Toxodontia examined here, the posterior cingulum is enlarged, persistent, and comes into wear much earlier than other parts of the cingulum. The presentation of the cingulum in these taxa is such that it is convenient to discuss them as independent structures, e.g., lingual cingulum, posterior cingulum, etc.

Often a fossette is formed between the posterior cingulum and the metaloph. This fossette will be referred to as the "posterior fossette" (Post *f*). Labial fossettes may also be formed. In some taxa these are formed between cristae, but most commonly are encircled by the crista-crochet, metaloph, and ectoloph. With these structures a general topographical description "labial fossette" is given, but require a description as to their origin.

Lower cheek teeth and the terminology used to describe them are shown in Figure 2.2. Their most general form may be described as an anterior and posterior crescent, with the trigonid forming the anterior crescent and the talonid forming the posterior. The trigonid is presumed to be formed by the protoconid, metaconid, and paraconid, though it is likely that the paraconid is not homologous with those of other eutherians (see Cifelli, 1993). The medially directed lophid of the talonid is referred to as the "entolophid."

Fossettids are named in regard to their topography and etiology. The fossettid formed by the fusion of the metaconid with the entolophid at the trigonid-talonid border is referred to as the "trigonid-talonid fossettid" (tri-tal *f*). Several taxa (see Chapter 3) have an early-formed fossettid in the entolophid which is referred to as the "entolophid fossettid" (entlph *f*). An additional talonid fossettid is sometimes formed by the union of the posterior portion of the talonid ("hypoconid") with the entolophid. In all cases it is the most posterior fossettid and is thus called the "posterior fossettid" (post *f*).

All measurements were taken using dial or digital calipers and are given in mm. In general, anteroposterior and transverse dimensions are given for teeth. These dimensions for cheek teeth are simply termed "lengths" for the anteroposterior dimension and "widths" for the transverse dimension. The upper lengths (L) of cheek teeth were measured at the occlusal surface at the anterolabial corner of the tooth to the posterolabial corner. Upper cheek teeth widths (W) is the distance in mm from the external ectoloph at the paracone ridge to the internal surface of the protocone (see Fig. 2.3). These were taken at the occlusal surface, except with leontiniids, with which a slightly different procedure was used. Their occlusal W changes so radically with wear that it was determined to measure W of these brachydont animals away from the occlusal surface, with W being at the level of the lingual cingulum to the labial ectoloph at the paracone.

Relative crown heights, or hypsodonty indices (HI) were determined by dividing the crown height by the length (L) of the occlusal surface, which in all cases was the greatest occlusal dimension. Crown heights (PCRH) were

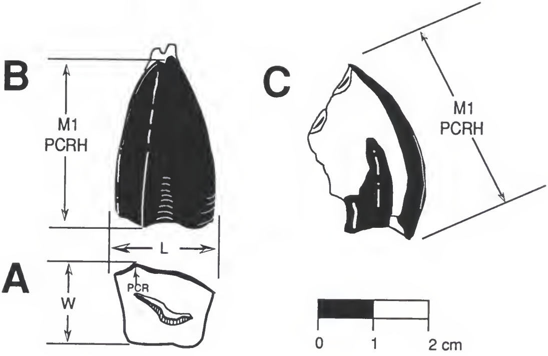

Figure 2.3. Upper molar of a notohippid indicating the methods used to determine length (L), width (W), and crown height (PCRH) at the paracone ridge (PCR). The molar is shown in occlusal (A), lateral (B), and anterior (C) views.

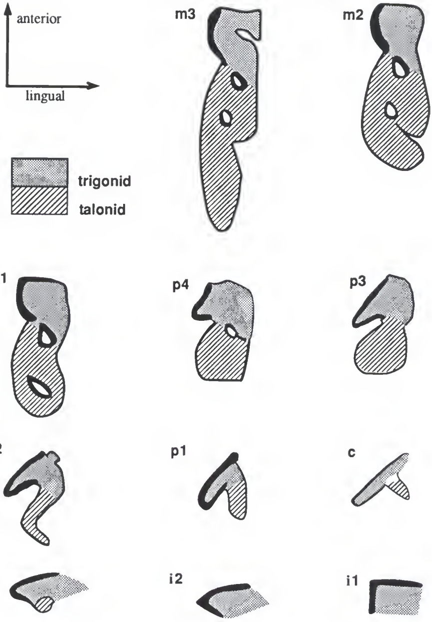

Figure 2.4. Graded transition in the form of lower teeth of a notohippid indicating putative homologous regions of the occlusal surfaces. (Based upon sketch of Rhynchippus equinus, FMNH P13410.)

taken along the paracone ridge of M1s from the occlusal level to the termination of the enamel at the root (see Fig. 2.3). Linear measures are given for crown heights, even in specimens in which the molars were strongly curved (an underestimate for the external enamel curvilinear dimension, but an overestimate of the internal curvilinear dimension [see Fig. 2.3C]).

Lengths (l) of lower cheek teeth were taken from the anterolabial corner to the posterolabial portion of the tooth. Widths (w) were determined by measuring the greatest transverse dimension of the trigonid.

Inspection of Figure 2.4 should convince one that the anteroposterior dimensions of incisors are not homologous to anteroposterior dimensions of the cheek teeth. The anteroposterior dimension of incisors is thus referred to as the "depth" (D for uppers and d for lowers), whereas the transverse dimension is the breadth (B for uppers and b for lowers.) Incisiform canines are treated in a like manner. Obliquely oriented incisiform canines are measured along the oblique axis.

Relative width of the muzzle was determined from the ratio of the width of the muzzle (MW) to the width of the palate (PW) (Janis and Ehrhardt, 1988). MW is the width of the snout at the premaxilla-maxilla border and PW is the distance between the lingual borders of the protocones on the opposite M2s. Janis and Ehrhardt's method was modified in animals having snouts that become broader anterior to the premaxilla-maxilla boundary (e.g., Eomorphippus and the new notohippid genus). In these taxa, the greatest width of the premaxilla (MW_{max}) was measured and divided by the PW.

Statistics

Statistical analyses of characters included Model II regressions and principal component analysis (PCA), as well as the standard sample descriptors such as means, standard deviations, and coefficients of variation (see abbreviations below). PCAs were accomplished by use of JMP IN 3.1.5 of the SAS Institute.

Abbreviations for descriptive statistic techniques are given in Table 2.3.

Table 2.3. Descriptive Statistic Abbreviations and Definitions.

CV = coefficient of variation (CV = $s/\bar{x}$)
Model II **slope** = (Model I slope)/r
r, correlation coefficient
r^2, coefficient of determination
PCA, principal component analysis
s, standard deviation
$\bar{X}$, mean
SAS, Statistical Analysis System, SAS Institute ®

Phylogenetic Analysis

Cladistic analysis was used as a tool to generate hypotheses regarding the phylogeny of the "advanced" Toxodontia (i.e., notohippids, leontiniids, and toxodontids). Included in this analysis are some primitive taxa previously regarded as isotemnids (Simpson, 1967) but referred to Notohippidae by Bond and Lopez (1993). Character states were determined and scored for morphological features in advanced Toxodontia. Specimens of all taxa in this analysis were directly examined for character state determination except *Argyrohippus praecox*. Character states for this taxon were obtained from the original description by Patterson (1935). Other literature consulted for character assessment include: Simpson (1967) for *Pleurostylodon modicus*, *Plexotemnus complicatissimus*, *Puelia coarctatus*, and *Eomorphippus obscurus*; Bond and Lopez (1993) for *Pampahippus arenalesi*; Ameghino (1897) for *E. latirostris*; Ameghino (1897) and Loomis (1914) for *Rhynchippus equinus*; Simpson (1932) and Patterson (1934a) for *R. pumilus*; Loomis (1914) for *Proadinotherium leptognathum* and Patterson (1934a) for *P. muensteri*; Scott (1912) for *Adinotherium ovinum* and *Nesodon imbricatus*; Loomis (1914) and Patterson (1934a) for *Leontinia gaudryi*; and Chaffee (1952) for *Scarrittia canquelensis*. Some of the characters and character states used were based upon the work of Cifelli (1993). Dental characters were used almost exclusively, since most of the taxa are known only from teeth.

The well known isotemnid *Pleurostylodon modicus* Ameghino, 1897 provided information regarding dental characters regarded as ancestral (Simpson, 1967; Cifelli, 1993). The data matrix (29 morphological characters; 18 taxa) was analyzed, using the Branch-and-Bound algorithm of PAUP (Swofford, 1989).

The taxa consisted of 12 species of notohippids, two genera of leontiniids, and three genera of toxodontids plus the outgroup (see Chapter 7). Although cladistic techniques were used to generated hypothetical phylogenetic relationships, conventional paraphyletic names are used.

Locality Coordinates

Latitude and longitude of localities of Salla were obtained with a Trimble Scout ® GPS (global positioning system). The error for the coordinates reported in Table 1.4 should be considered ± 100 m, since with but one GPS it is not possible to correct for the governmental degradation.

CHAPTER 3
SYSTEMATIC PALEONTOLOGY

Order Notoungulata Roth, 1903

Whereas Ameghino emphasized the similarities of South American ungulates to those of the rest of the world (see Chapter 1), Santiago Roth (1903) emphasized how different many of these taxa were from fossil and extant ungulates from other continents. He described derived characters of the auditory region that appeared to unite many of the South American ungulates, but excluded herbivores of other continents and some of the South American forms. The Toxodontia, Typotheria, and some early primitive taxa, such as notostylopids were included in the order Notoungulata (Roth, 1903), but some native taxa, such as litopterns, and astrapotheres, were excluded.

The monophyletic status of the notoungulates has never been seriously challenged. Indeed, the scrutiny of Simpson (e.g., 1934c, 1948, 1967), Patterson (1936), and Cifelli (1993) has supported this natural grouping, though some of the included taxa have varied (For example, Patterson [1977] included pyrotheres among the notoungulates, but this assessment has been generally rejected [Simpson, 1978; McKenna, 1981; Cifelli, 1983b]).

Cifelli (1993) recently summarized putative synapomorphies for the Notoungulata. His list included the following: 1) distinctive upper molar coronal pattern, including ectoloph, protoloph, metaloph, and, especially, the crochet (see Fig. 2.1); 2) entoconid of lower molar expanded into medially directed entolophid (see Fig. 2.2); 3) posterior zygomatic arch originating high on skull; and 4) auditory characters including epitympanic sinus in squamosal and tubular ectotympanic with crista meatus. Cifelli also included provisional tarsal synapomorphies, however, in general there is little support for postcranial synapomorphies in this diverse order (Bergqvist, 1996).

Suborder Toxodontia Owen, 1853

Owen described the first genera of notoungulates known, Toxodon (Owen, 1840) and Nesodon (Owen, 1846). He united these under the Toxodontia (Owen, 1853), which was recognized as having ordinal status until the time that Roth noted common morphological features among both toxodonts and typotheres (Roth, 1903). To differentiate the hierarchical levels, Scott (1912) proposed the alternate spelling "Toxodonta" for the suborder. This was followed by Simpson (e.g., 1945) and other workers, but Mones (1988) regarded the alternative spelling as unnecessary and a violation of the principle of priority.

The Toxodontia are presently considered to be composed of the families Isotemnidae, Homalodotheriidae, Leontiniidae, Notohippidae, and Toxodontidae (Simpson 1945; Cifelli, 1993). Of these, the leontiniids, notohippids, and toxodontids appear to form a natural group, informally called "advanced Toxodontia" (e.g., Cifelli, 1993). Cifelli (1993) indicated that synapomorphies for this group included loss of astragalocuboid contact, contact of navicular and calcaneum, and development of well developed trochlear fibular facet of the calcaneum. He noted that the addition of a "talonid fossettid" (= entolophid fossettid of this work, see Figure 2.2 and

Cifelli, 1993: fig. 15.6) was a presumed synapomorphy for these three families, however, this character is absent in pre-Deseadan notohippids such as Eomorphippus obscurus and ?Eomorphippus pascuali (see Chapter 7 and references therein). This fossettid may have been secondarily lost in the Deseadan Eurygenium sp. and Morphippus imbricatus (see Chapters 3 and 7).

Family Leontiniidae Ameghino, 1895

(Includes Colpodontidae Ameghino, 1906)

Ameghino honored his wife Leontina (see Simpson, 1948) by naming the genotype for this family Leontinia (Ameghino, 1895). In the same publication he also named three other genera of leontiniids, Ancylocoelus, Rodiotherium, and Loxocoelus, the latter two of which were represented by mere fragments (an "imperfect mandibular symphysis" for Rodiotherium and an indeterminate left molar for Loxocoelus). Three species of Leontinia were named in this first paper regarding the Deseadan (Ameghino, 1895). Leontinia gaudryi is regarded as the type for the genus, whereas L. lapidosa was named based on a mandibular fragment containing an m1. Leontinia lapidosa was virtually the same size as L. gaudryi and was differentiated based on a somewhat reduced cingulum around the m1. Leontinia garzoni, however, is clearly differentiated from L. gaudryi by its distinctly small size, but was considered indistinguishable from Ancylocoelus frequens by Patterson in his unpublished catalog of the Ameghino collection.

Ameghino's initial description of the family was based on somewhat fragmentary material, leading him to erroneously report that Leontinia lacked canines and that the caniniform incisors were I3 and i3. After receiving and studying superior material of Leontinia spp. collected by his brother at Cabeza Blanca, he corrected these errors (Ameghino,1897), noting that the caniniform incisors were I2 and i3 and that Leontinia had both upper and lower incisiform canines. In this second work on the Deseadan (Ameghino, 1897), Ameghino named three additional species of Leontinia, all of which were the same size as L. gaudryi and differed only in minor details.

Loomis (1914) synonymized several species in four genera of leontiniids, regarding these as Leontinia gaudryi. Based on his large sample of leontiniids from Cabeza Blanca (the most commonly encountered animal there), he inferred that the species was sexually dimorphic and regarded those with large caniniform incisors as being males and those with smaller ones (L. oxyrhynca Ameghino, 1897) females. He believed that the sexual dimorphism and changes in the appearance of the teeth that occur with wear accounted for much of the variation seen within this species.

Soon after the discovery of Scarritt Pocket, Simpson (1934a) named and hastily described the "most common quarry species" from that locality. Without adequate explanation, he designated "a specimen not collected and now unidentifiable (Simpson, 1934a: p. 2)" as the holotype for Scarrittia canquelensis, despite the fact that many specimens were at hand, though unprepared.

In naming Scarrittia, Simpson (1934a) did not closely compare it to Leontinia. Of it he wrote that "there is no reasonable possibility of very close relationship" (Simpson, 1934a: p. 2), but indicated that it was similar in the reduction of the canine and "some other details" which he did not specify. He believed that it was closest to Henricofilholia, but did not indicate which species (species then referred to Henricofilholia are now referred to both Astrapotheria and Leontiniidae) but tentatively referred Scarrittia to Leontiniidae.

Chaffee (1952) revised the diagnosis of Scarrittia and indicated that it was "very close to Leontinia" (1952: p. 517) differing only in that it was the I1 of Scarrittia that was caniniform, its lower incisors were more procumbent, and P2-4 lacked lingual grooves on the protocones. He proposed an informal grouping of these two genera and suggested that Scarrittia may be found to be a subgenus of Leontinia.

Although a Colhuehuapian genus, Colpodon warrants discussion here as it has been compared closely to Deseadan leontiniids (e.g., Ancylocoelus) and with notohippids. Ameghino once considered it to be a leontiniid, but later (Ameghino, 1904) put it in its own family, Colpodontidae, and regarded it as being closely aligned with the Notohippidae. Recent workers (Soria and Bond, 1988) have placed Colpodon in the Notohippidae, citing similarities of their astragali and muzzles and the absence of caniniform incisor. This referral to the Notohippidae is not followed here because Colpodon has a strong premolar external cingulum, like leontiniids and unlike notohippids, and because some specimens do indeed have a caniniform incisor (e.g., FMNH P 13304), unlike any notohippid. Similarities in the muzzle may be an ecomorphological effect (see Chapter 5). Any similarities of Colpodon astragali to notohippid astragali may indicate the conservative nature of tarsals among the advanced Toxodontia.

The poorly known and poorly defined genus, Henricofilholia, should be discussed since it has been noted on faunal lists of Salla as a leontiniid

(Hoffstetter, 1976) and an isotemnid (MacFadden et al., 1985). The genus was based largely on inadequate type material and the resulting chaos illustrates the futility of naming fragmentary remains. Henricofilholia (Ameghino, 1901) was first applied to the ?Parastrapotherium cingulatum Ameghino, 1894, with Ameghino explicitly designating ?Parastrapotherium cingulatum as the type species for Henricofilholia (Ameghino, 1895). He simultaneously named two new species of Henricofilholia, all of which he considered as belonging to the Astrapotheria.

Later, (Ameghino, 1904c) indicated that Henricofilholia was closer to Colpodon than Astrapotherium and included it among the Leontiniidae. Though he clearly stated in the text that he placed the genus in the Leontiniidae, the heading was erroneously printed as "Isotemnidae." This "typo" is the apparent source of erroneous assignment of Henricofilholia to Isotemnidae by later workers (i.e., Loomis, 1914 and MacFadden et al., 1985).

Ameghino's inclusion of Henricofilholia (and Colpodon) in the Leontiniidae seemed tentative since he added that the definitive allocation depended upon the familial placement of Colpodon. This "colocación definitiva" appeared soon after (Ameghino, 1906) and Henricofilholia was placed in the Colpodontidae which in turn was placed in the order Hippoidea. Hippoidea was composed of "colpodontids", notohippids, and equids (see Notohippidae section in this chapter).

With one exception, species of Henricofilholia were based upon one or two, isolated teeth. Some appear to be fragments of a large astrapothere (Chaffee [1952] regarded H. intercincta and H. lemoinei as synonyms for

Parastrapotherium ephebicum). Other species of Henricofilholia are based on such inadequate type material that they are best regarded as dubious.

Henricofilholia inaequilatera (Ameghino, 1901) is based upon a nearly complete cheek-tooth row (MACN A 52-528, P2-M3, see Ameghino, 1904a: fig 466). It is, however, indistinguishable from the leontiniid Ancylocoelus frequens. This specimen shows the same suite of characters seen in A. frequens and is well within the size range of this species (see Fig. 3.2). Bryan Patterson regarded it as a junior synonym of A. frequens in his 1952 unpublished catalog of specimens in the Ameghino Collection. Patterson also listed L. garzoni as a junior synonym of A. frequens.

In his first publication regarding Salla, Hoffstetter (1968) mentioned the probable presence of leontiniids there, but noted that the remains were rare and the material collected was too fragmentary to rule out the possibility that they were homalodontotheriids. On a later faunal list (Hoffstetter, 1976), he noted the absence of homalodontotheriids and listed Henricofilholia as the genus of leontiniid present. MacFadden et al. (1985) did not include leontiniids on their faunal list, but mentioned leontiniid genera (i.e., Henricofilholia, Leontinia, and Ancylocoelus) in their discussion of isotemnids, suggesting that the two families were confused.

Although leontiniids are common members of Deseadan faunas of Patagonia (e.g., Cabaza Blanca [Loomis, 1914] and Scarritt Pocket [Chaffee, 1952], and the tropical Tremembé Formation of Brasil [Soria and de Alvarenga, 1989]) they are remarkably uncommon at Salla. The two specimens described below, however, are complete enough to improve our understanding of the leontiniids of Salla. These demonstrate that at least two taxa lived in the region (though about two million years apart). Both display affinities with Leontinia, though they lack an enlarged I2. The plastic nature of the caniniform incisors prompts a revision of the definition of leontiniids offered by Chaffee (1952). His comment that the fossettid of the trigonid is formed by the union of the entolophid and metalophid is also revised based on the observation in an unworn molar of L. gaudry (FMNH P13285) that the fossettid forms early in the entolophid, before the entolophid and hypolophids unite.

Revised definition. Brachydont Toxodontia with reduced canines. Canines incisiform or absent. Tendency for enlargement of an upper incisor to caniniform or tusk-like form. Molar protolophs much greater length than metaloph. Anteroposteriorly oriented median valley containing simple cristae, forming small fossettes in some species. Lingual wall of molar ectolophs with longitudinal grooves, obscured early with wear. Third lower incisor enlarged or caniniform. Broad, robust entolophid of molars containing early-formed fossettid. Hypolophid of m1-2 less than half the total length of the talonid.

Unnamed Leontiniid Genus

Proposed type species. The smaller leontiniid described below (Species A) will be designated as the type species.

Generic diagnosis. I1 larger than I2. Anterior snout short with corresponding loss of an anterior upper tooth (apparently, but not definitely, the canine). Size variable, ranging from close to that of Leontinia gaudryi and Scarrittia canquelensis to nearly as small as Ancylocoelus frequens. P3-4 with longitudinal, lingual grooves (as in Leontinia), but indistinct or lacking in P2. Differs from Leontinia by incisiform I2 and apparent loss of canine. As in Scarrittia, I1 is larger than I2, but differs from Scarrittia by presence of grooved premolar protocones.

Geographic and temporal range. Both species are from Salla, Bolivia. The horizon from which the larger species (Species B) comes has an ^{40}Ar-^{39}Ar date of 27 Ma. The smaller species (the genotype) is constrained above and below by ^{40}Ar-^{39}Ar dates of 24.9 - 24.8 Ma (Table 1.3 and Figure 1.2).

Small Leontiniid in Unnamed Genus (Species A)

Fig. 3.1 and Table 3.1

Proposed holotype. Uncataloged MNHN-Bol specimen, tempory ID number, F-93-10 (see Appendex A for indentification of uncataloged specimens). Nearly complete upper dentition, lacking the right I1-2 and the left P1.

Horizon and locality. The proposed holotype was found at Tapial Pampa in the Salla Beds in Unit 5 below the El Planimiento. The specimen was found by Ruben Andrade of the MNHN-Bol.

Diagnosis. Size small, considerably smaller than L. gaudryi, Scarrittia canquelensis and the leontiniid described below. Size similar to Ancylocoelus frequens. I1 larger than I2 and I3, but not tusk-like. Upper canine appears to be lost. Protocone P3-4 with lingual groove, lacking on protocone of P2.

Description. MNHN-Bol-F-93-10 (Fig. 3.1) preserves nearly the entire upper dentition of this small leontiniid. Only the right I1-2 are missing as is the left P1. I1 is caniniform, and it is the largest incisor. It is incompletely

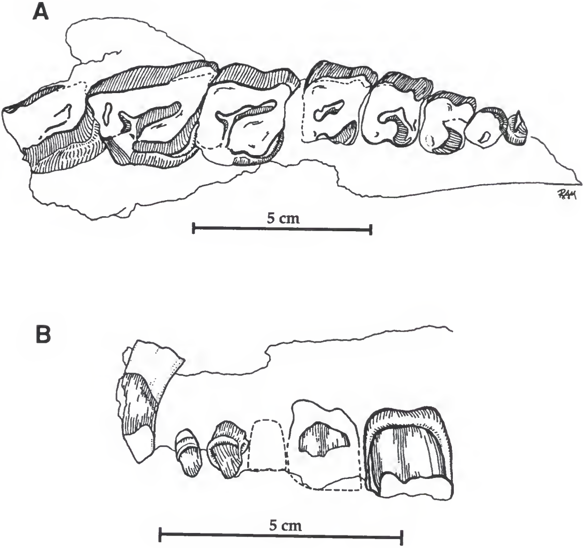

Figure 3.1. Salla leontiniid species A, MNHN-Bol-F-93-10 . Palatal view (A) of right I3 (C?)-M3 and lateral view (B) of the left I1-P3.

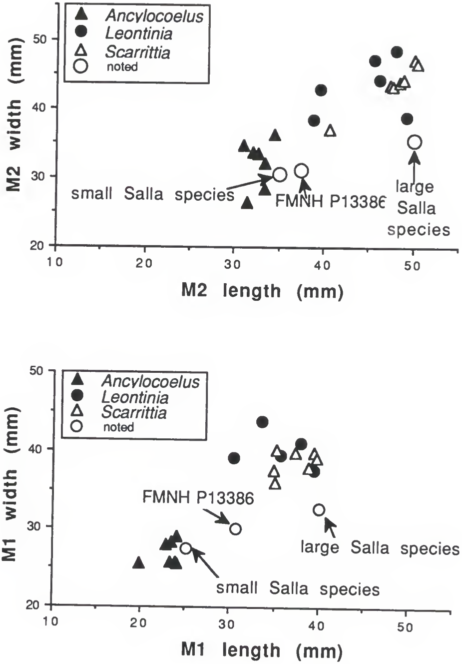

Figure 3.2. Widths vs. lengths of first and second upper molars from selected leontiniids.

Table 3.1. Dental dimensions (mm) of small leontiniid of Salla compared to the small species referred to Leontinia from Pico Truncado.

	Salla small species MNHN-Bol (Bol-F-93-10)	Leontinia sp. FMNH P 13386
P1 length	11.1	---
width	12.5	---
P2 length	12.1	---
width	18.0	---
P3 length	15.3	---
width	21.0	---
P4 length	16.8	18.8
width	22.6	25.5
M1 length	24.8	30.7
width	28.3	30.0
M2 length	34.7	37.4
width	30.5	31.2

erupted, but the enamel development had terminated. It has a weak external cingulum and a robust root, which is broken before showing any sign of tapering. I2 and I3 (C?) are significantly smaller than I1, are anteroposteriorly compressed, and have strong cingula. Either the I3 or C is lost. The exact determination of the absent tooth is difficult because the premaxilla and maxilla are solidly fused. Cracks and scratches on the specimen are more conspicuous than any suture that may remain. One palatal suture-like line follows immediately from the anterior root of the P1, suggesting that the absent tooth is the canine. This feature, however, may be a crack and not a suture. In any event, the animal lacks a complete upper dentition. The formula of the upper dental series is likely 3-0-4-3, but may be 2-1-4-3. The lower series is unknown.

P1 is much smaller than the following premolars and is preserved only on the right side. It is so worn that its crown is essentially featureless, except for a shallow fossette. A deep, conspicuous cingulum is present on the external surface. The tooth has worn down nearly to the external cingulum and has worn to such an extent that the anterolingual cingulum has formed a fossette.

Though heavily worn, P2-4 are comparable to those of FMNH P13386, an unnamed species described and figured by Patterson (1934a: fig. 10c) and referred to Leontinia sp. The external enamel undulates around a distinct parastyle and paracone ridge, then follows a smoother path to a shallow metacone ridge. A distinct external cingulum is present on P2-4, but absent on the molars. The paracone is not connected at the occlusal level to the parastyle, except on the more heavily worn P4. An anterolingual cingulum, deep to the level of occlusion, contacts the paracone with the protoloph. The paracones of P3-4 have longitudinal lingual grooves, as in L. gaudryi and the unnamed P13386 (and unlike Scarrittia canquelensis [Chaffee, 1952]).

The molars have the same general appearance as those of Leontinia and Scarrittia. M1 is roughly square in occlusal view, but has a projection of the anterolabial corner such that it imbricates the P4. Though the I1 and M3 have not come into complete occlusion, the M1 is worn to the level of the internal cingulum. Its protoloph is narrow labially, but broadens rapidly to form a bulbous structure at the protocone. The valley between the protoloph and ectoloph is narrow and lacks branches or fossettes. M1 lacks a posterior fossette. The M2 is relatively and absolutely longer than the M1, has a narrower protoloph, and a narrow, transversely oriented posterior fossette. M3 is incompletely erupted and badly damaged. A distinctive internal cingulum is present on it, and all the molars, but none of these upper molars have external cingula.

Discussion. The Salla leontiniid species A is small for Deseadan leontiniids, which are sometimes compared to rhinos (e.g., Loomis, 1914). Ancylocoelus frequens is the smallest Deseadan leontiniid and is comparable in size to the small Salla species A (See Figure 2.2). This species A is, however, readily differentiated from A. frequens by its I1 being larger that the I2, its lack of bifurcation of the central upper molar valley, and the groove in the protocone of P3-4.

Two unnamed taxa of leontiniids from Patagonia are roughly comparable in size to leontiniid specie A. These are FMNH P 13386, collected from Pico Truncado during the Marshall Field Patagonian Expedition (noted above), and AMNH 29607, collected during the Scarritt Expedition.

Patterson (1934a) referred FMNH P 13386 to Leontinia sp. The lack of wear of these teeth (P1-M2) made the specimen particularly useful in understanding the premolars and molars in this family. The specimen, however, is missing the diagnostic anterior dentition that distinguishes Leontinia from Scarrittia. This Pico Truncado animal is similar to L. gaudryi as both have the longitudinal grooves in its upper premolars. The protocone groove of P2 is distinct on the Pico Truncado animal whereas, the Salla animal lacks this feature of the P2. The Salla leontiniid species A differs from P 13386 by being somewhat smaller, having cheek teeth with relatively greater transverse dimensions (see Fig 3.2), and having a squarer M1. The M1 of leontiniid species A of Salla has a distinctive projection of its anterolabial corner that imbricates the P4. These differences are fairly trivial and the two may prove to be the same species should the anterior dentition of the Pico Truncado animal be discovered to be similar to that of Salla species A.

Chaffee (1952) described, but (wisely) did not name, a fragmentary leontiniid (AMNH 29607) from Scarritt Pocket. This specimen is of similar to the Salla leontiniid species A in size and by having an unbifurcated central valley of the upper molars (see Chaffee, 1952: fig 3). The small leontiniid of Scarritt Pocket, however, has a distinctive P2 that has but a single cusp.

Of the two extrapatagonian leontiniids of the Taubaté Basin, São Paulo, Brasil, one, Taubatherium paulacoutoi, is approximately the same size as leontiniid A of Salla. Molars of Taubatherium, however, have distinct cristae which give the anterior valley its branching appearance. Neither of the Salla leontiniids are referable to Taubatherium.

Large Leontiniid (Species B)
Fig. 3.3 and Table 3.2

Proposed Holotype. UF 90959. Right maxilla with P3-M2 and portion of M3, premaxilla with left I1, and left premaxilla with P3-4. Crowns of incisor and premolars are damaged.

Locality and Horizon. From Unit 2 of Pasto Grande of the Salla Beds (see Figs. 1.2 and 1.4). The name of the collector was not recorded.

Diagnosis. Size similar to Leontinia gaudryi, Scarrittia canquelensis, and Taubatherium major. Muzzle shorter that those of L. gaudryi and S. canquelensis. Alveolus of I1 larger than that of I2. I1 not greatly enlarged, but similar to I1 of L. gaudryi. Differs from L. gaudryi by small size of I2 and reduction of anterior dentition (no apparent canine). Differs from S. canquelensis by smaller I1, reduction of anterior dentition, and presence of longitudinal lingual groove in protocone of upper premolars (lingual protocone groove absent in S. canquelensis). Lacks the distinct molar cristae of T. major.

Description. The first upper incisor of UF 90959 has the same general form as that of Leontinia gaudryi. An external cingulum is present, but indistinct. The crown of I1 of leontiniid species B is broken. No posterior cingulum is seen, but this may have been lost in the breakage of this tooth since the posterior cingulum occurs closer to the occlusal level than the anterior cingulum. Both I2s are missing, but the alveoli and roots of I2 are not enlarged, as in L. gaudryi (see Loomis [1914] and discussion below).

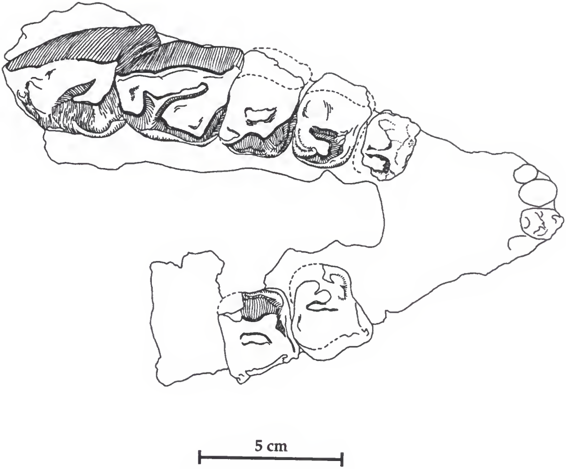

Figure 3.3. Occlusal view of Salla leontiniid species B (UF 90959).

Table 3.2. Upper dental dimensions (mm) of the large Salla leontiniid (Species B), UF 90950.

I1 (right aveolus)	breadth	10.0	I1 (left)	breadth	11.1
	depth	13.2		depth	14.0
I2 (right aveolus)	breadth	8.3	I2 (left aveolus)	breadth	10.0
	depth	8.0		depth	10.2

P3 (right)	length	21.7
	width	28.0
P4 (right)	length	(22.5)
	width	-----
M1 (right)	length	39.4
	width	32.3
M2 (right)	length	48.2
	width	36.4

The first premolars are missing and P2 is badly damaged. P3 is not heavily worn and preserves some of the crown features. The protocones of P3-4 have the vertical, lingual grooves as seen in L. gaudryi and in Leontinia sp. of Patterson, 1934a: fig. 10c. The badly damaged P2 lacks the protocone groove. On the P3 of the Salla specimen, the occlusal surface of the protocone is isolated, save for a connection to the metaloph. An unworn ridge connects the protocone with the posterior cingulum. The anterior cingulum is well removed from the occlusal surface and becomes incorporated into the protoloph. The parastyle is distinct and a sharp groove cuts into the ectoloph between the parastyle and the paracone ridge. P3-4 have an external cingulum. Damage prevents the assessment of this character on the P2.

The M1 is moderately worn. Cingula are present from the anterolingual portion of the tooth to the posterior border. All are removed from the occlusal level, except for the posterior cingulum which has come into wear. None of the molars have a labial cingulum. The central valley is Y-shaped, with the anterior arm being conspicuously longer. This anterior arm lacks any bifurcation such as is present in Ancylocoelus, Taubatherium and Colpodon.

The posterior cingulum of the M2 had not come into occlusion. This tooth has a similar form to the M1, though with significantly less wear.

Only the anterior-most portion of the M3 had broken the gum line. Most of this tooth is missing, but part of the ectoloph was recovered. The internal wall of this ectoloph demonstrates the vertical ridges described by Patterson (1934a: fig. 10b) of an unworn molar of Leontinia gaudryi (FMNH P14659).

Discussion. The grooved premolar protocones in the two Salla leontiniid species described above are suggestive of generic affinities with Leontinia, however, the greater size of the I1 compared to I2 is more similar to the condition seen in Scarrittia. This mosaic of characters tempts the hypothesis that the Salla leontiniids are intermediate between the two Patagonian genera, however, the loss of an anterior tooth in the Salla species argues against this since both Leontina and Scarrittia retain a full complement of teeth. In regard to dental formula, the Salla species are more derived than either L. gaudryi or Scarrittia.

Ancylocoelus and Colpodon both lack canines (Patterson, 1935; contra Loomis, 1914), but the cheek teeth of the Salla species are nearly identical to those of Leontinia and Scarrittia and differ from those of Ancylocoelus and Colpodon. Clearly, Leontinia and Scarrittia form a clade (the informal "sub-group" of Chaffee, 1952; see also Villarroel and Danis, 1997) distinct from Ancylocoelus and Colpodon. The two Salla species at hand appear to be members of this Leontinia-Scarrittia "subgroup". The vertical groove in the upper premolar protocones appear to be derived traits (these are not seen in either the proposed isotemnid or primitive notohippid outgroups, nor are they found in other known leontiniids. As such, the Salla species likely share a common ancestor with L. gaudryi and the unnamed leontiniid from La Flecha (P13386 of Patterson, 1934a).

The caniniform upper incisor of these species appears to be somewhat plastic. In L. gaudryi, it is the I2 that is caniniform and, following Loomis (1914) is dimorphic. He regarded L. oxyrhynca to be a synonym of L. gaudryi, offering the reasonable hypothesis that since the two morphs were male and female since they were equally represented at Cabeza Blanca. The L. oxyrhynca morph, which had a smaller tusk, was regarded as being a female of L. gaudryi. The larger Salla species B is not regarded here as being a female of L. gaudryi since even in these animals the I2 was not only larger than that of Salla species B, but the I2 of female L. gaudryi (L. oxyrhynca) is larger than the I1 on those specimens. The diameter of the I2 alveoli are greater than those of the I1 alveoli on ACM 3293 (printed as 3291x in Loomis, 1914: fig. 73 and pp. 116 - 119), whereas the alveolar diameter of I1 are greater than I2 of Salla leontiniid species B.

The caniniform I2 of Leontinia and the caniniform I1 of Scarrittia prompted Chaffee (1952) to propose an evolutionary shift from caniniform C to caniniform I1. In this scenario the canine was reduced and initially the I3 was enlarged in a hypothetical ancestor to both Leontinia and Scarrittia. In the next stage (as represented in Leontinia) I3 became reduced and I2 was enlarged. The most derived condition was where the I1 was enlarged, exemplified by Scarrittia. The Salla leontiniids approach the later condition in that I1 is enlarged but not to the extent seen in Scarrittia. As noted, these leontiniids are not good models for ancestors to Scarrittia since they appear to have lost the upper canine.

The Salla leontiniids do, however, suggest that the upper caniniform incisor is a fairly plastic feature, perhaps strongly influenced by exogenous factors such as use in feeding or use in sexual selection. This plasticity of the morphology of the incisors suggests that this character state may not be useful in determining phylogeny. Indeed, as Loomis (1914) demonstrated, it may be variable even at the specific level.

Given the lack of synapomorphies of the Salla leontiniids with known genera and the probable synapomorphies of reduction of anterior snout and loss of upper canine uniting these two species, they are best considered in a genus unto themselves.

Leontiniids however, are exceedingly rare at Salla. Only one specimen each (the two described above) are certainly leontiniids in the extensive Salla collections of MNHN-Bol and UF. Fragmentary remains of a few other specimens may represent leontiniids, but are in too poor condition to rule out possible referral to other taxa (e.g., Astrapotheria, Notohippidae, or cf. Acamana). A few molar fragments in the PU collection are likely, but not certainly, referable to Leontiniidae.

The scarcity of leontiniids at Salla may indicate that local conditions were not favorable to this animal. Since Salla is at a much lower latitude than the classical Deseadan localities of Patagonia one might consider the possibility there was a regional effect, that is, conditions were more favorable in higher latitudes than the more tropical latitude of Salla. The relative abundance of leontiniids in the Deseadan of Brasil, however, does not support the notion that there was a gross regional effect. Soria and de Alvarenga (1989) noted that leontiniids were the most commonly encountered fossil in the Taubaté Basin, which lies near the Tropic of Capricorn (about 6° south of Salla). Also, the fact that leontiniids survived into the middle Miocene at La Venta, Columbia (Villarroel and Guerrero Diaz, 1985), 13.8 - 11.8 Ma (Flynn et al., 1997), but became extinct at the end of the Colhuehuapian in Patagonia also argues against any notion that tropical regions were unfavorable to them.

A more discrete regional effect may involve the scarcity of leontiniids at Salla. The likely uneven terrain around Salla during this time of early mountain-building may have been a factor. The region surrounding the Salla Basin were apparently raised relative to it at that time, except to the southwest, as suggested by the Sempere scenario (Sempere et al., 1990, see also Chapter 1). The relatively large leontiniids may not have been well-suited for locomotion on uneven substrates. This may also explain the scarcity of astrapotheres. Only one fragment in the UF collection is referable to the Astrapotheria and there is but a single incisor of this animal in the MNHN-Bol collection.

Another ecological consideration is that, in general, low-crowned ungulates, like leontiniids, are uncommon at Salla, whereas hypsodont animals (e.g., several species of typotheres and notohippids) are the most common ungulates encountered. Possible explanations include the hypothesis that the local vegetation included mostly grass or that much of the vegetation was covered with volcanic grit or both (see Chapters 5). The extreme wear of the cheek teeth prior to the eruption of I1 and M3 in Salla Species A suggest that abrasives were a likely pressure on these animals.

Another possibility is that the scarcity of these Leontinia-like leontiniids at Salla is indicative of the continental demise (extinction) of this group of animals. Given that the Leontinia-Scarrittia taxa are unknown in the Colhuehuapian and that Salla is a young Deseadan locality, it is possible that the scarcity was related to factors that led to their extinction. As Darwin pointed out in his Voyage of the Beagle (1845), one might expect an animal to become scarce before it goes extinct.

Family Notohippidae Ameghino, 1894

The type genus for this family was based on two lower molars from the Santacrucian of Patagonia (Ameghino, 1891). Ameghino's initial naming of the family Protequidae (Ameghino, 1891) illustrates that he believed from his first description that this species was close to the base of the radiation of equids. He did not place Notohippus among the Toxodontia (which then had ordinal status, conceptually similar to the modern Notoungulata) but in the Litopterna. Ameghino (1897) noted that the morphology of Notohippus molars was similar to that of both equids and toxodonts; thus the binomen Notohippus toxidontoides. He believed that the similarity to toxodonts was merely "superficial" (Ameghino, 1897: p. 456), but felt that the similarity to horses was profound. He then, and for the rest of his life, argued that notohippids were ancestral to horses (Ameghino, 1897, 1902, 1906). He gave the family the genus-based name Notohippidae (1894) and later (Ameghino, 1902) removed this family from Litopterna and erected the order "Hippoidea," which included notohippids and equids.

His assertion that equids had their origins in the notohippids never enjoyed a following. Subsequent workers (e.g., Scott, 1912; Loomis, 1914; Simpson, 1945) regarded the notohippids as belonging to Toxodontia.

Loomis (1914) offered cranial and postcranial evidence from the notohippid Rhynchippus that demonstrated the close affinity between notohippids and toxodontids. Loomis argued that since the type genus was so poorly known the family name should be suppressed and replaced with

Rhynchippidae (see Loomis 1914, footnote p. 86). For a time, both families were recognized, with cementum being the character determining the familial placement of a genus. Notohippids were those that had cement (e.g. Notohippus and Argyrohippus Ameghino, 1901) and the rhynchippids were those that lacked cement (e.g. Rhynchippus and Morphippus).

Patterson (1934a) regarded the distinction of the two families as being somewhat dubious, in part because the presence of cement among the genera of Rhynchippidae and Notohippidae is variable. For example, Morphippus had been consistently placed among the non-cement group (Rhynchippidae) and it typically has no cement. Patterson detected cement on some specimens and he noted that Ameghino (1904, p. 222) had reported cement on specimens of Rhynchippus and Morphippus.

In his Classification of Mammals, Simpson (1945) reduced the two families to subfamilial rank under the Notohippidae (Notohippinae and Rhynchippinae) but later stated that it was "decidedly moot" as to whether the separation was justified "by phylogeny or convenience" (Simpson, 1967: p. 179).

Cifelli (1993) performed a cladistic analysis of advanced Toxodontia (Leontiniidae, Toxodontidae and Notohippidae) which suggested that Simpson's subfamilial designation is inadequate to describe all the genera of notohippids. The presence of both a diastema and cement (presumably thick cement) united Notohippus, Argyrohippus and Coresodon in the Notohippinae. A smooth, rather than undulating, ectoloph of upper molars appeared to unite Rhynchippus and Morphippus (an apparent tautology, since these uppers represent the same species; see discussion under

Eurygenium sp.), but excluded the Mustersan-Tinguirirican Eomorphippus. Eomorphippus, regarded among the Rhynchippinae by Simpson (1967), appeared as a sister taxon to the remaining Rhynchippinae (Rhynchippus), the Notohippinae, and the Toxodontidae.

Bond and Lopez (1993) described Pampahippus from the Lumbrera Formation (Casamayoran) of Argentina. It shows notohippid characteristics of an incisiform canine and an incomplete protoloph, but retains isotemnid traits, such as the accessory trigonid cuspule of the lower molars, short molar talonids, and brachydont cheek teeth. Bond and Lopez (1993) referred Pampahippus to the Notohippidae and revised the family definition to include taxa having more than two molar cristae. With this broader definition, they specifically included taxa that had formerly been regarded as being isotemnids (e.g., Plexotemnus complicatissimus, Puelia coarctatus, P. sigma). (Simpson [1967] had united these taxa under the genus Acoelohyrax, but this is now regarded as having been erroneous [see Bond and Lopez, 1993 for discussion]). Simpson (1967) noted the notohippid characteristics of his "Acoelohyrax" lineage and doubted that these were convergent. He preferred, however, the interpretation that this clade and notohippids had a common isotemnid ancestor and demonstrated parallel evolution. The revised concept of Notohippidae of Bond and Lopez essentially includes this presumed common hypothetical ancestor.

Unnamed Notohippid Genus

Type species. The species name is currently in press.

Diagnosis. Premaxillary dentition linear, formed with only I1 and I2 until advanced wear. Second incisor lateral to and conspicuously broader than I1. I3 posterior to I2 and much reduced, as are canines. Narrowing of snout occurring posterior to I3 with width decreasing to narrowest point at level of P1. Palate broadening posterior to P1. M1 having well-formed anterolingual cingulum not seen in other Deseadan notohippids. Anterior nasals not simply rounded, but having projecting lateral margins. Anterior dentition linear and transverse, not semicircular. Distinct from Eomorphippus obscurus by leading edge formed with only first two incisors; whereas, all three incisors form leading edge of E. obscurus. Incisors not procumbent as in E. obscurus. Differs from toxodontids by having rooted incisors. Further differentiable from toxodontids by mid-metaloph origination of upper molar crochet instead of lingual origination, and lack of bifurcation of anterior arm of lingual infolding of upper molars. Similar size, but differentiable from Rhynchippus equinus by the transverse muzzle, greater reduction of I3 and C, I2 broader than I1, and retention of anterolingual cingulum of M1.

Unnamed Notohippid Species

(Figs. 3.4, 3.5; Table 3.3)

Proposed Holotype. MNHN-Bol-V-003642 (UF 91400 cast). Anterior part of skull preserving the snout and upper dentition, lacking the left M3 and the posterior part of the right M3.

Referred Specimens. UF 149221, left I1-P4, right I1-C, P3-4, M3; uncataloged PU specimen, having field number "Salla 17017", from the collection made by Leonardo Branisa for Princeton University from 1964 through 1966, premaxilla with right and left I1-I2.

Horizon and Locality. The proposed holotype and UF 149221 came from Unit 2 (see Fig. 1.2) of a northern region of the Salla Beds known as Pasto Grande (Fig. 1.4). Gonzalo Barriga of GEOBOL and Roger Portell of UF discovered and collected the holotype in 1984. The PU specimen is just noted as having come from Salla.

Diagnosis. Same as for genus.

Description. The broad, blunt snout, with the first two incisors forming a transverse line across the anterior premaxilla followed by a narrowing of the snout is similar to the muzzle of nesodontine toxodontids. Unlike these toxodontids, the incisors form roots, and the cheek-teeth of this species do not resemble those of the early toxodontids, such as the Deseadan Proadinotherium leptognathum (Loomis, 1914:fig. 80) or the Colhuehuapian P. muensteri (Patterson, 1934a: fig. 12). The molars of this species lack the bifurcation of the central valley as seen in these toxodontids. The posterior fossette is smaller and the paracone ridge of the ectoloph is less pronounced than in species of Proadinotherium.

M2 of the proposed holotype retains the infolding of the lingual enamel which has, with wear, become isolated as the major fossette on the M1. Neither molar has a branched anterior arm of the fossette/infolding. Only a portion of the M3 is preserved, of which only the anterior most part has come into wear.

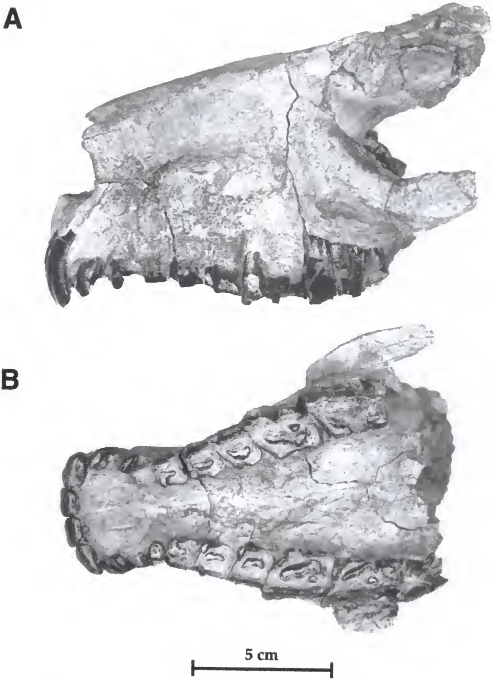

Figure 3.4. Proposed holotype of unnamed new notohippid genus (MNHN-Bol-V-003642), lateral (A) and occlusal (B) views.

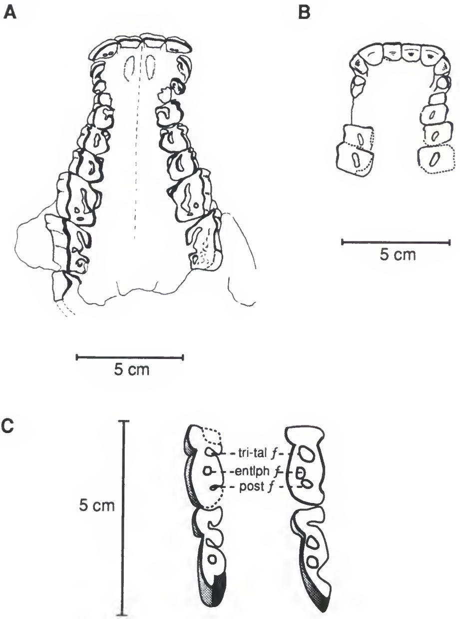

Figure 3.5. Unnamed new notohippid genus from Salla. Palatal views of MNHN-Bol-V-003642 (A), UF 149221 (B), and occlusal views of lower m2-3 (C) of specimens referred to this genus; UF 149219 (left) and UF 149224 (right).

Table 3.3. Upper dental dimensions (mm) of Salla notohippids.

	new genus of Salla	Eurygenium sp.		Rhynchippus sp., cf. R. brasiliensis
	MNHN-Bol-V-003642	MNHN-Bol-V-003643	MNHN-Bol-V-003644	MNHN Bol-V-003456
I1 length	9.3	8.3	---	7.4
width	6.0	7.8	---	4.8
I2 length	12.8	8.7	---	---
width	6.9	7.4	---	---
I3 length	6.9	8.7	---	7.8
width	4.8	6.9	---	5.1
C length	7.0	7.8	---	9.0
width	3.8	(2.4)	---	4.3
P1 length	5.6	4.8	---	---
width	6.8	7.1	---	---
P2 length	10.5	7.8	7.9	6.8
width	9.6	9.7	9.8	7.9
P3 length	12.0	7.9	8.2	7.8
width	11.5	11.0	10.8	9.2
P4 length	12.6	10.4	8.9	9.3
width	11.5	12.0	11.6	10.8
M1 length	22.2	17.0	17.5	14.0
width	16.4	16.0	15.9	12.6
M2 length	24.1	23.6	24.5	18.5
width	12.9	15.3	13.1	12.6

An anterolingual cingulum is present on P3-M1, which is distinct from the fossettes of these teeth. No anterolingual cingulum is visible on M2. The cingulum on the premolars resembles that seen in Rhynchippus equinus and Salla specimens of R. sp., cf. R. brasiliensis, described below. The distinct anterolingual cingulum of M1, however, is unique to Deseadan notohippids. The upper dentition is complete and lacks a diastema. (See Table 3.3 for measures of the dentition of the proposed holotype.)

A broad, shallow depression occurs in the preorbital region of the maxillae, extending from the infraorbital foremen, above the M1, to the area above P2. This depression is not adjacent to the nasal bone, as is the dorsal preorbital fossa of Miocene horses (see MacFadden, 1992: fig. 5.16) but may be at least analogous to the lower or "malar" fossa of many of these Miocene equids (Gregory, 1920).

UF 149219 is referred to this genus because the M1 has the distinctive anterolingual cingulum. This specimen contains associated upper (right P2-4, M1-2) and lower (left p2-3, m2-3, and left and right i1) teeth. The little-worn m3 (Fig. 3.5C) has a lingual fold partly bisecting the trigonid. The posterolingual projection of the trigonid is just coming into contact with the broad ectolophid defining the trigonid-talonid fossettid. An entolophid fossettid is present. The m2 is damaged, but shows the trigonid-talonid fossettid, the entolophid fossettid, and the newly formed posterior fossettid, which developed as a result of the posterolingual portion of the talonid coming into contact with the entolophid. UF 149224, left and right m2 and m3 (see Fig. 3.5C), are similar though show greater wear. The lingual trigonid fold persists in the m3 which has the trigonid-talonid fossettid and the entolophid fossettid. The m2 has three fossettids and no trace of the trigonid lingual fold seen in the m3s.

Eurygenium Ameghino, 1895
(= Eurygeniops Ameghino, 1897)

Type Species. Eurygenium latirostris Ameghino, 1895. Holotype MACN A 52-70 (an edentulous premaxilla). MACN A 52-71, an anterior cranium with dentition, was incorrectly regarded as the holotype by Loomis (1914: fig. 68). From Patagonia, although the specific localities are unknown.

Included Taxa. Eurygenium, sp. nov. and, provisionally (see discussion below), Morphippus imbricatus Ameghino, 1897.

Revised Diagnosis. Anterolingual cingula of upper premolars absent; cingula of lower incisors and canines absent or reduced; p4 and molars lack entolophid fossettids, having but one fossettid at the trigonid-talonid border. Short muzzle with anteroposterior dimensions of premolars reduced. Palate width variable, conspicuously broad in E. latirostris. Manus tetradactyl, and third trochanter proximally placed in the Salla species, whereas, manus tridactyl and third trochanter projecting from femur at mid-shaft level in Rhynchippus equinus. Loss of entolophid fossettid of molars, reduction or loss of lingual incisive cingulae, reduction of anteroposterior dimension of upper premolars, and loss of upper premolar anterolingual cingulae regarded as synapomorphies uniting E. latirostris, M. imbricatus, and E. sp. of Salla.

Eurygenium sp. nov.
(Figs. 3.6 - 3.8; Table 3.4)

Proposed Holotype. MNHN Bol-V-003643 (UF 137882, cast): Rostrum with complete and well-preserved upper dentition (Fig. 3A). The portion posterior to the orbits is missing, and the nasals and premaxillae are crushed. Both maxillae, the right frontal, and anterior zygomatic arch are intact.

Referred Specimens. UF 146400, right I12, P1-M1 and left I12, P1-4; UF 90981, premaxilla, left and right maxillae with left and right P3-M3; UF 146398, right P3-4; UF 146399, right P4-M2; UF 149210, left P4-M2; UF 137887, right P2-M3 with posterior cranium; UF 90996, right M2; UF 137883, left M1-3; UF 137884, left M1-3; UF 149216, partial skull and basicranium of juvenile with left and right dC, dP1-4 and M1; UF 149217, right dP34 and M1; MNHN-Bol-V-003644, nearly complete skeleton; MNHN-Bol-V-003645 mandible with complete lower dentition; MNHN-Bol-V-003646, left dp4-m1, premaxilla with I1 and 2, LM1; UF 149209 mandible with nearly complete dentition; UF 149212 mandible with left p4-m3 and right m1-3; PU 20696, associated palate and mandible; PU 22105, right P4-M3; PU 21928, right I2-M1 and left C-P3; PU 22106, right P3-M3; PU 22107, I1-M2; PU 22103, left P2-M3; PU 20699, left P4-M3; right M2-M3; PU 22136, left M2-M3; PU 21929, mandibular symphysis with right ramus, left i1-i3 and right i1- m3; PU 21934, mandibular symphysis and partial right ramus, with right i1-m1 and left i1-p2.

Horizon and Locality. The author collected the proposed holotype from the Upper White Level (Unit 6), 300 meters above the base of the beds, at Tapial Pampa East in the Salla Beds in 1992. Specimens referable to this species have been found from the lowest faunal regions of Salla (Unit 1 at

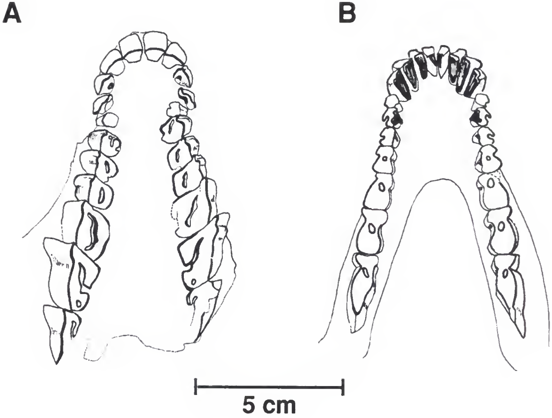

Figure 3.6. Eurygenium sp., occlusal view of palate (A) MNHN-Bol-V-003643 and mandible (B) MNHN-Bol-V-003645.

Willa Kkollu) and at various localities up to the Upper White Level (see Figs. 1.2 and 1.4). The "cf. Rhynchippus sp" reported from the from the Petaca Formation in Southern Bolivia (Senjinés and Jiménez, 1976) is referable to this species.

Diagnosis. Palate and muzzle not conspicuously broad, as that of E. latirostris; no bifurcation of anterior arm of upper molar lingual infolding of enamel (or fossettes with wear); protoloph of M2 long, giving tooth distinctive oblique appearance. Lower incisors lack labial longitudinal groove, and canines do not project laterally as occurring in Morphippus imbricatus. Size similar to Rhynchippus equinus, but entolophid fossettids of lower molars absent, upper premolar anterolingual cingulae absent, anteroposterior dimension of upper premolars shorter, manus tetradactyl, and third trochanter more proximally placed. Size greater than R. pumilus and R. brasiliensis. Differentiable from the previous species by rounded muzzle, I3 less reduced, labial upper molar fossette absent, and anterolingual cingulae of upper premolars absent.

Description. The well-preserved dentition of the holotype shows a slight pinching behind the rounded premaxillary dental arcade. I1 and I2 are roughly equal in size, both in occlusal area and crown height. The reduction in I3 is not great, being slightly smaller and lower crowned. It shows less wear than the I1 and I2 and retains a posterior cingulum, which has nearly worn to a shallow fossette on the right I3. The canines are a little smaller than I3 and show same general form, but having less wear.

The premolars of UF 146400 are but lightly worn. The upper canine is unerupted. The parastyle and protocone are not connected at the occlusal level of the well-worn dP1. P2 and P3 of this young individual are but slightly worn and show a distinct parastyle having a short protoloph which does not connect with the paracone. The valley projecting through the parastyle and protocone enlarges and becomes the premolar fossette once wear unites the protoloph with the protocone. This completed protoloph occurs on the more heavily worn P4. A posterolingual cingulum is apparent in these slightly worn premolars; however, there is not even a trace of the anterolingual cingulum as seen in the premolars of the new genus described above and species of Rhynchippus.

M1 of the proposed holotype lacks the anterolingual cingulum seen on the M1 of the previously described Salla notohippid. This tooth is roughly square in occlusal view, whereas M2 of the holotype has an elongated protoloph as compared to the posterior border of the tooth. M2 retains the pronounced infolding of the lingual enamel, but this feature has become isolated as the major fossette by wear on the M1. M2 has a small fossette posterior to the lingual enamel infolding. This posterior fossette originates from the posterior cingulum, as seen in juvenile specimens UF 149216 and UF 149217 and confirmed by serial cross sections of the M1 of UF 149217.

M3 has erupted, but only the anterior half of the tooth has come into wear. The posterior most part of this tooth still lies about 7 mm from the occlusal plane of the tooth. The posterior border of M3 lacks enamel.

The bones surrounding the right orbit almost completely encircle it, except for a small gap (< 2 cm) between the distinct postorbital process and the ascending zygomatic arch. A lacrimal tuberosity lies at the anterior point of the orbit. The infraorbital canal has a dorsoventral diameter of 6 mm.

Mandible. MNHN Bol-V-003644, MNHN Bol-V-003646, and PU 20696 contain associated upper and lower dentitions. The lower molars and premolars (Fig. 3.6B) are distinct from those of other genera of Deseadan notohippids, early toxodontids (e.g. Proadinotherium, Adinotherium), and leontiniids (e.g., Leontinia, Scarrittia, Ancyloceolus, Colpodon, Huilatherium) in the lack of the entolophid fossettid. The anterior mandibular dental arcade is rounded, and the canines are contained within the arch. They do not protrude laterally as in Morphippus imbricatus (Fig. 3.9 and Ameghino 1897:fig. 46). The lower incisors of E. sp. nov. also lack the external longitudinal grooves seen on MACN A 52-76 and noted by Ameghino (1897).

Postcranial skeleton. MNHN Bol-V-003644 was discovered by Roger Portell of UF in the Upper White Level (Unit 6) in May 1992. This nearly complete articulated skeleton is the first of Eurygenium , or any notohippid, to be reported.

The forelimb (Fig. 3.7A) appears to have been adapted for strength, rather than speed. This strength is inferred from the large surface area for attachments of the deltoids and pectorals. The crests for the attachments of these muscles extend ventrally, two-thirds of the way along the humeral shaft. Additionally, the olecranon process is relatively long (25% of the total ulnar length) and would have provided a significant mechanical advantage for the elbow extensors, the triceps and anconeus muscles. The ability to supinate is implied by the independence of the ulna and radius, and the subspherical shape of the capitular region of the trochlea. Both forelimbs were found flexed and supinated, showing a degree of dexterity suggesting

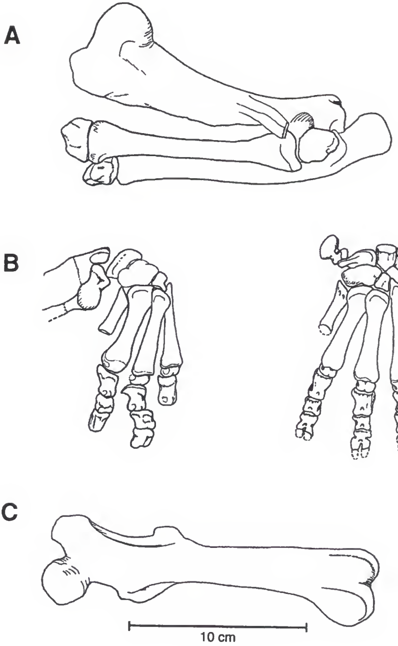

Figure 3.7. Postcranial elements of Eurygenium sp. (MNHN-Bol-V-003644). A, left humerus, ulna, and radius; B, right manus (left) as found in matrix (flexed and supine) and (right) reconstructed as pronated and unflexed; C, left femur.

Table 3.4. Dimensions of postcranial elements of MNHN-Bol-V-003644. All dimensions (mm) are greatest lengths, unless indicated as greatest transverse widths (TVW).

L. humerus	156
L. ulna	167
R. ulna	166
R. radius	126
L. cuneiform (TVW)	21.9
L. lunar (TVW)	11.9
R. lunar (TVW)	12.0
R. scaphoid (TVW)	12.2
L. unciform (TVW)	23.2
R. metacarpal II	52.1
R. metacarpal III	52.1
R. metacarpal IV	48.5
R. metacarpal V	≈30
L. femur	176
R. femur	174
L. tibia	164
R. metatarsal III	44.5
L. metatarsal III	44.3
L. metatarsal IV	42.5

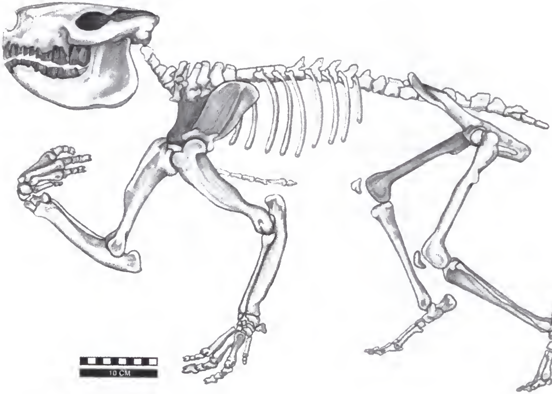

Figure 3.8. Reconstruction of the composite skeleton of Eurygenium sp. Postcranial skeleton is based upon MNHN-Bol-V-003644. Cranium is a composite based upon PU 20680, MNHN-Bol-V-003643, and UF 137887. Mandible is based upon MNHN-Bol-V-003645.

that the animal would have been capable of scratching its right shoulder with its right digits. There is no entepicondylar foremen on the humerus, but a supratrochlear foremen is present.

The manus is tetradactyl (Fig. 3.7B), with no evidence of digit I. Metacarpal V is reduced, but not to the extent seen in Rhynchippus equinus (Loomis, 1914) nor early toxodontids, such as Adinotherium and Nesodon (see Scott, 1912). Metacarpals II, III, and IV are nearly equal in length (see Table 3.5), while metacarpal V is shorter and thinner (total length minus the missing epiphysis is 26 mm; estimated total length would have been about 30 mm). These metacarpals are not closely compacted as in R. equinus. Furthermore, they are both relatively and absolutely shorter than the metacarpals of R. equinus. The distal phalanges have the distinctive medial grooves as seen in R. equinus.

The femur (Fig. 3.7C) is teardrop-shaped in cross section, with the cross-sectional apex pointing medially. The greater trochanter does not extend above the head, while the lesser and third trochanters are developed about one-third of the way down the femoral shaft. The head is hemispherical and the diameter of the neck is smaller than the diameter of the head. The angle of the neck to the shaft approaches 45°. The femur of this Salla species of Eurygenium is shorter than that of R. equinus (175 mm to 202 mm), but more gracile than that of the R. equinus specimen (ACM 3291) described by Loomis (1914). The more distal position of the third trochanter in E. sp. distinguishes it from Adinotherium and Nesodon (Scott, 1912), as well as from R. equinus, all of which have third trochanters projecting at the mid-shaft level.

The pes is not well preserved; however, there is sufficient material to infer that it was tetradactyl, although functionally tridactyl. Metatarsals II, III, and IV are roughly equal in size (see Table 3.5), and although metatarsal V was not recovered, the right cuboid and metatarsal IV show evidence for articulation with a much-reduced metatarsal V. The metatarsal/femur ratio is 0.25, which is more similar to that in carnivorans than to extant ungulates (Garland and Janis, 1993). The astragalus is broad, certainly broader than the astragalus of R. pumilus (see Chaffee, 1952), and relatively shorter than that astragalus of Rhynchippus. There is no cubo-astragular contact. The neck of the astragalus is quite short and unconstricted. The trochlear groove is not distinctively deep. In the right pes, the ectocuneiform and the mesocuneiform are fused, whereas, the left ectocuneiform is a separate element. (The left mesocuneiform was not found.) The few preserved phalanges are short, and the distal phalanges lack the medial groove seen in the distal phalanges of the manus.

The partially articulated vertebral column suggests an estimated head and body length of 760 mm and an estimated mass of 9.6 kg based upon the regression of Damuth (1990) for all ungulates, or 11.8 kg for nonselenodonts. Damuth found head and body lengths to be a better predictor of body mass than dental measurements. Regression equations derived from proximal limb elements of extant ungulates (Scott, 1990) predict masses of 34.3 kg and 27.5 kg based on the lengths, respectively, of the humerus (156 mm) and femur (177 mm). The mean of these masses is 20 kg, which is consistent with a qualitative estimate of an 18 liter volume derived from a clay model of the animal. A reconstruction of this skeleton is given in Figure 3.8.

Discussion. In erecting the genus Morphippus, Ameghino (1897) mistakenly combined characters from a mandible with those of a cranium from a different genus (Fig. 3.9). In his description of Morphippus imbricatus, Ameghino figured and gave measurements of a cranium (MACN A 52-59, cataloged as coming from Cabeza Blanca) and a mandible (MACN A 52-56, noted as being from La Flecha). The cranium is indistinguishable from R. equinus and is nearly identical to FMNH P13410, figured by Scott (1937: fig. 319). This FMNH specimen has an associated mandible and demonstrates the characters noted by Ameghino as diagnostic for Rhynchippus (Ameghino, 1897) and are illustrated in the type specimen of R. equinus (Ameghino, 1897:figs. 50 and 51; specimen MACN A 52-31).

The mandible of Morphippus imbricatus (MACN A 52-76) is similar to that of Eurygenium sp. of Salla in that the cheek teeth lack the entolophid and posterior fossettids seen in most advanced Toxodontia. It differs from that of Eurygenium sp. in having laterally projecting lower canines and pronounced longitudinal grooves in the external surface of the incisors. This distinctive mandible should be regarded as the holotype of Morphippus imbricatus, whereas the cranium MACN A 52-59 is referred to Rhynchippus equinus.

The absence of entolophid and posterior fossettids in p4-m3 in M. imbricatus and the Salla species of Eurygenium suggests a synapomorphy uniting these taxa. A close relationship of E. latirostris to this Salla notohippid may also be indicated in the apparently derived condition of their upper premolars (loss of anterolingual cingulum and reduced L). The absence of associated cranial material of M. imbricatus and lack of an associated

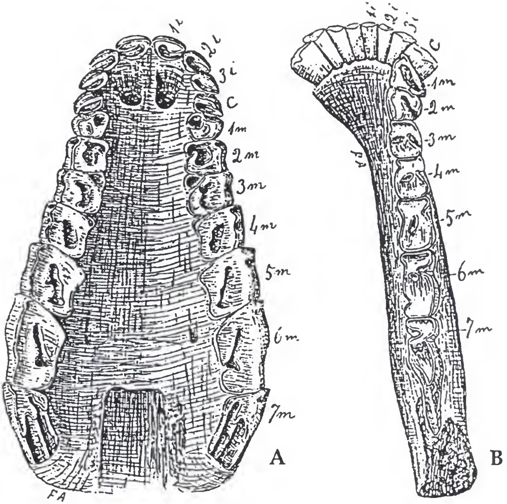

Figure 3.9. Ameghino's figure of cranium and mandible of *Morphippus imbricatus* from his intial description (Ameghino, 1897). These are regarded in this work as belonging to distinct species. The cranium is referred to *Rhynchippus equinus* (see text).

Table 3.5. Morphometric data are given for specimens of Eurygenium spp. and Rhynchippus equinus. The P4 of Eurygenium sp. of Salla is relatively narrower than that of R. equinus as shown by the significantly lower P4/M1 ($p<0.05$). The specimen of E. latirostris also has a relatively short P4. The specimen of E. normalis has a P4/M1 more similar to that R. equinus.

Taxon	**Specimen**	**PL**	**MW**	**P4ap**	**M1ap**	**P4/M1**
Eurygenium sp.	PU 20680	116	43.3	10.0	14.4	0.69
Eurygenium sp.	PU 20696	108	40.0	9.4	13.6	0.69
Eurygenium sp.	UF 146400	---	---	10.2	17.0	0.60
Eurygenium sp.	UF 90981	109	32.0	9.8	15.0	0.65
Eurygenium sp.	Bol-V-003643	104	---	10.4	17.0	0.61
Eurygenium sp.	Bol-V-003644	---	---	8.9	17.5	0.51
E. latirostris	MACN A 52-71	142	54	10.5	16.5	0.63
E. normalis	MACN A 52-85	--	--	10.3	13.8	0.74
R. equinus	ACM 3028	140	--	13.0	15.5	0.84
R. equinus	FMNH P13420	122	35	12.2	16.6	0.73
R. equinus	FMNH P13410	127	42.7	12.6	16.2	0.78
R. equinus	FMNH P13287	129	36	12.7	15.9	0.80
R. equinus	MACN A 52-31	123	--	12.4	14.3	0.87
R. equinus	MACN A 52-49	134	--	12.3	17.1	0.72
R. equinus	MACN A 52-59	112	36.7	12.6	16.9	0.74

mandible of E. latirostris prevent direct comparison of these two taxa. However, since they both appear to be closely related to Eurygenium of Salla, one may conclude that they too are closely related. It is even possible that M. imbricatus and E. latirostris represent a single species. The laterally projecting canines of M. imbricatus gives the lower cropping arcade sufficient breadth to occlude with the unusually wide premaxillary arcade of E. latirostris. The nature of the M. imbricatus upper dentition, however, will remain unknown until both dental series are found in association. Although there is no associated mandible known for E. latirostris, Ameghino did refer some lower molars to this taxon (e.g., MACN A 52-72 and MACN A 52-75). These, like M. imbricatus and Eurygenium sp. of Salla, lack entolophid fossettids.

In 1952, Bryan Patterson, then with the Field Museum, visited and organized much of the Ameghino Collection of MACN. He noted the mispaired cranial and mandibular material for M. imbricatus in an unpublished catalog that he prepared. The catalog indicates that he would have considered the mandible to be the holotype of M. imbricatus, and he cataloged and labeled the cranium (MACN A 52-59) as R. equinus. His referral of the holotype of Eurygenium normalis to M. imbricatus indicates that he believed that these upper teeth represented the unknown uppers of M. imbricatus.

Unfortunately, E. normalis is known only from the fragmentary holotype (MACN A 51-85), which has no associated lower teeth (it consists only of P4-M3). It is too poorly known to be confidently referred to Eurygenium. Ameghino referred it to Eurygenium because the P4 does not show the anterolingual cingulum. The absence of this cingulum, however, is not diagnostic, because the P4 had worn beyond the point where it would have appeared. A bulge in the anterolingual corner of the tooth is suggestive of the former presence of this cingulum, which would have caused such an increase in the occlusal surface area once it came into wear. This bulge is seen on P4s of older individuals of R. equinus (e.g., ACM 3028 in Loomis 1914:fig. 54; and MACN A 52-31). Moreover, the ratio of the anteroposterior length of the P4/M1 is more similar to those of R. equinus than those of Eurygenium (Table 3.5).

Specimens of this species have been found at various localities of Salla ranging from the lowest section at Willa Kkollu to the Upper White at Tapial Pampa. In July 1996 I had the opportunity to examine the notohippid (YPFB, Pal.-0932) found just above the base of the Petaca Formation near Santa Cruz, Bolivia. This specimen, reported in the literature as "cf. Rhynchippus sp." (Sanjinés and Jiménez, 1976) is indistinguishable from the Salla species of Eurygenium. The conspecific assignment of a Salla taxon with that of the Petaca Formation supports the hypothesis that these two localities are contemporaneous (Sempere et al., 1990).

Rhynchippus sp., cf. R. brasiliensis Soria and Alvarenga, 1989

Figs. 3.10 and 3.11; Tables 3.3 and 3.6

Holotype. DGM 1092-M, fragment of left mandible containing m3 and the talonid of m2 from the Tremembé Formation, Municipio de Tremembé, Estado de São Paulo, Brasil.

Referred Salla specimens. MNHN-Bol-V-003456, upper dentition, lacking right M3, left and right P1, and left P2; MNHN-Bol-V-003457, cranium with mandible; MNHN-Bol-V-003458, rostrum with right and left I1-P3; MNHN-Bol-V-003647, left P2-M1; UF 149201, mandibular ramus with p2-m3; UF 149202, mandibular symphysis with left ramus and left i1-m3 and right i1-p3 and associated distal right humerus; UF 149203, left m2-3; UF 149205, right m1-2; UF 149227, distal left humerus; UF 91927, mandible with left di1-2, dp2-4, m1-2 and right di1-2, dp3, and m2.

Description. This species is the smallest notohippid of Salla (Figs.3.10 and 3.11; Table 3.7). The upper premolars retain distinct anterolingual cingula; however, the molars do not. The labial border of the lingual infolding of enamel in the upper molars is more undulating than that in the previous two taxa described. The lingual infolding of the M2 of MNHN-Bol-V-003456 has a small bifurcation of the anterior arm, and the ectoloph is modestly undulated (Figs. 3.10 and 3.11). The M2 retains the posterior fossette but has no lingual fossette. The incomplete premaxillary dental arcade of MNHN-Bol-V-003456 appears rounded, and this condition is confirmed in the intact premaxilla of MNHN-Bol-V-003458. Lower molars form fossettids at the trigonid-talonid border, in the entolophid, and, with significant wear, just posterior to the entolophid when the caudal region of the talonid contacts the lingual ectolophid. The molar trigonids have infoldings of lingual enamel.

The Salla specimens are slightly larger than specimens of R. pumilus from Patagonia, and there are sufficient numbers of lower molars of the Bolivian and Patagonian specimens to suggest that the size difference is significant ($p < 0.05$) (Table 3.6). There was virtually no overlap of the dental and cranial measures between the Bolivian and Patagonian specimens. The

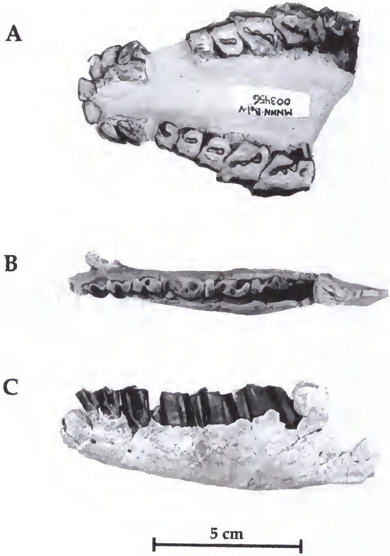

Figure 3.10. Rhynchippus sp., cf. R. brasiliensis. Palatal view of MNHN-Bol-V-003456 (A) and occlusal (B) and lateral (C) views of mandible UF 149201.

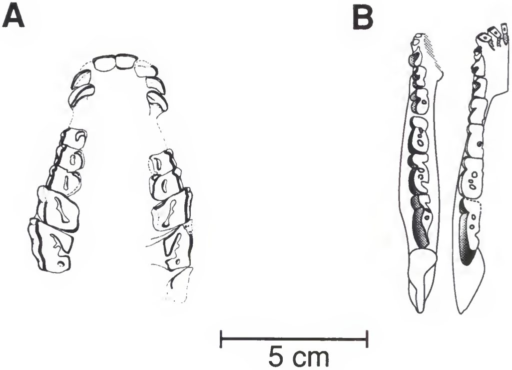

Figure 3.11. Rhynchippus sp., cf. R. brasiliensis. Palatal view of MNHN-Bol-V-003456 (A) and occlusal views of mandibles (B) UF 149201 (left) and 149202 (right).

Table 3.6 Palatal lengths (PL) and anteroposterior lenghts (AP) of upper and lower fourth premolars and first two molars are given for specimens of Rhynchippus pumilus from Patagonia and for specimens of R. sp., cf. R. brasiliensis from Salla. Specimens of R. sp., cf. R. brasiliensis from Salla are larger than the Patagonian specimens with virtually no overlap. The holotype of R. pumilus is indicated by the asterisk (*).

Upper Dentition

Locality	Specimen	PL	P4 AP	M1 AP	M2 AP
Cabeza Blanca (?)	*MACN A 52-61	85	7.8	8.7	12.4
Cabeza Blanca	AMNH 29555	68	7.4	12.5	15.1
Scarritt Pocket	AMNH 29579	80	9.3	12.4	14.8
Salla	Bol-V-003456	90	9.3	14.0	18.5
Salla	Bol-V-003647	--	--	15.3	--

Lower Dentition

Locality	Specimen	p4	m1	m2
Gran Barranca	MACN A 52-62	--	10.3	11.0
Cabeza Blanca	MACN A 52-63	--	11.5	--
? unknown	MACN A 52-64	--	--	12.3
La Flecha	MACN A 52-67	--	10.9	--
Cabeza Blanca	FMNH P14691	8.2	10.5	12.1
Cabeza Blanca	FMNH P14673	--	10.7	12.8
Scarritt Pocket	AMNH 29579	--	9.8	12.4
Salla	PU uncataloged	8.6	12.3	--
Salla	MNHN Bol (GB101)	8.5	12.9	14.5
Salla	UF 149201	8.7	--	13.5
Salla	UF 149202	9.3	11.7	15.8
Salla	UF 149203	--	--	14.7
Salla	UF 149205	--	--	15.0
Salla	UF 91927	--	--	16.0

The larger size of the small Salla notohippid suggests that it is not referable to Rhynchippus pumilus, but may be referable to R. brasiliensis, which is a little larger than R. pumilus (Soria and Alvarenga, 1989). Unfortunately, R. brasiliensis is known only from the fragmentary holotype. The only tooth from which an anteroposterior measurement can be obtained is the m3. Soria and Alvarenga (1989) reported its anteroposterior length as 20 mm which is larger than that of R. pumilus (Soria and Alvarenga, 1989) but within the range of measurements of Salla specimens (17 - 21 mm, n=3). UF 149201 (Fig. 3.11B, left) and the holotype of R. brasiliensis show similar wear and morphology. Both their m3s have lingual trigonid infoldings and their entolophids contain a single fossettid. The m2s of these specimens have trigonid-talonid fossettids, as well as entolophid fossettids. The trigonid of the m2 on the holotype of R. brasiliensis is missing, but the Salla specimen has lingual infolding in its trigonid. In addition to having a trigonid-talonid fossettid and an entolophid fossettid, the m1 of UF 149201 has a posterior fossettid.

The distal part of a right humerus was found with UF 149202. Its trochlea is similar to that of R. equinus figured by Loomis (1914:fig. 58).

Because the holotype of R. brasiliensis is so fragmentary, the referral of the Salla species of Rhynchippus to this taxon is considered tentative.

Toxodontidae Owen, 1845

Toxodontids were among the first endemic South American taxa described (see Chapter 1). They are characterized by ever-growing incisors, tridactyl manus, tusk-like I2, concave upper molar ectoloph. Primitive genera have distinctive, elongated upper molar cristae (second crista unites with crochet), and lingual origination of molar crochet (Cifelli, 1993).

The origin of the family is obscured by the pre-Deseadan depositional hiatus. In his first work regarding the Deseadan, Ameghino (1895) described five species, which he placed in four genera (Proadinotherium leptognathum, Pronesodon cristatus, P. robustus, Senodon platyarthrus, and Scaphops grypus). Most of these are regarded as synonyms of P. leptognathum (Simpson, 1945) and Ameghino later referred Scaphops to the leontiniidae (Chaffee [1952] regarded Scaphops as a synonym of Leontinia).

Proadinotherium appears the only valid Deseadan toxodontid genus, known not only from Patagonia, but also Colombia (Stirton, 1947) and Salla (Hoffstetter, 1968 and below). One species (P. muensteri) is known from the Colhuehuapian of Patagonia.

Proadinotherium Ameghino 1895, cf. Proadinotherium sp.

Figs. 3.12 and 3.13; Table 3.7

Referred specimens. UF 149222, mandible with complete lower dentition, found in Unit 3 of Pasto Grande; UF 149223, mandible with right and left p3-m3, found in Unit 3 of Pasto Grande; MNHN-Bol (sin numero), badly damaged P4-M3, found in the Upper White at Tapial Pampa.

Description. UF 149222 (Fig. 3.12) preserves the lower incisive battery which is transversely linear and generally similar to that of Adinotherium (see Scott, 1912: Plate XVII, 10). The incisors of the Salla specimen, however, have shorter crowns. As in Adinotherium the lower incisors form an

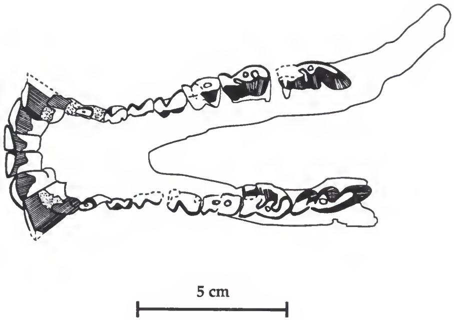

Figure 3.12. Occlusal view of mandible of Proadinotherium sp. (UF 149222).

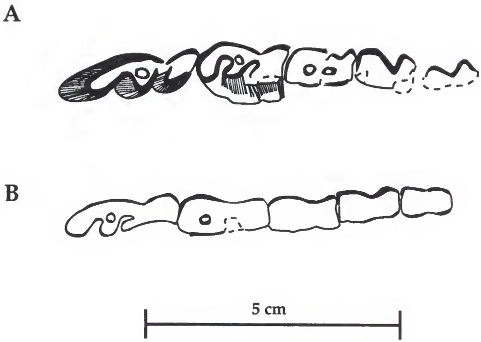

Figure 3.13. Occlusal views of p3-m3 of two specimens of Proadinotherium sp., UF 149222 (A) and the onotgenetically older UF 149223 (B).

Table 3.7. Dental dimensions (mm) of cf. Proadinotherium sp.

tooth	**UF 149222**	**UF149223**
i1 breadth	8.4	------
depth	4.8	------
i2 breadth	11.8	------
depth	4.8	------
i3 breadth	(13.3)	------
depth	4.6	------
c breadth	6.9	------
depth	2.5	------
p1 length	5.5	------
width	3.5	------
p2 length	8.5	------
width	4.3	------
p3 length	9.5	10.0
width	5.5	5.7
p4 length	10.8	12.5
width	6.5	6.6
m1 length	12.6	14.5
width	6.9	7.3
m2 length	16.9	18.2
width	6.8	7.7
m3 length	23.0	24.3
width	6.9	7.6
p3-m3	76	81
i3-i3	(51)	---

irregular triangle in occlusal view. The lateral incisors have a greater breadth than the medial (see Table 3.7). These teeth form roots, unlike most other toxodontids. The roots of i3 are quite long but ultimately come to a closed point. All the lower incisors are procumbent. Also, i1-3 have enamel on both the internal and external surfaces, which differs form the condition seen in the specimen of Proadinotherium leptognathum described by Ameghino (1895) which had only external enamel. The lingual surface has less enamel than the labial, so presumably with greater wear one might see just the external enamel.

The canine is much smaller than any of the incisors, is not caniniform but is unlike the incisors of this animal. It is gently curved in occlusal view, with the labial side convex and the lingual concave. It has a blunt internal cingulum. It is so small that it appears vestigial, an interpretation supported by its unworn state.

No diastema occurs between the c and p1 as in the P. leptognathum specimen figured by Loomis (1914: fig. 81). The p1 is smaller than the canine, but shows some sign of use. It 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 premolars of UF 149222, nor the more heavily worn UF 149223 (Fig. 3.13), have any fossettids. The labial infolding of enamel between the trigonid and talonid is deep on the p4 of UF 149222.

The m1 has formed a trigonid-talonid fossettid and an entolophid fossettid. The m2 is less heavily worn and the posterolingual portion of the trigonid has not come in contact with the entolophid at the occlusal level so that the only fossettid seen is that of the entolophid. The occlusal internal enamel undulates on the m2, having pronounced infoldings between the trigonid and entolophid and between the entolophid and hypolophid. The m3 has a similar form, except that the hypolophid is elongated and not directed medially.

Though the crowns of upper teeth of the MNHN-Bol specimen are damaged, the coronal pattern is persistent enough to demonstrate the long, distinct first cristae of the molars, the presence of a labial fossette (enclosed by the crochet, metaloph, ectoloph, and second cristae), and an irregular posterior fossette (between the metaloph and posterior cingulum). The crown patterns of the molars are comparable to the specimen of P. leptognathum described by Loomis (1914: fig. 80), who repeatedly misspelled the species name.

Discussion. The Salla toxodontids referred to Proadinotherium sp. differ from the Amherst referred specimen of P. leptognathum by its smaller size, lack of diastema, presence of molar entolophid fossettid, and a more transversely oriented entolophid. The distance between the anterior i3 to posterior m2 is 25% greater on the Loomis specimen (115 mm of ACM versus 91 mm on UF 149222). The m2 is only comparable grinding tooth present in the Loomis specimen, which is larger, has an obliquely oriented entolophid, and does not show an ectolophid fossette.

Specific referral of the Salla toxodontid should be deferred until it is compared with the holotype of P. leptognathum and additional referred specimens.

CHAPTER 4
ONTOGENY OF TWO NOTOUNGULATES OF SALLA

Introduction

Collecting at Salla over the past five years has yielded sufficient numbers of juvenile specimens of the notohippid Eurygenium sp. and the mesotheriid Trachytherus spegazzinianus to document the ontogenetic changes of their teeth. The upper milk teeth of these two species are described below. This represents the first descriptions of the milk teeth of any notohippid or mesotheriid. Descriptions of these teeth are necessary so that isolated low-crowned teeth may be properly identified. Otherwise, it would be impossible to discriminate a deciduous notohippid premolar from that of a mesotheriid or even an adult postcanine tooth of an isotemnid.

Study of deciduous premolars has long been regarded as a useful means of understanding the development and homologies of the permanent molars (Matthew, 1937; Butler, 1952). This is considered valid since the deciduous premolars and permanent molars are believed to represent the same series; that is, they are derived from the same germ, whereas the permanent premolars represent a second dental series (Luckett, 1993).

An unworn dP2 referred to Eurygenium sp. suggests an alternative, parsimonious hypothesis to Patterson's interpretation regarding notoungulate cusp homologies (Patterson, 1934a). He believed that the posterior loph of the anterior deciduous teeth was composed of the protocone, which split going from dP3 to dP4 to form the "pseudohypocone" of the posterolingual loph and the "protocone" on the anterolingual loph (see Fig. 4.1). The alternative hypothesis presented here is that the protocone formed part of the anterolingual loph (not the posterolingual) of the anterior milk molars and that no protocone splitting between the dP3 and dP4 occurred. The posterolingual loph is interpreted as being composed of the "hypocone" and the posterior cingulum.

One juvenile specimen of Trachytherus described below is so little abraded that it likely was still nursing at the time of death. The milk molars of this animal retains details of the crown pattern that illustrates the ancestral notoungulate "face" pattern and the genesis of the upper molar mesotheriid median loph, a feature characteristic of geologically younger mesotheriids.

Survey of Studies of Juvenile Notoungulates

The profound ontogenetic changes that occur in the dentitions of notoungulates have provided challenges for students of South American paleomammalogy since its beginning. Unknowingly, Owen (1846) gave two names to a single species of toxodontid, one of which was a juvenile (Nesodon imbricatus) and the other (N. sulivani) an adult. The proliferation of names for this species continued to such a point that Scott (1912) listed 41 synonyms in nine genera for N. imbricatus. Ameghino (1891b and 1894) noted the pronounced changes in the dental morphology with ontogeny and wear of Nesodon and listed 12 stages which included descriptions of the

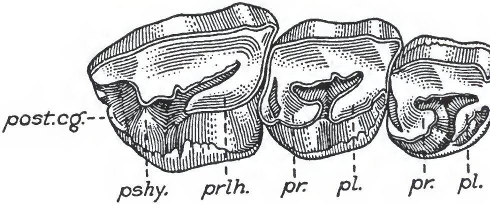

Figure 4.1. Deciduous upper premolars (dP2-4) of Leontinia gaudryi (FMNH P14659). The figure and terminology of the tooth topography is from Patterson, 1934a. pl., protoconule; post. cg., posterior cingulum; pr., protocone; prlh., protoloph; pshy., "pseudohypocone". (See text and Fig. 4.2 for different interpretation.)

"prelacteal" dentition (!), the milk-teeth, eruption sequence of the permanent teeth, and descriptions of their changes in appearance, and size, with wear. Scott (1912) presented Ameghino's stages with minor modifications and also described the milk-teeth, eruption sequence, and wear of adult teeth of Adinotherium ovinum.

The extreme morphological changes in notoungulate teeth appear related to hypsodonty. Madden (1990) noted that the teeth of brachydont species of notoungulates did not show greater intraspecific variation than expected for extant species. However, hypsodont notoungulates had much greater variation in their tooth dimensions. He found that the coefficients of variation (CV) of the the cheek teeth of the hypsodont toxodontid Adinotherium ovinum to be typically well over ten per cent, despite the fact that he controlled for geographic and temporal effects. (Usually CV values within a species are under 10% [Simpson et al., 1960; Gingerich, 1974]). The CV values of the brachydont cheek teeth of leontiniids, Leontinia gaudryi and Ancylocoelus frequens, however, were under ten per cent.

In addition to the change in occlusal size and shape that occurs with abrasion, the repeated evolutionary trend of many notoungulates to develop simplified crowns confounds attempts to use teeth to determine phylogenetic relationships. In many cases the simplification is of such an extreme that the grinding teeth of these animals is rendered a featureless surface lacking identifiable cusps, lophs, or fossettes. Geologically younger notoungulates having dentitions grossly simplified compared to their putative ancestors included toxodontids, interatheriids, mesotheriids, and hegetotheriids (see Cifelli, 1993). The notohippid Eurygenium sp. also has simple tooth crown patterns compared to its assumed sister taxa (Chapters 3 and 7).

The crown patterns of many of these taxa are so superficial that they disappear with the slightest abrasion. Thus, the only way to determine dental characters and their homologies is to examine specimens in which very little abrasion has taken place. This is possible with juvenile specimens which were either still nursing or which had permanent teeth that incompletely erupted. Some such characters are obtained from the notohippid and mesotheriid juvenile specimens described below.

Juvenile Notoungulates of Salla

Eurygenium sp.

Referred juvenile Eurygenium sp. specimens. UF 149216, palate with right and left (d?)C, P1, dP2-dP4 and M1, found in the Upper White (Unit 6) of Tapial Pampa West; UF 149217, right dP3-4 and M1, found in the Upper White of Jaccha Huay Kallumi; UF 91833, left dP2; from the Upper White of Jiska Tapial Chuchu; MNHN-Bol-F-94-21, right dP2; found in the Branisella Zone at Poco Poconi.

Description. The milk molars of UF 149216 (Fig. 4.2B) are well worn, but preserved enough of the crown pattern so that it is worthwhile to compare them to the deciduous teeth of other notoungulates. The M1 was newly erupted, with only the anterior portion having come into wear. The M1 of UF 149217 was similarly worn, but in a better state of preservation. The milk molars, however, had been worn to a greater degree than those of the previous specimen, such that the description of the deciduous uppers will be taken from UF 149216.

The (d?)C is broken on the left, but intact on the right. It is low-crowned, though not obviously heavily worn. Its long axis is obliquely oriented (anterior end medial) and shows but a trace of an internal cingulum.

The first post-canine tooth of UF 149216 appears to be the P1. It is higher crowned than the dP2-4 and is relatively unworn. The paracones and protocones of the P1 remain somewhat pointed, with the paracone being larger and higher than the protocone. The protocone is isolated at the occlusal level, with but a shallow loph connecting it with the metaloph. The parastyle is shallow and anteriorly placed. No protoloph connects the parastyle to the protocone.

Dp2-4 are low-crowned and well worn. This brachydont condition combined with the hypsodonty of the erupting M1 unambiguously identifies them as being milk molars. These compare more closely with the deciduous dentition of Leontinia gaudryi (see Patterson, 1934a) than those of early toxodontids (Scott, 1912). The juvenile dental series described below can not be compared to any other notohippid, since they represent the first description of milk teeth in the family.

The dP2 has the same general form as the dP2 of Leontinia gaudryi (Fig. 4.1). Two worn lophs lie on the lingual side, with the posterior being more robust than the anterior. Patterson interpreted the posterior cusp of the dP2 of Leontinia as the protocone since it occupied most of the area of the lingual portion of the tooth and appears to have emanated from the root. He called the anterolingual cusp the protoconule. A similar condition occurs in an isolated dP2 (UF 91833), which has three roots, two external and one internal. The anterior and posterior lingual lophs are more evenly placed over the lingual root than Leontinia in which the posterior loph overlaid the root. The posterior loph of Leontinia was also much larger than the anterior. The dP2 of Nesodon also had a larger posterior cusp (Scott, 1912, noted the large size of the posterolingual cusp ["tetartocone" using his terminology, with the anterolingual cusp being the "deuterocone"]). The major differences in the Eurygenium dP2 and that of Leontinia, aside from the overall smaller size of Eurygenium, is that the anterior loph of the notohippid dP2 is larger. It also lacks an lingual and anterolingual cingula.

An isolated, unworn dP2 (Fig. 4.2A) shows that the "protoconule" consists of two small cusps, with the more lingual being smallest. The posterior loph is composed of the posterior cingulum and the cusp that Patterson believed was the protocone. This "protocone" has the same general form and relative position to the posterior cingulum as the "hypocone" of adult molars.

The anterior and posterior lingual lophs of the dP3 of UF 149216 have united, isolating the internal valley as a fossette. The labial wall of this fossette has several undulations, suggestive of the presence of minute crista, as seen in specimens of the isotemnid Pleurostylodon (Patterson, 1934a; Simpson, 1967).

As in Leontinia, the dP4 of Eurygenium sp. is molariform, being much longer than the dP3. It also has a greater anteroposterior dimension than the permanent tooth that will replace it. The mean P4 length from adult specimens of Eurygenium sp. is only 9.6 mm (n = 8, OR: 8.5 - 10.4), whereas the dP4 lengths of the juvenile specimens at hand range from about 14 to 16.3 mm (see Table 4.1). The dP4 is sub-rectangular in occlusal view and the protoloph is united with the posterior loph (the "pseudohypocone" of Patterson,1934a) to form the major fossette. A posterior fossette, formed by the posterior cingulum, is also present.

The M1s of these juvenile specimens are little worn, with but the anterior portion of the teeth showing signs of use. The region of the metaloph and posterior to it apparently had not broken the surface. The posterior cingula of these specimens lie about 5 mm below the occlusal plane. The protoloph is narrow and does not unite with the metaloph until a depth of about 6 mm. A distinct crista is present on the UF 149216 specimen. This feature is not seen in any of the UF adult specimens.

The M1 of UF 149217 was sectioned (Fig. 4.3) to demonstrate the occlusal pattern that would have occurred with wear in this animal and to confirm the referral of this specimen to Eurygenium sp. With wear, the M1 length decreases, whereas the width increases (Table 4.1). The protoloph joins the metaloph at a depth of about 13 mm of wear as measured from occlusal surface along the paracone ridge. The posterior fossette disappears at a depth of about 17 mm. At this point, the M1 of the juvenile specimen has a similar cross-sectional appearance to the occlusal surface of the M1 of specimens ontogenetically older individuals (compare Fig. 4.3 A and B). The anterior lingual enamel production ceases at this depth and within about 5 more mm of wear the entire internal enamel is lost.

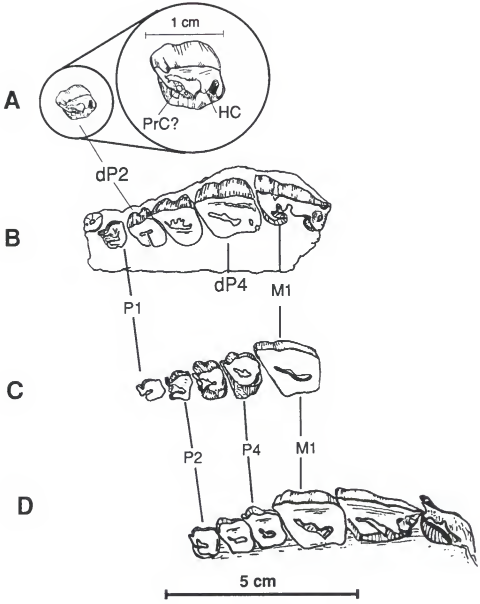

Figure 4.2. Cheek-tooth ontogenetic series of Eurygenium sp. A, UF 173285, enlarged at right. (Scale bar within right circle applicable only within the circle.) B, UF 149216; C, UF 146400; D, MNHN-Bol-V-003644. PrC, protocone; HC, "hypocone, as interpreted in this study. The hypocone of the anterior teeth is homologous to the "protocone" of Patterson, 1934 (see text for discussion).

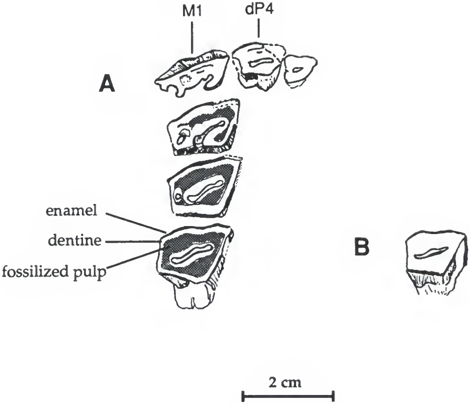

Figure 4.3. M1 of Eurygenium sp. A, serial section of juvenile specimen, UF 149217; B, occlusal view of M1 from UF 146400 (reversed for comparison).

Table 4.1. Dental dimensions of juvenile specimens referred to Eurygenium sp.

Upper Milk Molars

Museum Nº	dP2		dP3		dP4	
	l x	w	l x	w	l x	w
UF 149216 (right)	8.4	9.1	10.8	11.7	16.3	13.5
(left)	8.5	9.3	11.7	12.1	15.6	12.8
UF 149217 (estimated due to damage)	---	---	9.4	11.2	14	12
MNHN-Bol sin num	8.5	9.2	---	---	---	---
UF 91833	8.3	9.0	---	---	---	---

Sectioned M1 of Juvenile
(UF 149217)

depth below labial occlusal surface (mm)	M1 (mm)	
	l x	w
9	21.2	14.4
12	20.8	(13.5)
16	19.5	16.5
20	19.6	16.8
25	18.0	17.8

Discussion regarding juvenile notohippid. The deciduous notohippid teeth described above could easily be mistaken for worn isotemnid teeth. They are low-crowned, of similar size and morphology. These differ in that they retain only a posterior cingulum, which comes into wear quite early in ontogeny, whereas isotemnids typically have internal, anterior, and often external cingulae (see Fig. 2.1A).

The dP1 is unknown in this taxon and perhaps the first premolar is not replaced. The presence of both a dP1 and P1 is demonstrated in an anomalous specimen of Rhynchippus equinus from the Deseadan of the Gran Barranca (FMNH P13410; Fig. 5.6B). Both dP1s in this specimen were not shed when the P1s developed. The dP1s deflected the P1 medially such that they did never came into contact with the lower teeth and thus remained unworn.

As in Nesodon (Scott, 1912) and Leontinia (Patterson, 1934a), P1 of Eurygenium sp. comes into wear considerably earlier than the other permanent upper premolars. It is but a peg-like stub even in young adult specimens of Eurygenium (see Chapter 3: Fig. 3.6).

The dP2 of Eurygenium sp. lacks the distinct crista projecting from the metaloph and ectoloph seen in juvenile specimens of Nesodon (Scott, 1912). The longitudinal metacone ridge on the ectoloph of the Nesodon dP2 is persistent, whereas little undulation of the ectoloph occurs on the Eurygenium dP2, except along the paracone ridge before much wear had occurred (Fig. 4.2A).

The relative positions of the lingual cusps to the roots do not support Patterson's (1934a) interpretation regarding the cusp homologies. He considered the posterior deciduous loph of dP2-3 as being homologous with both the posterior and anterior lingual lophs of the dP4 and adult molars. He hypothesized that the protocone split to form the "pseudohypocone" of the posterior loph of dP4 and the permanent molars and and the elongation of the anterior loph. The "protoconule" became the protoloph. It is more parsimonious, however, to consider the anterior loph of the deciduous tooth the homologue to the anterior loph of the adult molars. This interpretation requires no significant change in the series, whereas Patterson's interpretation requires the both splitting the posterior cusp and attaching the anterior portion to the "protoconule".

DP3 of Nesodon is elongated and molariform, whereas there is not such a great elongation of the dP3 in Eurygenium or Leontinia. The notohippid milk molar has several small cristae projecting from the ectoloph, whereas there is a single, conspicuous cristae in Nesodon and Adinotherium.

DP4 is molariform in the toxodontids, Leontinia and Eurygenium. True to its specific name, the protoloph of the dP4 overlaps the preceding tooth in Nesodon imbricatus. The notohippid deciduous cheekteeth do not imbricate one another.

In its general appearance, the deciduous premolars of Eurygenium sp. are more similar to those of Leontinia than the early toxodontids. The Eurygenium deciduous teeth, however, like those of toxodontids, lack the lingual and anterolingual cingula seen in Leontinia.

Trachytherus spegazzinianus

Referred juvenile specimens of Trachytherus spegazzinianus. MNHN-Bol-94-09, unworn left dP2-4, found in the Upper White Level at Tapial Pampa East; UF 91651, nearly complete cranium, missing the premaxilla and frontals, found in the Branisella Level of Tapial Pampa West; UF 91832, left dP3-4, from the Upper White Level at Jiska Tapial Chuchu; UF 136062, cranium with palate, right dP3-M1 and left dP2-M1, from the Branisella level of Chaccha Tapial Chuchu; UF 137846, palate with right dP2-4, M1 and left dP3-4 and M1, mandible with right i1-2, dp3-4, m1 and left i1-2, dp2-4 and m2, and partial skeleton, found in the Branisella Level of Irupata Loma; UF 137845, partial skeleton, skull containing right and left dP2-4, found in the Upper White Level of Tapial Pampa East; MNHN-Bol-V-003459, palate with right and left dP2-4, M1 and left (d?)P1 found in Unit 5 at Tapial Pampa.

Description. The left maxillary fragment with dP2-4 (MNHN-Bol-94-09) is an instructive specimen because it little worn (Fig. 4.4). This minimal wear and early ontogenetic stage suggest that the animal was not weaned.

In occlusal view, the dP2 of the MNHN-Bol specimen has the coronal pattern of fossettes that give the tooth the "happy face" appearance of archaeohyracids and primitive notoungulates (Fig. 4.5; Simpson, 1967; Cifelli, 1993). The protoloph of dP2 has united with the metaloph, isolating the major fossette (the "smile"). The anterior cristae has not yet contacted the protoloph, but the posterior cirstae meets the crochet. An irregular-shaped fossette is isolated by this union of cristae-crochet and the metaloph and ectoloph. The greatest transverse occlusal dimension is at the posterior portion of the tooth, which is not molariform.

Dp3 is molariform, having a conspicuously greater length than the dp2 (see Table 4.2). The protoloph and metaloph have not yet united at the occlusal surface, nor has the anterior cristae contacted the protoloph. The union of the posterior cristae and crochet forms a slight, lingually oriented apex. The posterior cingulum is occluded and somewhat worn, leaving the trace of a posterior fossette between the cingulum and metaloph.

The dP4 is similar in appearance to the dP3 except that it appears less worn. A median cusp is united with the posterior cristae, but is not connected to the crochet at the occlusal level. At this level of wear the crochet is but a small projection from the median loph. The median cusp appears to be homologous with the median lobe of later mesotheriid upper molars (see Villarroel, 1974: fig. 1). The posterior cingulum is connected to the ectoloph, but is free on the lingual side at the occlusal level. It appears as a loph running parallel to the metaloph. The tooth crown is high, having a metaloph crest length of 23.1 mm, giving it a crown height to length ratio (HI) of 1.42, making this a rather hypsodont tooth, particularly considering that it is deciduous.

Several juvenile specimens demonstrate that the crown patterns of the milk molars obscure early with wear (Fig. 4.6). Their occlusal surfaces appear as nearly featureless except for the major fossette which initially has an asymmetric "V" appearance, then ultimately as a simple oblique line.

The MNHN-Bol specimen (Fig. 4.4 and 4.6A) is the least worn with only the dP2 having formed the fossette which results form the union of the protoloph and metaloph. The infolding of lingual enamel is not isolated as a fossette in dP3-4, but has appears as an asymmetric "Y" shape as in little worn adults (Sydow, 1988). Several specimens (UF 91651, UF 91832, UF 173273) are at the same stage in regard to the fossette development.

The dP4s of UF 137845 and UF 137846 retain the infolding of lingual enamel, but dP2-3 have formed fossettes. The M1 of UF 137846 has broken the gum and shows signs of wear at its anterior occlusal surface. The posterior cingulum is well removed from the occlusal plane and is unworn.

The dP4 of MNHN-Bol-V-003459 has formed the fossette (Fig. 4.6B). The anterior surface of M1 is heavily worn, but the posterior cingulum is still unoccluded. The cusp formed by the cristae-crochet union presents itself as a distinct loph between the protoloph and metaloph, the "median lobe" of Patterson's terminology for the Trachytherus molar (Patterson, 1934b). Patterson (1934b) and Sydow (1988) have described the wear of adult specimens of Trachytherus, so this will not be repeated here.

Several specimens indicate that the dP2-4 are retained after the M1 has completely erupted. The M2 of UF 90989 (Fig. 4.6D) is erupted and all of the deciduous premolars have been shed. P2-4 are newly erupted on this specimen with the P4 being the most developed and worn and P2 the least. These findings suggest the following eruption sequence for the adult upper cheek teeth of Trachytherus: M1-M2-P4-P3-P2-M3. The lophs of these newly erupted premolars are not as well developed as those illustrated and described by Patterson (1934b).

Discussion regarding juvenile trachytheres. The unworn deciduous dentition of the Trachytherus specimen described above is remarkable for its similarity to adult molars of archaeohyracids and because the dP4 illustrates how the characteristic mesotheriid median lobe was formed.

The unworn juvenile dentition has a similar, likely homologous, crown topology as Deseadan archaeohyracids. The presence of the adult form of one species in the juvenile form of another provokes the question as to the phyletic relationship of these animals and as to whether it is an example heterochrony. In this case, since the two animals are placed in separate families, the question has relevance at the familial level.

The "face" topology, however, is seen in several notoungulate lineages, including archaeopithecids, primitive interatheriids, archaeohyracids, and oldfieldthomasiids (Simpson, 1967; Cifelli, 1993). These families represent two notoungulate suborders, Typotheria and Toxodontia. The broad representation of this feature and its occurrence in older taxa and disappearance in geologically younger taxa suggest that it is the plesiomorphic condition and does not imply a unique relationship of mesotheriids and archaeohyracids. As such, it has little or no utility in aiding in the determination of the relationship of mesotheriids and archaeohyracids.

Whereas the "face" topology of the dP2-3 records the evolutionary history of Trachytherus, the dP4 illustrates the origin of the median lobe. Though this feature is inconspicuous in Trachytherus (Patterson, 1934b), it becomes well developed in later mesotheriids (see Villarroel, 1974: fig. 1).

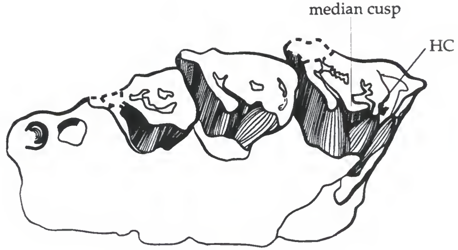

Figure 4.4. Unworn milk molars of Trachytherus spegazzinianus, dP2-4. MNHN-Bol-F-94-09.

Table 4.2. Dimensions of upper deciduous premolars of specimens of *Trachytherus spegazzinianus*.

Specimen	**dP2**		**dP3**		**dP4**	
Nº	(l x w)		(l x w)		(l x w)	
MNHN-Bol-F-94-09	7.5	6.8	12.6	7.4	16.3	9.0
UF 91832	--	--	12.4	8.4	---	8.7
UF 136062	10.5	8.7	11.0	---	15.5	10.2
UF 137846	9.2	--	11.0	10.2	15.6	11.5
UF 137845	8.0	8.5	---	---	14.0	12.0
MNHN-Bol-V-003459	10.1	8.8	10.8	11.4	13.8	12.0
$\bar{x}$	9.06	8.2	11.56	9.35	15.04	10.57
s	1.30	0.94	0.86	1.79	1.09	1.49
CV	14.32	11.48	7.48	19.16	7.23	14.07

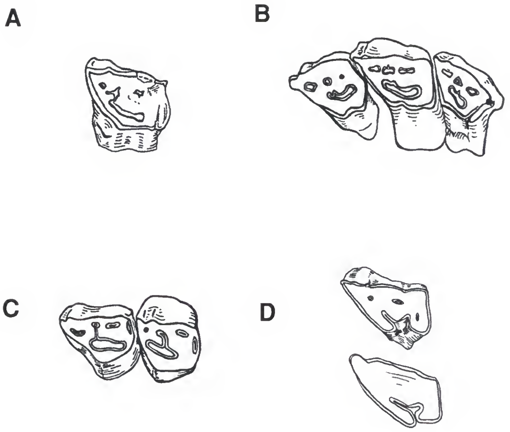

Figure 4.5. "Face" topology of some notoungulates upper molars. The major (lingual) fossette has the appearance of a "mouth", whereas labial fossettes form the "eyes" and, in some specimens, a "nose". A, left M2 of *Eohyrax isotemnoides* (redrawn from Simpson, 1967: plate 18.1); B, right (reversed) M1-3 of *Pseudhyrax eutrachyteroides* (from Simpson, 1967: plate 20.2); C, left M1-2 of *Acropithicus tersus* (redrawn from Ameghino, 1904: fig. 280); D, a little worn left M2 of *Archaeohyrax* sp. of Salla (upper: UF 91885), and a more heavilly worn M2 (lower: UF 91370) in which the labial fossettes (the "eyes") have worn away just prior to the closure of the major fossette (the "mouth").

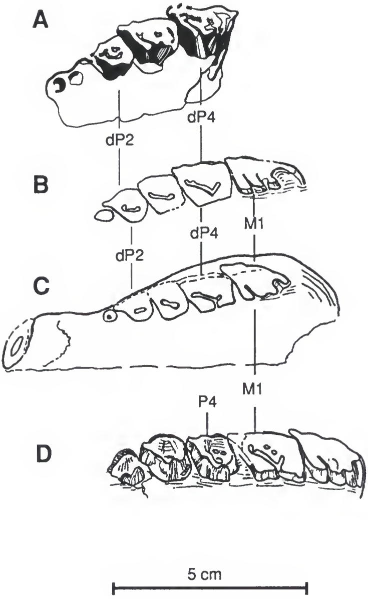

Figure 4.6. Cheek-tooth ontogenetic series of Trachytherus spegazzinianus. A, Unworn deciduous teeth of MNHN-Bol-F-94-09; B, MNHN-Bol-V-003459; C, UF 137845; D, UF 90989.

Ontogeny and Evolution

The development and evolution of high crowned teeth in these notoungulates may be thought of as an overdevelopment due to the delay of the closure of the tooth-roots. In modern heterochronic terms, this is an example of "hypermorphosis" a type of "peramorphosis" (sensu McNamara, 1986; and McKinny and McNamara, 1991). The hypermorphosis (enlarged tooth crown) occurs due to the delayed termination of a developmental stage (root closure). In this case, the tooth becomes higher crowned because of the retardation of a developmental stage. Overdevelopment may also be caused by increased rate of development ("acceleration") or an earlier onset of growth ("predisplacement") (McKinny and McNamara, 1991).

The hypertrophy of the cristae of Trachytherus into a median cusp or loph is also an example of a peramorphosis. It is impossible to determine as to whether the peramorphosis is due to acceleration, predisplacement or hypermorphosis with the limited material at hand. This determination would require not only a series teeth from unweaned and prenatal trachytheres, but also a similar series from an ancestral species.

The hypertrophy of the median cusp appears to cause the loss of the "face" appearance of the molars of Trachytherus. The enlarged median cusp occupies areas which had defined the labial fossettes (the "eyes"). The brief appearance of the "eyes" in the unworn juvenile specimen occurred only when little more than the apex of the median cusp had come into occlusion. The median loph of newly formed molars is so enlarged that labial fossettes are not formed (note the newly erupted M1s of Figs. 4.6B and 4.6C).

Chapter Summary

The study of juvenile specimens has utility for alpha taxonomy and deepens our understanding of phylogeny, and evolutionary history. Since the milk molars represent the same series as the permanent molars, they have the potential for aiding our knowledge of the development and homologies of the adult dentition.

The description of the deciduous cheek teeth of Eurygenium sp. and Trachytherus spegazzinianus permits differentiation of these taxa from one another, and also allows them to be differentiated from isotemnids, with which they may otherwise have been confused. The most notable difference between the deciduous and adult dentitions of these two taxa is the high-crowned state of the adult molars. In Eurygenium sp., the rooting of the molars are ontogenetically delayed such that they become high-crowned. The rooting of the true molars of Trachytherus is halted such that the molars are essentially ever-growing or hypselodont (Patterson, 1934b).

The hypothesis of Patterson (1934a) regarding molar cusp homologies of Toxodontia is not supported by the morphology of the deciduous notohippid teeth. A more parsimonious interpretation offered here is that the anterolingual loph of the anterior deciduous cheek teeth is the homologue of the anterolingual loph of the dP4 and adult molars. The protocone is regarded here as a component of the anterolingual loph in both the milk molars and permanent molars and is not "split" as suggested by Patterson (1934a).

Homologies of the upper molars of Trachytherus are implied by the deciduous premolars. These illustrate an intermediate state containing both the primitive notoungulate condition and the derived mesotheriid character. The plesiomorphic "happy face" topology records the phylogenetic history of Trachytherus, whereas the unworn dP4 demonstrates the source of the novel median loph that becomes so pronounced in geologically younger mesotheriids.

CHAPTER 5
FUNCTIONAL MORPHOLOGY AND FEEDING ECOLOGY

Introduction

Principals regarding the ecomorphology of feeding are derived from studying adaptations of extant taxa are used to generate hypotheses about the feeding ecology of Toxodontia.

The limitations of using modern analogs is acknowledged, particularly since there are no extant notoungulates. The phylogenetic distance of the notoungulates from extant ungulates may make a rigorous, quantitative assessment of their biology difficult, but a major premise here is that the principles derived from phylogenetically diverse extant taxa will be general enough to apply to extinct herbivores whose diets are unknown.

Three simple morphological indices associated with feeding are examined in extant ungulates: hypsodonty, relative muzzle width, and relative breadth of the lower lateral incisor. These indices were determined in the extinct Toxodontia notoungulates of Salla and were compared and interpreted in terms of modern taxa whose dietary habits are known. Scaling is also considered as an explanation for apparent "phylogenetic constraint" that appears as exceptions to some of the general trends in modern taxa.

Adaptations for Herbivory

Acquiring energy from plant material is no small challenge for multicellular animals. This difficulty is due to the structure of plant cells. They are surrounded by rigid, durable cell walls composed of cellulose, other polysaccharides and lignin (Wainwright et al., 1976). As far as the multicellular animal is concerned, the digestible food stuff of plants is encapsulated within indigestible shells.

Herbivorous animals need to break the cell walls in order to extract the energy-rich contents (carbohydrates and proteins), and do so by physical or chemical methods. Physical methods include crushing the plant material with teeth (as commonly seen in mammals), pharyngeal grinders (e.g., fish), gizzards (e.g., some birds), and gizzard stones (e.g., some herbivorous birds and dinosaurs). Chemical means for disrupting the cell wall involve the use of some cellulase enzymes. These enzymes have not evolved in multicellular animals, but occur in numerous unicellular organisms that live as symbionts within the digestive tracts of multicellular animals.

Since the proportion of cellulose in plants is variable, the difficulty in extracting energy and nutrients also varies. For example, mature leaves have more cellulose in their cell walls than do roots, fruits and sprouting young leaves (Janis and Fortelius, 1988). Some plants, especially grasses, present further difficulties for animals by being studded with opaline phytoliths which result in the plant becoming more abrasive (Walker et al., 1978).

Of extant vertebrates, mammals are the most successful at exploiting plant products for energy. Several mammalian orders are exclusively herbivorous (e.g. perissodactyls, proboscideans, and sirenians). Several others are predominantly herbivorous (e.g. artiodactyls and rodents) (Janis and Fortelius, 1988).

The success of mammals in exploiting plant material for food appears to be related to their more efficient mechanical breakdown of the plant substances during mastication. Modern herbivorous reptiles and birds lack such effective mastication, but have digestive adaptations that are similar to those of mammals. These include elongated large intestines, reverse peristalsis, transverse partitions across the colon, and symbiotic microfauna in foregut and hindgut fermentation chambers (Farlow, 1987).

The mechanisms mammals use to masticate plant material involve jaw and tooth structure. The more permanent nature of mammalian teeth permits the development of occlusal patterns that can facilitate mastication. This initial mechanical breakdown of the vegetation is of considerable importance for herbivorous animals because the cell walls of plants need to be broken in order to for digestive enzymes to have access to the contents of the plant cells. This is important even for animals that have microfauna capable of digesting cellulose (See Janis, 1976). Exposing a greater surface area of the plant material sent to the gut gives the endogenous and symbiotic enzymes greater access to the food; thus, chemical breakdown is facilitated.

Because of the variation in the difficulty of obtaining energy from plants, animals exploiting different plants will require different adaptations to deal with the particular types of food. The requirements for an animal consuming soft, high energy fruits are different for an animal consuming coarse, low energy grasses; thus, the grazer would likely develop different adaptations for feeding than the browser. Such differences have been observed in browsing versus grazing herbivores (see references below). Three morphological features that appear to be related to feeding ecology include relative crown height, relative muzzle width, and relative lateral incisor breadth.

Relative cheek-tooth crown height. Hypsodonty has long been regarded as an evolutionary response to consuming abrasive grasses and, thus, an indication of grazing in extinct herbivores (Kowalevsky, 1873; Osborn, 1910; Van Valen, 1960; MacNaughton et al., 1985). Since grass rapidly wears away teeth, a low-crowned (brachydont) animal would soon be unable to masticate grass, or anything else, and have a shorter life. Life, and presumably fitness, is increased in grazers that have high-crowned (hypsodont) teeth (see Fig. 5.1).

Patterson and Pascual (1972) and Simpson (1980) noted that hypsodonty developed earlier in South America than in other continents. Stebbins (1981) suggested that this "precocious" hypsodonty was due to an early development of grasslands in South America. Simpson (1980) did not believe that grassland evolved earlier there, but favored a hypothesis in which grasses were equally abundant in North and South America, but that "some notoungulates simply had the genetic background" for developing hypsodonty and were thus able to exploit grasslands earlier than other ungulates of the world (Simpson, 1980: p. 144). Pascual and Ortiz Jaureguizar (1990) argued that the precocious hypsodonty had little to do with grasses, but instead, was a response to abrasive volcanic ash that had dusted the plants, suggested by the pyroclastic derived sediments of many Tertiary localities of

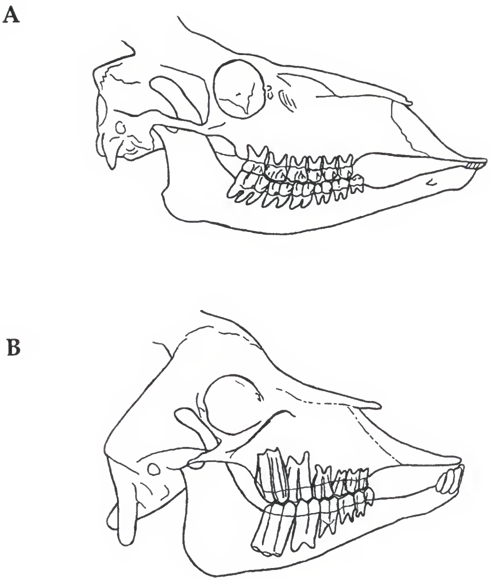

Figure 5.1. Brachydont (low-crowned) and hypsodont (high-crowned) dentitions are exemplified by two artiodactyls. The browsing deer, Odocoileus (A), has brachydont teeth, whereas, the teeth of the grazing goat, Capra hircus (B) are hypsodont. (Adapted from Solounias and Dawson-Saunders, 1988.)

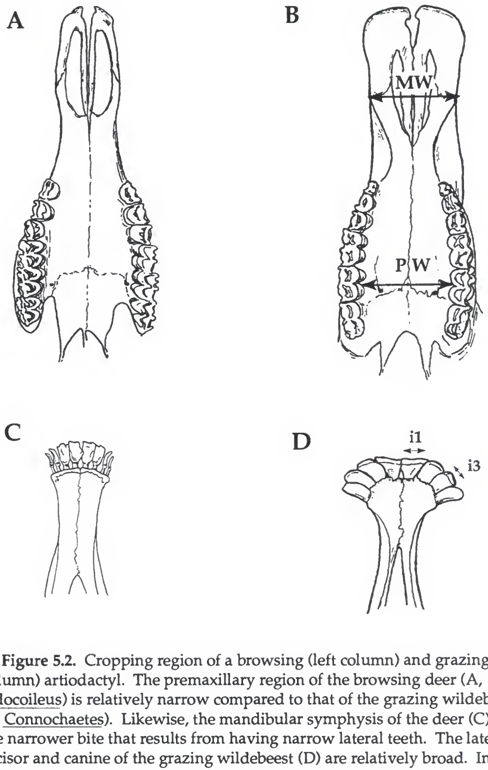

Figure 5.2. Cropping region of a browsing (left column) and grazing (right column) artiodactyl. The premaxillary region of the browsing deer (A, Odocoileus) is relatively narrow compared to that of the grazing wildebeest (B, Connochaetes). Likewise, the mandibular symphysis of the deer (C) shows the narrower bite that results from having narrow lateral teeth. The lateral incisor and canine of the grazing wildebeest (D) are relatively broad. Indicated on the widebeest are the regions measured to obtain the raw data for determining relative muzzle width (MW/PW) and relative lateral incisor breadth (i3/i1).

Patagonia. The latter possibility is supported by the observation of Janis (1988) that hypsodonty occurs in animals feeding on any type of low level vegetation subject to being covered with abrasive dust and grit.

Crown height to quantified to determine if the apparent trend toward hypsodonty in notohippids was just an increase in diversity of relative crown heights or if low-crowned taxa were selected against. This quantification also serves to document the initiation of hypsodonty in the Toxodontia.

Muzzle morphology. Because hypsodonty may have been the result of some function other than grazing, additional morphological characters associated with grazing should be examined. The morphology of the muzzle is an example of a character useful in determining the diets of extinct herbivores (Solounias et al., 1988; Dompierre and Churcher, 1996). Qualitative observations by Gwynne and Bell (1968), Jarman (1974), and Owen-Smith (1985) suggest that browsers evolved narrow muzzles, whereas grazers evolved broader muzzles (Fig. 5.2). This is supported by the quantitative work of Janis and Ehrhardt (1988) and Solounias et al. (1988), and is explained by the need of browsers to select particular nutrient-rich food items (e.g., buds, young leaves, fruits) without getting a mouthful of coarse twigs (as occurs, for example, in broad snouted elands; see Nge'the and Box, 1976). For animals that use their anterior snout to crop vegetation, a narrow muzzle facilitates selective feeding, whereas a broad snout aids a grazer in readily obtaining the required high volumes of relatively low-energy grasses.

Narrow muzzles may be adaptive for browsers foraging for particular food substances. For example, in an animal that specializes on high energy, easy-to-digest new sprouts, the ability to grasp these particular sprouting leaves without getting a mouth full of coarse, low energy, hard-to-digest old leaves will be advantageous. Wide, blunt muzzles, on the other hand, may be advantageous to grazers because they need to consume large quantities of this relatively low energy food in order to extract sufficient energy. Also, grasses tend to be more evenly distributed in the environment, thus the ability to discriminate and hit a small target is unnecessary. Quantity will be the driving force for grazers and a wide muzzle makes for a more efficient lawn mower.

Relative incisor breadth. Gordon and Illius (1988) noted wider lateral incisors in grazing animals compared to those that browse (see Fig. 5.2). The driving force behind the wide lateral incisors appears to be conceptually similar to broad premaxillae of grazers. These teeth aid in cropping larger quantities of grass, but would be a hindrance to a selective feeder.

Methods

Methods to Analyze of Modern Analogs

The findings of Janis and Ehrhardt (1988) and additional analyses of their extensive data set were used infer relationships between morphology and diet. The dietary categories given in Janis and Ehrhardt (1988) were followed, however their indices for muzzle widths and incisor widths were modified so that (as in hypsodonty) larger values are associated with grazing and smaller values with browsing. Thus, the index for relative muzzle width here is MW/PW rather than the inverse listed by Janis and Ehrhardt (1988).

Likewise, lateral incisor breadth is i3/i1 rather than i1/i3. Janis and Ehrhardt did not report measures of lower incisors of perissodactyls, so these were obtained from specimens in the Mammalogy and Vertebrate Paleontology collections of the Florida Museum of Natural History (Appendix B).

To gain insights into the most general principles governing ungulate ecomorphology, a broad taxonomic range should be observed and analyzed. Ideally, all herbivorous mammals should be examined for comparison of the phylogenetically distant notoungulates. However, the premise behind relative muzzle width and lateral incisor width make proboscidians and hyracoids irrelevant candidates for this study. Neither uses its snouts to crop vegetation. Elephants use their trunks for grasping a variety of food items and hyraxes crop vegetation with their cheek teeth (Kingdon, 1971). The samples of modern taxa were limited to artiodactyls and perissodactyls. Unfortunately, rhinos had to be excluded from some of the analyses because they lack an i3.

The statistical program JMP of the SAS Institute was used to perform principal components analysis of relative tooth crown height, relative muzzle width, and relative lateral incisor width of equid and tapirid perissodactyls (2 each) and ruminant artiodactyls (n = 55). The artiodactyls were mostly bovids (n = 40), but also included seven cervids, two giraffids, an antilocaprid, and a tragulid. The species and their dietary categories and morphological indices are given in Table 5.1.

An explicit size component was added to the data set to determine effects of scaling on these variables. Body mass estimates of the taxa examined were obtained from several sources which are given in Appendix C.

Table 5.1. Feeding indices of extant ugulates (n= 59). Indices are hypsodonty index (hi), relative muzzle width (MW/PW) and relative lower lateral incisor breadth (i3/i1). Data and feeding catagories were derived from Janis and Ehrhardt (1988) with perissodactyl data added from Florida Museum of Natural History specimens. Feeding categories include grazers (g), mixed feeders (m), and browsers (b). Fresh grass grazers (f), mixed feeders in closed habitats (c), and high level browsers (h) are also designated.

Taxon	diet	hi	MW/PW	i3/i1
Bovidae				
Aepyceros melampus	m	1.57	0.82	0.23
Alcelaphus buselaphus	g	1.66	1.07	0.42
Connochaetes gnou	g	1.84	1.19	0.58
Connochaetes taurinus	g	2.16	1.05	0.61
Damaliscus dorcas	g	1.51	1.10	0.28
Damaliscus hunteri	m	1.19	1.01	0.52
Damaliscus lunatus	g	2.33	1.10	0.43
Boselaphus tragocamelus	m (c)	1.03	0.85	0.62
Tetracerus quadricornis	m (c)	1.12	0.72	0.41
Bison bison	g	1.42	0.97	0.88
Bos gaurus	m	1.59	0.97	0.72
Syncerus caffer	m	1.79	1.13	1.01
Capra ibex	m	1.60	0.50	0.68
Ovis canadensis	m	1.34	0.64	0.95
Cephalophus monticola	b	1.12	0.56	0.25
Cephalophus silvicultor	b	1.22	0.76	0.44
Amodorcas clarkei	b (h)	1.17	0.62	0.23
Antidorcas marsupialis	m	1.69	0.62	0.15
Gazella granti	m	1.41	0.58	0.24
Gazella thomsoni	m	1.41	0.56	0.30
Litocranius walleri	b (h)	0.72	0.70	0.19
Hippotragus niger	g	1.67	0.89	0.68
Oryx gazella	m	1.41	0.89	0.67
Dorcatragus megalotis	m	1.65	0.53	0.26
Madoqua kirki	b	0.79	0.41	0.35
Neotragus moschatus	b	1.56	0.52	0.27
Orebia irebi	m	1.58	0.67	0.32
Oreotragus oreotragus	m	1.18	0.53	0.41
Raphiceru campestris	m	1.05	0.57	0.28
Raphiceru melanotis	m	1.07	0.53	0.25
Kobus ellipsiprymnus	g (f)	1.54	0.93	0.29
Kobus lechwe	g (f)	1.91	0.89	0.26
Pelea capreolus	m	1.25	0.68	0.20
Reduncia fulvorufula	m	1.46	0.82	0.18

Table 5.1. continued

Taxon	diet	hi	MW/PW	i3/i1
Bovidae (continued)				
Tragelaphus angasi	m (c)	1.22	0.76	0.20
Tragelaphus buxtoni	b	1.02	0.70	0.25
Tragelaphus euryceros	b	0.75	0.81	0.23
Tragelaphus imberbis	b	0.79	0.82	0.21
Tragelaphus scriptis	b	1.42	0.78	0.18
Tragelaphus strepsiceros	b	1.19	0.85	0.20
Cervidae				
Alces alces	b (h)	0.80	0.73	0.81
Cervis canadensis	m	0.96	0.90	0.52
Elaphurus davidianus	g (f)	1.39	0.91	0.52
Hippocamalus bisculus	m	0.96	0.75	0.44
Mazama mazama	b	0.75	0.59	0.32
Odocoileus hemionus	b	0.84	0.81	0.69
Odocoileus virginianus	b	0.83	0.75	0.28
Giraffidae				
Giraffa camelopardalis	b (h)	0.75	0.88	0.45
Okapia johnstoni	b (h)	0.74	0.68	0.55
Tragulidae				
Hyemoschus aquaticus	b	0.71	0.65	0.32
Antilocapridae				
Antilocapra americana	m	2.36	0.68	0.78
Camelidae				
Camelus bactrianus	m	1.07	0.89	1.20
Camelus dromedarius	m	0.83	0.88	1.25
Lama guanicoe	m	1.45	0.84	0.94
Vicugna vicugna	m	1.43	0.80	0.67
Equidae				
Equus asinus	g	2.50	0.84	1.25
Equus grevyi	g	2.48	0.84	0.96
Tapiridae				
Tapiris bairdii	b (h)	0.69	0.68	0.62
Tapiris terrestris	b (h)	0.56	0.74	0.68

Analysis of feeding morphology of extant ungulates

The indices used to quantify hypsodonty, relative muzzle width and lateral incisor width are based upon those of Janis and Ehrhardt (1988), but the later two are modified. Specifically, the index for relative muzzle width is given here as MW/PW (the inverse of the index used by Janis and Ehrhardt) so that relatively wide muzzles will have larger values than ones that are narrow. This inverse is used not just for the esthetics of giving greater numerical values for wider muzzles, but it is also consistent with hypsodonty indices, which generally have higher numerical values in grazers. Similarly, the index for breadth of lateral incisors is given here as i3/i1 rather than i1/i3 to help distinguish among the feeding ecologies in multivariate space.

Dietary categories

The dietary categories of Janis and Ehrhardt were based largely on the work of Hofmann and Stewart (1972). These categories are given as follows: dry grass grazers (G), fresh grass grazers (F), mixed feeders in open habitats (M); mixed feeder in closed habitat (W); unspecialized browser (B); selective browser (S); and high level browser (H) (See Table 5.1). These may be conveniently lumped into three general categories: browser, grazers, and intermediates.

Browsing ungulates. Browsers were defined as animals whose diets contained over 90% dicotyledonous material. Subcategories of browsing included "regular browsers" (consumers of a mixture of leaves, shrubs, herbs and succulent items), "selective browsers" (consumers of fruits and buds but very little leaf material) and "high level browsers" (consumers of tree leaves).

Grazing ungulates. Fresh-grass grazers were defined as grazers that resided and fed in moist habitats; areas near water. Greater than 90% of these animal's diet came from these grasses. Janis and Ehrhardt neglected to report their definition of dry-grass grazers, however, (by inference) they appear to be referring to animals whose diet consist of over 90% grass obtained in open savanna habitats. Animals classified as dry grass feeders are open grassland feeders such as zebras (Equus spp.), wildebeests (Connochaetes spp. and Damaliscus dorcas), and the American bison (Bison bison).

Mixed feeders. Animals that had between more than 10% but less than 90% grass in their diet were classified as mixed feeders. These were subdivided into those mixed feeders that fed in open savanna, prairie or arid desert habitats (mixed feeders in open habitats) and those that fed in forest (mixed feeders in closed habitats).

Methods to Evaluate Feeding Morphology of Toxodontia

Hypsodonty of Toxodontia. Relative crown heights, or Hypsodonty Indices (HI), were obtained from M1s showing minimal wear in 16 notohippids specimens (ten species in seven genera) (see Table 5.2). Temporally, these notohippids range from the Casamayoran (early Eocene) to the Colhuehuapian (early to middle Miocene). Hypsodonty indices were determined by dividing the crown height by the anteroposterior length (APL) of the occlusal surface, which in all cases was the greatest occlusal dimension.

Table 5.2. Notohippid specimens of Argentina and Bolivia from which hypsodonty indices (HI) were calculated. Cañandón Blanco is considered to be post-Mustersan/pre-Deseadan, or "Tinguiririrican". See abbreviations section for institutional names. Asterisk (*) indicates holotype.

Museum Nº	SALMA	Taxon	HI
PVL-S-4192	Casamayoran	**Pampahippus arenalesi*	0.54
MACN A 55-1	Casamayoran	**Plexotemnus complicatissimus*	0.65
AMNH 29405	Mustersan	**Eomorphippus*? *pascuali*	0.72
MLP 12-1508	Cn. Blanco	*Eomorphippus obscurus*	1.01
AMNH 27885	Cn. Blanco	*E. obscurus* (Padua cast)	0.91
Bol-V-003456	Deseadan, Salla	*Rhychippus* cf. *R. brasiliensis*	1.40
AMNH 29555	Deseadan, Arg.	*Rhynchippus pumilus*	1.56
MACN A52-59	Deseadan, Arg.	*Rhynchippus equinus*	1.65
MACN A52-83	Deseadan, Arg.	**M. complicatus* (=*R. equinus*)	1.86
FMNH P13420	Deseadan, Arg.	*Rhynchippus equinus*	1.50
FMNH P13628	Deseadan, Arg.	*Rhynchippus equinus*	1.51
FMNH P13410	Deseadan, Arg.	*Rhynchippus equinus*	1.64
UF 146400	Deseadan, Salla	*Eurygenium* sp.	1.70
Bol-V-003643	Deseadan, Salla	*Eurygenium* sp.	1.81
AMNH 29731	Colhuehuapian	*Argyrohippus fraterculus*	2.55

Crown heights were taken along the paracone ridge of M1 from the point of occlusion to the termination of the enamel at the root. Linear measures are given for crown heights, even in specimens in which the molars were strongly curved (an underestimate for the external enamel curvilinear dimension, but an overestimate of the internal curvilinear dimension). Anteroposterior tooth lengths were taken along the ectoloph at the occlusal surface.

Hypsodonty indices (HI) were plotted versus time, in millions of years (Ma). Age of the specimens was estimated using the mid-point of the range of ages of their respective South American Land Mammal Ages (SALMA) (Flynn and Swisher, 1995). Because of assumed errors on the x-axis (age), Model II (reduced major axis) regression equations were used to describe the change in HI over time. The mid-point for the Casamayoran SALMA is estimated to be 52.5 Ma and for the Mustersan 42.5 Ma. Specimens from Roth's Cañandón Blanco locality are considered here to be post-Mustersan/pre-Deseadan and roughly the same age as the Tinguiririca Fauna of Chile, about 34 Ma (see Wyss et. al, 1994 for discussion). The mean age estimate for specimens from the Deseadan of Patagonia is 27 Ma. The Salla specimens can be constrained more precisely. The new genus of notohippid from Unit 2 of Salla is placed at 27 Ma (see "Horizon" section of its description below), while the remaining two species from the higher sections are dated at 24 Ma. The Colhuehuapian SALMA is placed at 20 Ma for this comparison. M1s were selected so that the relative crown heights of notohippids could be compared to those of equids (MacFadden, 1992).

Evolutionary rates were estimated using the methods developed by Haldane (1949). Putative ancestor-descendant lineages are given and rates (r) of change of M1 length (L) and crown height (PCRH) were determined by:

$$r \text{ (in darwins)} = (\ln x_2 - \ln x_1)/\Delta t,$$

or the computationally convenient equality:

$$r \text{ (in darwins)} = \ln (x_2/x_1)/\Delta t;$$

where, Δt is the change of time, x_2 is the measure of the putative descenden and x_1 its ancestor.

To compare the relative crown heights of the Toxodontia with the those of the extant taxa, relative crown heights (hi) were also determined for lower teeth by the method used by Janis and Ehrhardt (1988) (m3 crown height/m2 length). These ratios from the Toxodontia were then compared to those of extant taxa whose diets are known.

Muzzle morphology of Toxodontia. Relative width of the muzzle was determined from the ratio of the width of the muzzle (MW) to the width of the palate (PW) (Janis and Ehrhardt, 1988). MW is the width of the snout at the premaxilla-maxilla border and PW is the distance between the lingual borders of the protocones on the opposite M2s. Janis and Ehrhardt's measure was modified in animals having snouts that become broader anterior to the premaxilla-maxilla boundary (e.g., Eomorphippus and the new Salla notohippid genus). In these taxa, the greatest width of the premaxilla (MW_{max}) was divided by the PW.

The breadth of i1 and i3 of notohippid and toxodontid specimens were obtained and relative incisor breadths (i3/i1) were determined and compared to the relative incisor breadths of modern analogs. Also, a measures of symphyseal breadth (i3 -i3, inclusive) and relative symphyseal breadth ([i3-i3]/m2 length) was determined in the Toxodontia.

Results

Diet and Morphology of Extant Ungulates

Hypsodonty of extant taxa. Extant grazers have significantly higher crowned teeth than browsers, while intermediate feeders have a broad and overlapping range of values of hi. Some overlap exist even among browsers and grazers, but this is largely resolved when a mass component is added (Fig. 5.3).

Mass has little predictive value of crown height of browsers ($r^2 = 0.18$). A weak effect for relative crown height to decrease in larger ungulates is suggested by the small, negative slope.

The scaling of relative crown heights of grazing ungulates is less ambiguously allometric (Fig. 5.3). Relative crown heights of grazers decreases as body size increases. The slope of log hi vs. log mass was -0.13 and the coefficient of determination (r^2) was 0.37.

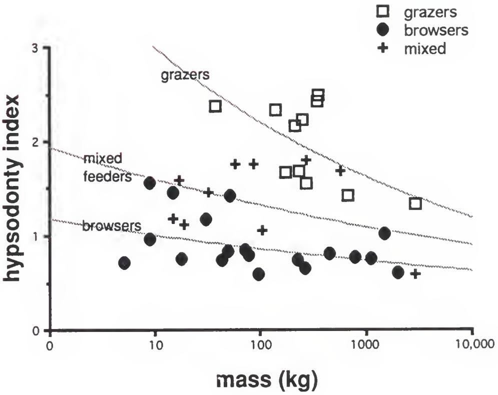

Figure 5.3. Hypsodonty indices of lower molars shown as a function of mass.

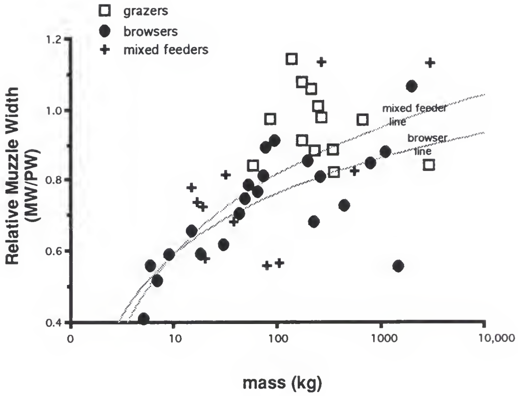

Figure 5.4. Relative muzzle widths (MW/PW) plotted as a function of body mass in kg.

Muzzle Morphology of Extant Taxa. As previous workers have noted, extant grazing ungulates tend to have broader muzzles. This is demonstrated by the shape analysis performed by Solounias et al. (1988) and the greater MW/PW, as noted by Janis and Ehrhardt (1988).

The broader relative muzzle width of grazers may also be inferred from the relationship demonstrated in Fig. 5.4. The relationship of relative muzzle width and mass suggests scaling effects for browsing and intermediate feeders, but not grazers. Relative muzzle widths of grazing ungulates was not highly correlated with body size ($r^2 = 0.08$).

Allometric scaling of RMW appears to occur in browsing ungulates ($r^2 = 0.52$). Larger bodied ungulates have relatively broader muzzles than small ungulates. A similar trend occurs in the intermediate feeders, which is best expressed by a first ordered regression ($r^2 = 0.41$).

Results of Principal Components Analysis of Artiodactyla

The results of the PCA of ruminant artiodactyls is given in Table 5.3. Hypsodonty, muzzle width, and relative incisor width contribute nearly equally to principal component 1 (PC 1), with relative muzzle width making the strongest contribution (see eigenvectors of Table 5.3). principal component 1 accounted for little over 50% of the variation, but completely discriminated between browsers and grazers (see discussion below).

Principal component 2 accounted for about 25% of the variation and was a component of incisor width ratio and the inverse of hypsodonty. Muzzle width had virtually no effect on PC 2.

Principal component 3 accounted for about 20% of the variation. Narrow muzzles contributed most to this axis, since the index for muzzle width had a negative eigenvector. Lateral incisor breadth and hypsodonty made smaller, but significant contributions to this axis.

Result from Analysis of Toxodontia

Crown height in Toxodontia of Salla. The hypsodonty indices for uppers (HI) and lowers (hi) are given in Table 5.4. Both upper and lower dentitions of Eurygenium sp. and Rhynchippus cf. R. brasiliensis could be evaluated for hypsodonty. The lower teeth of UF 149219 are tentatively referred to the new notohippid genus and an hi was calculated. No lower teeth of the two species of leontiniids were found. Only lower teeth of Proadinotherium sp. were suitable for determination of hypsodonty. The notohippids may be characterized as being hypsodont and the leontiniids brachydont. The toxodontid, Proadinotherium sp. may be characterized as mesodont or incipiently hypsodont.

Evolution of notohippid hypsodonty. The hypsodonty indices (HI) of the family Notohippidae from the Casamayoran to the Colhuehuapian sampled ranged from 0.5 to 2.6 (Table 5.2). The relationship of HI as a function of time (Fig. 5.5) is represented as $HI = 260\ t^{-1.49}$ (derived from a log-log, least squares regression), where t is time in Ma. (In this convention, the negative exponent indicates exponential growth, not decay.) The high coefficient of determination ($r^2 = 0.93$) indicates that most of the variance in HI may be explained as a function of time. This suggests a trend toward

Table 5.3. Eigenvalues and eigenvectors are given for the principal component analysis of indices of feeding of extant ungulates.

Principal Components	**PC 1**	**PC 2**	**PC 3**
EigenValue:	1.61	0.77	0.62
Percent:	53.60	25.57	20.84
CumPercent:	53.60	79.17	100
Eigenvectors:			
hypsodonty	0.57	-0.68	0.47
MW/PW	0.62	-0.04	-0.78
i3/i1	0.55	0.73	0.40

Table 5.4. Hypsodonty indices (HI/hi) of upper and lower molars of Toxodontia of Salla.

Taxon	**ID Nº**	**PCRH/M1L**	**HI**
Leontiniid (small) sp. A	Bol (sin numero)	21.4/24.8	0.86
Leontiniid (large) sp. B	UF 90950	29.5/39.4	0.75
Eurygenium sp.	UF 146400	28.9/17.0	1.70
Eurygenium sp.	Bol-V-003643	30.8/17.0	1.81
cf. R. brasiliensis	Bol-V-003456	19.2/13.7	1.40

Taxon	**ID Nº**	**m3 ch/m2L**	**hi**
Eurygenium sp.	Bol sin num	39.5/15.7	2.52
cf. R. brasiliensis	UF 149201	24.5/13.5	1.81
?New notohippid genus	UF 149219	37.4/20.1	1.86
Proadinotherium sp.	UF 149222	17.0/16.9	1.01

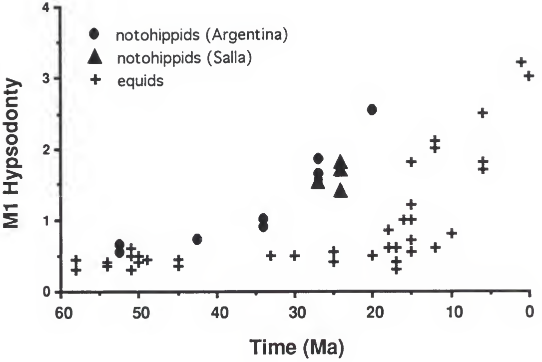

Figure 5.5 Hypsodonty indices of the M1s of notohippids and equids shown as a function of time.

evolving higher crowned teeth. Not only did higher crowned taxa appear, but brachydont forms failed to persist. The lack of variation in HI of contemporary notohippids might be explained by the small sample size, but it should be noted that 10 Deseadan specimens of four distinct taxa had an HI range of only 1.4 to 1.9. This variation in HI is too small to make confident inferences regarding niche separation and dietary preferences of these contemporaneous animals. Evidence for possible niche separation would need to be sought in some other morphological character, such as morphology of the muzzle (see discussion below).

The comparison of notohippid HI to equid HI over time (equid data from MacFadden, 1992) illustrates that hypsodonty developed earlier in notohippids than in equids (Fig. 5.5). This is consistent with the qualitative notion that hypsodonty occurred earlier in ungulates of South America than in those of other continents.

Inspection of Fig. 5.5 indicates that the relative crown height of horses remained constant from the Eocene to middle Miocene, but increased thereafter. This qualitative impression is supported by MacFadden (1988) who reported low rates of crown heights in Eocene to Oligocene genera and higher rates in younger genera.

The notohippids, however, demonstrated increases in crown heights in Eocene taxa as well as later genera. The relationship $HI = 260\ t^{-1.49}$ suggests a quasiexponential increase in relative crown heights. The rates of evolution in the crown heights are modest and fairly constant (Table 5.5).

Table 5.5. Evolutionary rates (r, in darwins [d]) of size change in the length (L) and crown height (PCRH) of the M1 in putative ancestor-descendant (a-d) pairs of notohippids.

Species Pair (putative ancestor-decendent)	n (a-d)	Δt (Ma)	r M1 L (d)	r PCRH (d)
Pampahippus - ?E. pascuali	1-1	10	0.0046	0.033
?E. pascuali - E. obscurus	1-2	8.5	0.024	0.055
Pampahippus - Eomorphippus	1-2	16.5	0.013	0.043
Eomorphippus - Rhynchippus	2-4	7	0.0044	0.077
Eomorphippus - Argyrohippus	2-1	14	-0.011	0.059

Table 5.6. Two indices of relative width of muzzles in notohippids. The index MW_{max}/PW is sensitive to anterior broadening of the premaxilla, as seen in the notohippid genus of Salla and Eomorphippus obscurus (see methods section of this chapter.)

Nº	**Taxon**	**MW/PW**	**MW_{max}/PW**
MLP 12-1508	Eomorphippus obscurus	1.12*	1.26*
FMNH P13410	Rhynchippus equinus	0.93	0.93
Bol-V-003456	R. sp., cf. R. brasiliensis	0.91	0.91
Bol-V-003643	Eurygenium sp.	0.76	0.76
UF 90981	Eurygenium sp.	0.74	0.74
Bol-V-003642	New notohippid genus	0.95	1.01
AMNH 29685	Argyrohippus fraterculus	0.97	0.99

*Palatal width estimated due to lateral compression of specimen.

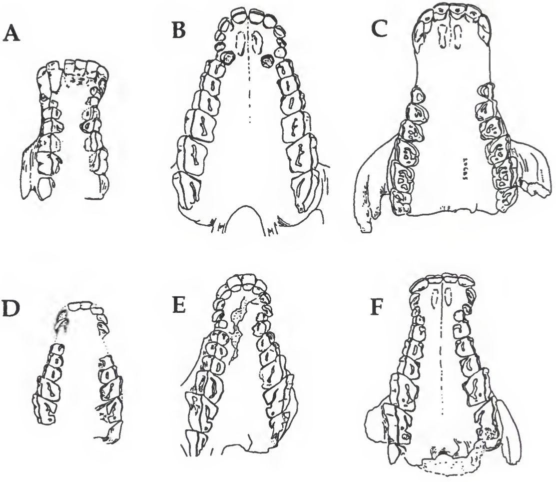

Figure 5.6. Muzzles of Patagonian notohippids (upper row) and the three notohippids of Salla (lower row). A, *Eomorphippus obscurus*; B, *Rhynchippus equinus*; C, *Argyrohippus fraterculus*; D, *Rhynchippus* sp., cf. *R. brasiliensis*; E, *Eurygenium* sp.; F, new genus.

Table 5.7. Lower incisive batteries of Toxodontia of Salla. Relative lateral incisor width (i3/i1) is given as well as measures for the width (i3 - i3) and relative width (i3-i3/m2) of the lower incisive arcade.

Taxon	**ID Nº**	**i3/i1**	**i3-i3**	**(i3-i3)/m2**
Eurygenium sp.	UF 149209	8.3/6.0 = 1.38	31.5	1.78
R. cf. *brasiliensis*	UF 149202	4.2/3.6 = 1.17	25.5	1.70
Proadinotherium	UF 149222	13.3/8.4 = 1.58	(50.5) > 49.0	3.07

Toxodontia relative muzzle width. The premaxillary regions of the two leontiniids have a generally pointed appearance. The RMW could not be quantified since the specimen of species A had lateral compression that would have given an underestimate of the PW. The border of the premaxilla and maxilla was undefined so that the dimension MW could not be determined with confidence either. An estimated MW/PW for species A is MW/PW = (24.5)/(33.5) = (0.73). Potential errors in both the numerator and denominator make this ratio a dubious value. The specimen of species B lacked both maxillary regions so a measure of PW could not be obtained. Qualitatively, the leontiniids appeared to have narrower snouts than Eurygenium sp.

Eurygenium sp. had the narrowest muzzle of all notohippids (see Table 5.6). The new genus of Salla had one of the broadest muzzles of all notohippids. This value was exceeded only by Eomorphippus obscurus. Considerable variation is seen in the RMW of notohippids (Fig.5.6).

Unfortunately, no premaxillary region of Proadinotherium sp. has been recovered from Salla. Presumably, it had a relatively broad premaxillary region like all other known toxodontids. This inference is also supported by the lower anterior dental battery (UF 149222, see Fig. 3.12) which shows evidence of occlusion on its widely separated third incisors.

Incisive batteries of Toxodontia. Proadinotherium sp. had the broadest lateral lower incisors of the Toxodontia of Salla (Table 5.7). It also had the broadest central incisor (i1), thus the ratio of i3/i1 was not as great as one of the specimens (MNHN-Bol-V-003645) of Eurygenium sp. Proadinotherium sp. had the greatest breadth of its incisive battery (i3-i3 ≈ 50 mm), a dimension three times greater than the m2 length. This ratio ([i3-i3]/m2 l) in

Eurygenium sp. and Rhynchippus sp. cf R. brasiliensis was less than two. Unfortunately, the broad-muzzled new notohippid genus of Salla was not represented by a mandibular symphysis. No mandibles of Salla leontiniids are known either.

Discussion

Extant Taxa of Known Diets

Hypsodonty. Analyses of extant ungulates indicates a strong relationship between hypsodonty and grazing (Janis, 1988; Janis and Ehrhardt, 1988). The addition of the mass component to the present analysis suggest that scaling effects explain the relatively low crowns of large bodied grazers, such as the white rhino, hippopotamus, and bison. It appears that absolute crown height is a significant factor in the dental durability required for consuming grasses. Thus, hypsodonty indices that are a simple ratios of crown height to tooth length are inappropriate for comparing species of very different body masses.

Relative crown heights of extant artiodactyl and perissodactyl grazers scale allometrically and are represented by the following relationship:

$$\underline{hi} = 4.07\text{mass}^{-0.134};$$

where mass is in kilograms and hi is the hypsodonty index of the lower molars ([m3 height] /[m2 length].

Relative Muzzle Width. Though grazers generally have broader muzzles than browsers (Janis and Ehrhardt, 1988; Solounias, 1988) there is considerable overlap among the relative muzzle widths (RMW) of browsers and grazers. A number of browsers (e.g., Rhinoceros sondaicus, Rangifer caribou, Giraffa camelopardalis, Tragalephus strepsiceros) have RMW values comparable to many grazers (0.8 - 1.1). This overlap is largely unresolved when body mass is considered (Fig. 5.4), though small browsing ungulates clearly have narrower muzzles than grazers.

A scaling effect is noted for the browsing ungulates (Fig. 5.4), but not for grazers. The narrower muzzles of small browsing ungulates is consistent with their greater need to be selective in their food choices. Because smaller animals will have a greater mass specific metabolic rates (Schmidt-Nielsen, 1990) they require food items rich in calories and protein. Ingestion and digestion rates, as well as relative abundances of rich (high in calories and protein) and poor quality food items are also related to body size (Owen-Smith, 1985).

Owen-Smith (1985) developed a model illustrating optimal feeding requirements of ungulates of various sizes. His model incorporated ingestion and digestion rates, as well as the expected relative abundances of food (abundant poor-quality food and less abundant rich food items). A very small ungulate, like the dik dik (Madoqua kirki) could acquire maximum energy profit by only consuming foods rich in protein (>11.8%). It would have to exclude poor quality foods, such as mature leaves. To obtain their optimal energy profit, larger taxa, like the eland (Taurotragus oryx), required much higher volumes of readily available, but poorer quality food (as little as 6%

protein). Thus, the dik dik would have to be much more selective than an eland. The increased digestion time that poor quality food requires would prevent a dik dik from meeting its high mass specific energetic demands. The dik dik has to select rich food items only. The dik dik's narrow muzzle permits it to select only the richest sprouting leaves or fruits. If it had a broader muzzle, it would obtain unwanted mature leaves and twigs, as occurs in the broad-muzzled eland when it browses (Nge'the and Box, 1976). The eland, however, can tolerate this poor quality food because of its larger body size.

Relative lateral incisor breadth. In principle, breadth of lateral incisors is similar to relative muzzle width. Narrow lateral incisors permit a browser to be selective, whereas broad lateral incisors help a grazer acquire large volumes of poor quality grass. Though browsers indeed have relatively narrower lateral incisors than grazers (Janis and Ehrhardt, 1988), considerable overlap is seen in these two groups. No particular scaling effect is noted in the relationship i3/i1 vs. body mass (Fig. 5.7) as was noted in the relative muzzle widths of browsers above.

Taken by itself, relative incisor breadth would fail to discriminate between browsers and grazers, except that taxa having i3/i1 values less than 1/4 would likely exclude grazers. Both browsers or mixed feeders have values less than 1/4. Curiously, most of the taxa with the highest i3/i1 values were mixed feeders (e.g., Camelus spp., Syncerus cafer). Equids were the only grazers having i3/i1 values close to 1.

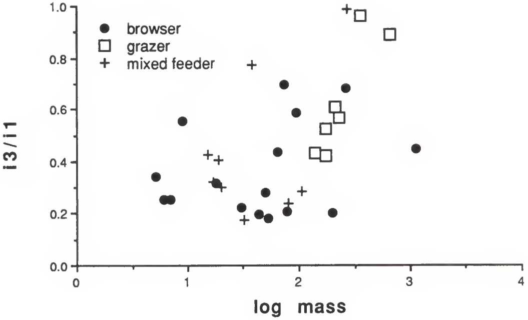

Figure 5.7. Relative lateral incisor breadth (i3/i1) shown as a function of the log of body mass (untransformed mass in kg).

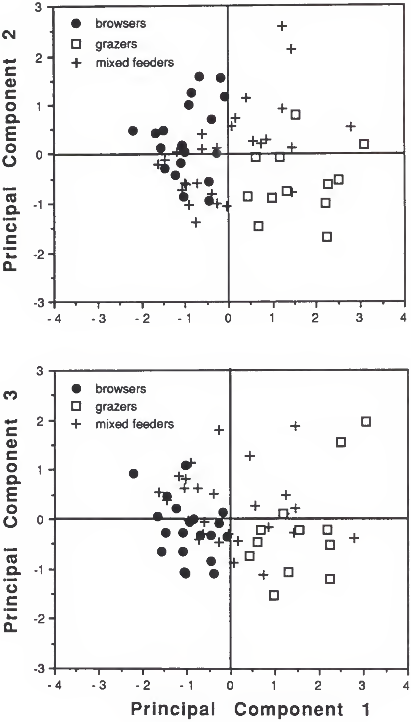

Figure 5.8. Principal components of browsing, grazing, and mixed feeding ungulates.

Discussion regarding the Principal Component Analysis

Though browsing and grazing artiodactyls overlap in regard to measures of tooth crown height, muzzle width, and relative incisor width, no such overlap occurs in the three dimensional combination of these variables. The major principal component (PC 1) unambiguously separated browsing and grazing ungulates (Fig. 5.8).

Principal component 1 accounted for just over half of the variation in the data (Table 5.3). Despite the rather modest alignment along this axis, PC 1 completely segregated browsers from grazers. All the grazing ungulates had PC 1 scores greater than zero, whereas, the browsers all had scores less than zero. Mixed feeders overlapped with browsers and grazers, having both negative and positive PC 1 scores. This is not surprising since this group represents animals that both browse and graze.

Fresh grass grazers (Kobus spp. and Elaphurus davidianus) have positive PC 1 scores that are lower than those of other grazers. They tend to have lower crowned molars and narrower muzzles and lateral incisors than other grazers.

Principal component 1 is a composite vector of the three variables examined. Each variable influenced PC 1 fairly equally (see eigenvectors of Table 5.3), with relative muzzle width making the greatest contribution.

Principal component 2 accounted for about a quarter of the variation among the three feeding indices and is related to relative incisor width and inversely related to hypsodonty. Muzzle width does not contribute to this axis.

A phylogenetic effect is noted on the second principal component axis. Almost all non-bovids had PC 2 scores greater than zero. The exceptions are a single cervid (Elaphuras davidianus), the antilocaprid (Antilocapra americana), and the zebra (Equus grevyi). The PC 2 score of Elaphurus (the grazing Père David's deer) was barely negative (-0.07). Antilocapra is also a questionable exception as a nonbovid having a PC 2 score less than zero since it is regarded as being a bovid by some (O'Gara and Matson, 1975). The zebra (E. grevyi.) is a clear exception having a PC 2 value of -0.51.

The PC 2 scores of the bovids ($\bar{x}$ = -0.35, s = 0.65) were significantly lower than those of the non-bovids ($\bar{x}$ = 0.74, s= 0.84; $p < 0.001$). This indicates that bovids tend to be higher crowned and have narrower lateral incisors than non-bovid artiodactyl ungulates.

Grazing ungulates are clustered in the lower right quadrant (positive PC 1 and negative PC 2 values) of the plot of PC 2 vs. PC 1 (Fig. 5.8). The only non-grazer in this quadrant is Antilocapra, a mixed feeder in open country. The only grazers sampled that do not appear in the lower right quadrant of PC 2 vs. PC 1 are the bison (B. bison) and an ass (E. asinus). These appear in the upper right quadrant (positive PC 1 and PC 2 scores).

The upper right quadrant is composed mostly of mixed feeders in open country. The only exceptions are the previously noted grazers and two mixed feeders in closed habitats. These closed-habitat mixed-feeders were the elk (Cervus canadensis) and the blue buck (Boselaphus tragocamelus), both of which had PC 1 scores close to zero. Most of the other taxa are mixed feeders living in open, sometimes arid, environments. The desert adaptive taxa include the camelids, the oryx (Oryx gazella), and ass (Equus asinus).

The upper right quadrant of PC 1 vs. PC 2 may be idealized as a region of morphometric space occupied by non-bovid mixed feeders, and the lower right an idealized grazing bovid quadrant. The equids straddle the border of these two regions of morphometric space, between the bovid grazers and the non-bovid taxa. The desert adapted ass falls within the upper right quad and the savanna adapted zebra falls in the lower right quad. The vast majority of taxa having positive PC 1 scores live in open habitats.

The upper left quadrant of the graph PC 2 vs. PC 1 (negative PC 1 and positive PC 2 values) was composed mostly of browsers. The exceptions are some mixed feeders along the fringes of this quadrant with the lower left quad (negative PC 1 & 2 values). All non-bovid browsers (tapirids, giraffids, cervids, and the tragulid) occur in the upper left PC 2 vs. PC 1 quadrant. The dik dik (Madoqua kirki) is the only browsing bovid clearly within this quadrant, though several others line the border of the lower left quad.

The lower left quadrant (negative PC 1 and 2 values) is composed solely of bovids. These are a mixture of browsers and mixed feeders completely overlapped in this perspective of their positions in multivariate space.

The graph of PC 3 vs. PC 1 (Fig. 5.8) also presents the browsing and grazing ungulates as two discrete groups. These are overlapped from above by mixed feeders. Curiously, a larger number of mixed feeders occur in regions where they overlap with the other either the browsers or grazers. The two equids occupy a region somewhat removed form the grazing bovids, which are clustered almost exclusively within the lower right quadrant of the PC 3 vs PC 1 plot. The equids lie in the upper right quad of the P3 vs. P1 plot.

The third principal component axis (PC 3) accounts for about 25% of the multivariate variation. It is most influenced by muzzle shape, with taxa having narrow muzzles having the higher PC 3 values since MW/PW has a negative eigenvector (Table 5.3). The isolation of the equids from other equids is due to the their unusually narrow muzzles compared to artiodactyl grazers. This example of phylogenetic constraint had been noted by Janis and Ehrhardt (1988).

The phylogenetic relationships were obscured on the plot of PC 3 vs. PC 2, but so too were the ecological relationships.

Reconstruction of Diets of Toxodontia

Leontiniid Feeding Ecology

The leontiniids of Salla are uncommon and the two specimens representing two species were too incomplete to be used for quantitative analysis. The material at hand indicates that they had pointed snouts and brachydont to mesodont molars. These characters give the qualitative impression that they were browsers. Chaffee (1952) suggested that Scarrittia was a browser based upon the low-crowned cheek teeth. The same dietary interpretation could apply to the Salla leontiniids.

Chaffee (1952) described the postcrania of Scarrittia and suggested that its broad feet would have aided locomotion on soft substrate. Based on the the numerous specimens of Scarrittia and the scarcity of cursorial taxa he suggested that the region was heavily forested. He also engaged in some interesting, "possibly far-fetched" (Chaffee, 1952: p. 553) speculation. He considered the possibility that Scarrittia may have fed upon some tuber that was a common food source for leontiniids and homalodotheres in South America and chalicotheres in North America.

Notohippid Feeding Ecology

Sufficient data were available for two species of notohippids to determine principal component scores (Table 5.8). Specimens of other species of Toxodontia are too incomplete for this analysis. No specimens of the new notohippid genus have an i3, the leontiniid specimens lack lower teeth, and no specimen of Proadinotherium sp. had a premaxilla.

The principal component scores of Eurygenium sp. and Rhynchippus cf. R. brasiliensis were determined by multiplying their standardized hi, MW/PW, and i3/i1 scores by their appropriate eigenvectors and then summing these. The standardized scale was such that the mean of each index (hi, MW/PW, and i3/i1) for all the ungulates was set at zero and the standard deviation was one. The PC scores and the means and standard deviations used to determine these scores are given in Table 5.8.

These notohippids may then be compared to the extant ungulates in multivariate space (Fig. 5.9). Both notohippid genera appear at the border of the grazing cluster on the plot of PC 2 vs. PC 1. This suggests that they could be primarily grazers or mixed feeders. The same interpretation applies to the relationship PC 3 vs. PC 1. This model indicates that these notohippids consumed grasses, either in moderate to large amounts, but would not have

Table 5.8. Data used for computing principle component scores for notohippids. For standardized scores the mean is zero and the standard deviation is one.

	$\bar{X}$, s (all ungulates)	*Eurygenium* sp.	cf. *R. brasiliensis*
hi :	1.31, 0.47	2.52	1.81
hi standardized:	— —	2.57	1.06
MW/PW:	0.78, 0.17	0.75	0.91
MW/PW standardized:	— —	-0.18	0.76
iwr:	0.49, 0.29	1.38	1.17
iwr standardized:	— —	3.06	2.34
notohippid eigenvector sums:			
	PC 1:	3.01	2.35
	PC 2:	0.50	0.85
	PC 3:	2.58	0.84

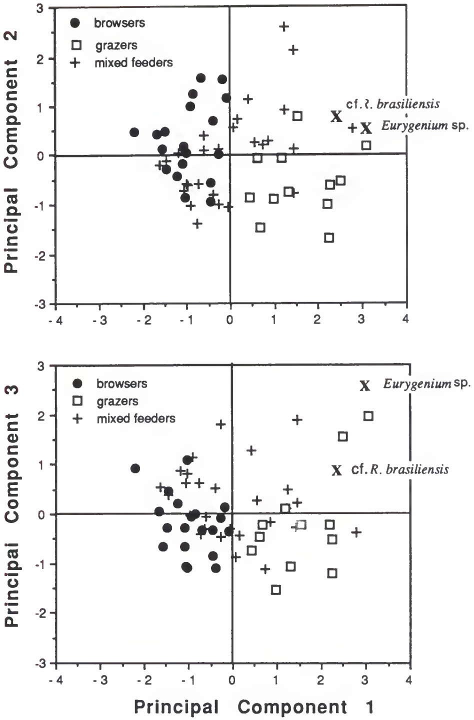

Figure 5.9. Principal components of notohippids superimposed on those of extant ungulates of known diets. The principal components of the notohippids were calculated from the eigenvectors of the extant ungulates.

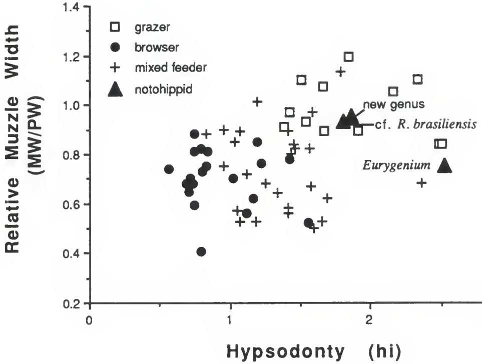

Figure 5.10. Relative muzzle width (MW/PW) shown as a function of hypsodonty (hi). Points are for extant ungulates of known diets and three notohippids of Salla.

subsisted primarily on browse. The notohippids, perhaps to Ameghino's delight, occupied positions in multivariate space close to equids. The Cape Buffalo (a mixed feeder) is another near neighbor on PC 2 vs. PC 1.

The lack of a mandibular symphysis of the new notohippid genus prevents its inclusion in this multivariate analysis. Its molar crown heights are comparable to the other notohippids (Table 5.4), but its relative muzzle width was greater (Table 5.6). The functional significance suggests that it would be more of a grazer than the other notohippids.

Although a multivariate quantitative comparison cannot be accomplished with the specimens at hand, a qualitative assessment may. The larger MW/PW value for the new notohippid genus will yield larger PC 1 scores, slightly smaller PC 2 scores, and much smaller PC 3 scores than other notohippids. This would put it more squarely among the grazing taxa.

The bivariate relationship of relative muzzle width and hypsodonty likely has some predictive utility since browsers and grazers do not overlap in two-dimensional bivariate space. These two indices have overlap among browsers and grazers when considered separately, but this overlap is resolved in bivariate space. The new notohippid genus lies among grazers when relative muzzle width (MW/PW) is plotted as a function of hypsodonty (hi) (Fig. 5.10). It lies close in bivariate space to smaller Rhynchippus cf. R. brasiliensis. The small size of R. cf. brasiliensis suggests that it would have required foods richer in calories and protein than available from just grass stems and leaves.

In addition to the Salla notohippids, I studied several other notohippid taxa in terms of hypsodonty and relative muzzle width. Of all the notohippid muzzles examined, Eomorphippus obscurus had relatively the broadest muzzle, as suggested by the highest MW/PW and MW_{max}/PW (see Table 5.6). Eomorphippus obscurus is known from the lost Cañandón Blanco locality of Argentina, which is here considered to be post-Mustersan; roughly the same age as the Tinguiririca fauna (≈ 35 Ma [Wyss et al., 1994]).

The blunt muzzle of E. obscurus suggests it was a grazer. Its molars approach hypsodonty (HI of M1 ≈ 1), being among the earliest notoungulates to develop high crowned teeth (Patterson and Pascual, 1972). Given this early mesodont condition, combined with the broad muzzle, the hypothesis that E. obscurus was a grazer seems credible, indicating that grasses were present, at least to some degree, by 35 Ma in South America (about 10 million years before Salla).

Argyrohippus fraterculus also had a relatively broad muzzle (MW_{max}/PW = 0.99) and was the most hypsodont of the notohippids sampled (HI = 2.5). Additionally, it had a thick coating of cement on its teeth and a large diastema. These characters suggest that it was a grazer.

Toxodontid Feeding Ecology

The absence of a specimen of Proadinotherium containing the upper anterior dental arcade prevents its inclusion in the multivariate analysis. Two lines of evidence indicate it had a broad relatively high MW/PW: 1) other specimens in this genus have broad muzzles (e.g., P. muensteri, AMNH 29722) and 2) the lower incisors are transversely arranged, wide, and show wear from occlusion with the upper teeth. Such a broad muzzle, wide symphyseal region with transversely arranged incisors would have facilitated grazing. The molars are hypsodont, though not to the extreme seen in the notohippids.

A qualitative assessment suggests that Proadinotherium sp. was a grazer. Its broad anterior dental arcade would have hindered selective feeding. Also, its hypsodont molars could have tolerated some degree of wear.

Chapter Summary

Multivariate analysis can help resolve ambiguities that plague one-dimensional attempts to interpret function. For example, a couple of neotragini browsers (i.e., Neotragus moschatus and Dorcatragus megalotis) have molars as high-crowned as several grazers (e.g., Elaphurus davidianus, Bison bison, Damaliscus dorcas). One could not judge the diet of a fossil taxon having a similar relative crown heights (hi ≈ 1.5).

The determination of PC scores for extinct taxa derived from taxa of known diets demonstrates a multidimensional means of comparing animals of unknown diets with those of known diets. This method suggests that grasses were a considerable component of notohippid diets.

Since many of the indices do not scale isometrically, body size should be considered in making interpretations. For example, the bison (a grazer) appears in the upper right quadrant of the plot of PC 2 vs. PC 1 among mixed feeders. Its PC 2 score is higher than other grazers, largely because it is low-crowned compared for a grazer (hi = 1.42). The index, hi, assumes isometry, apparently an inappropriate assumption in this case (see Fig. 5.3, but see also Janis, 1988). Allometrically scaling indices, such as hi, should be adjusted for effect of scaling. With such a correction, bison have a functionally higher hypsodonty index and would thus have a lower PC 2 score (since the eigenvector for hypsonty of PC 2 is negative).

A weakness of such a multivariate method is that fossils are often fragmentary and lack sufficient structures to determine even three simple indices. This is exemplified by the less common taxa of Salla such as the leontiniids and the toxodontid. A two dimensional method was used to predict the diet of the new notohippid genus. The leontiniids required a qualitative two dimensional method since the condition and incompleteness of the material prevented the determination of feeding indices.

CHAPTER 6
COMPARATIVE AND FUNCTIONAL SKELETAL ANATOMY OF SOME MEDIUM-SIZED UNGULATES FROM SALLA.

Introduction

Fragmentary fossil remains of vertebrates are scattered throughout the Salla Beds and rarely are reasonably complete skeletons encountered. Notable exceptions include two partial skeletons of Trachytherus spegazzinianus (Sydow, 1988), an interatheriid (Hitz, in preparation), the notohippid Eurygenium sp. (Chapter 3), as well as the partial skeleton of an undescribed anuran.

Eurygenium sp. is the only member of the Toxodontia of Salla that is represented by fairly complete postcranial elements. Rhynchippus cf. R. brasiliensis is represented by a distal humerus as well as a tentatively referred astragalus. A partial pes (UF 172410) is referred with some doubt to the new notohippid genus. The similarity to this pes and those of early toxodontids suggests that cf. Proadinotherium sp. should be considered as a differential diagnosis, though the similarity may be due to the speculated close phylogenetic relationship of the new notohippid to the Toxodontidae (see Chapter 7).

Though a brief description of the postcranial skeleton of Eurygenium sp. was provided in Chapter 3, a functional and comparative description is provided here to demonstrate the variety and degree of locomotor adaptations that had occurred by the Oligocene in Bolivia. This is accomplished by comparing Eurygenium sp. to Trachytherus spegazzinianus and a macraucheniid, cf. ?Coniopternium primitivum. These are also compared to extant taxa of known locomotor behavior.

The tarsal elements are described in some detail since they are particularly instructive regarding both function and phylogeny (Szalay, 1985).

Materials and Methods

Specimens Studied.

Postcranial specimens referred to Eurygenium sp. MNHN-Bol-V-003644, nearly complete, articulated skeleton, found in the the Upper White of Irupata Loma by Roger Portell in May 1992; UF 172432, right tarsal elements (astragalus, calcaneum, navicular, and cuboid) associated with fragmentary left m3, from Unit 2 of Pasto Grande, collected by Bruce J. MacFadden in Sept. 1984; UF 172431, right astragalus, collected from the Branisella Level (locality unrecorded); MNHN-Bol-004077, right astragalus, collected from the Branisella Level of Tapial Pampa West during a joint MNHN-Bol/Duke University expedition during May-June 1996.

Postcranial specimens referred to the new notohippid genus (rule out referral to Proadinotherium sp.). UF 172410, distal crux and tarsals (calcaneum, astragalus, navicular, cuboid) from Unit 2 "nowhere ash", the type locality of the new notohippid genus.

Postcranial specimens referred to Trachytherus spegazzinianus. UF 90960, partial skeleton, the "female" described by Sydow (1988); UF 91933 ("male"), skeleton lacking hind limbs, found in the Branisella level of "Ciudad de los Cranios"; UF 172437, left astragalus associated with a right tibia, from the "Buff Rubbly" of Unit 1 at Willa Kkollu; MNHN Bol-F-94-11, left calcaneum, astragalus, navicular, cuboid, and proximal Mt III, and Mt IV, associated with left tibia and several phalanges, from the "Upper White" (Unit 6) at Irupata Loma; MNHN Bol-F-94-10, left navicular, ectocuneiform, mesocuneiform, entocuneiform, cuboid, proximal Mt III and IV fused together by the matrix and associated with left astragalus (missing the neck and head), and left distal tibia and fibula, from the Branisella Level of Poco Poconi North West; MNHN Bol-F-94-01, left astragalus, from the Branisella Level of Poco Poconi North West; MNHN Bol-F-94-02, right astragalus, from the Principal Guide Level of Calaboza Pata.

Postcranial specimens referred to cf. ?Coniopternium primitivum. UF 172426, associated left calcaneum, astragalus, navicular, cuboid, and distal tibia and fibula, from Unit II at Pasto Grande; left astragalus, from the Principal Guide Level at Calaboza Pata; UF 172425, distal left femur, right navicular, metatarsal III, and proximal phalange from the "Red Rodent Zone" of Unit 3 at Calaboza Pata; MNHN-Bol-V-005305, associated left calcaneum, cuboid, ectocuneiform, distal fibula, metatarsal III (lacking distal end), proximal and distal portions of metatarsal IV, and one proximal and medial phalange each; UF 149207, right humerus from Unit II at Pasto Grande; MNHN-Bol-F-94-30, right femur, left distal femur, right astragalus, left cuboid, proximal humerus, and two vertebrae, from Unit 3, northeast of

Poco Poconi from northern section of Salla Beds along western wall of Quebrada Kollpajahuira; MNHN-Bol/UF sin numero, right femur, from the Principal Guide Level (Unit 4) at Poco Poconi.

Taxonomic determination of isolated tarsals. The nearly complete, articulated skeleton (MNHN-Bol-V-003644) of Eurygenium sp. permits unambiguous referral of tarsal elements to this taxon. Though many of the skeletal elements are abraded, the general form of the astragalus and calcaneum is sufficient to refer isolated tarsal elements to this species. The astragalus of MNHN-Bol-V-003644 has a distinctively short neck, lacking any constriction behind the broad, oval head. This nearly neck-less condition of the astragalus of Eurygenium sp. clearly differentiates it from astragali of Trachytherus. Thus, they could only be confused with other species of notohippids or Proadinotherium sp. It is easily differentiated from Rhynchippus cf. R. brasiliensis by size, so, of the known taxa of Salla, these may only be confused with astragali of the new notohippid genus or Proadinotherium sp. The description of the Eurygenium sp. limb elements below is based upon MNHN-Bol-003644 and the description of the tarsals is based largely upon UF 172432.

Partial skeletons of Trachytherus spegazzinianus (UF 90960 and UF 91933; see Sydow, 1988) permit confident referral of postcrania to this species. Hind limbs were preserved only of UF 90960 and the tarsals of this specimen, though imperfectly preserved, are sufficient to refer isolated elements to this species.

The macraucheniid limb elements lack associated teeth. The referral to this family is based upon comparison to postcrania described by Scott (1910) and Loomis (1914). The only named macraucheniid from Salla is ?Coniopternium primitivum (Cifelli and Soria, 1983a). These litoptern postcranial elements are certainly too large for an adianthid and are also larger than known proterotheriids.

Comparative Postcranial Anatomy of Ungulates of Salla

Forelimb.

Humerus. Several features of the humerus of Eurygenium sp. were noted in Chapter 3 as being indicative of strength and dexterity. These included the large surface area for deltoids and pectorals, a subspherical capitulum, and distinctive supinater crests. The humeral crests are distinctive compared to the notohippid Rhynchippus equinus (Loomis, 1914) but are similar to those of the humerus of the small adult ("female") of Trachytherus spegazzinianus (UF 90960). The putative male trachythere (UF 91933) however, has very distinctive crest for attachments for the pectoral, deltoid, and supinator muscles (Fig. 6.1).

The notohippid and trachythere humeri have prominent, undivided greater tuberosities that project above the humeral heads (this feature is not preserved on the cf. ?Coniopternium specimen). Though a paradigm interpretation (see discussion) suggest that a high greater tuberosity may indicate greater leverage, and thus strength (Taylor, 1974), it is noted that modern ungulates and cursorial non-ungulate mammals have this character (O'Leary and Rose, 1995). Tall greater tuberosities in cursorial animals may function to restrict humeral mobility to the parasagittal plane (O'Leary and Rose, 1995).

The humeral heads of Eurygenium and Trachytherus are displaced such that they lie posterior to the long axis of the shaft. The degree of this displacement is comparable to that seen in the domestic pig (Sus). The displacement of the humeral head is greater in the macraucheniid humerus (UF 149207) referred to cf. ?Coniopternium primitivum.

A litoptern humerus (UF 149207) is small (Table 6.1) relative to the femur described below. Though macraucheniids are characterized by their relatively short humeri, this specimen is probably too short to have come from animals as large as those represented by the macraucheniid femora described below. Cifelli and Soria (1983b) noted considerable variation in size of macraucheniid teeth and speculated that they may represent more than one species.

This macraucheniid humerus is similar to that of Notodiaphorus crassus (= Coniopternium andinum) described and figured by Loomis (1914: fig. 6). Both lack a distinctive capitulum, but have deep, symmetric, pool-shaped articular surfaces for the antebrachium. Like the Loomis specimen, the Salla macraucheniid lacks an entepicondylar foremen but has a large supratrochlear foramen. The supinator crest is inconspicuous and there is no evidence of pronounced pectoral or deltoid crest, though the proximal anterior surface of the humerus is damaged. The Salla element is somewhat smaller than the humerus described by Loomis (he reported anterior and posterior trochlear widths of 37 and 28 mm, whereas the Salla macraucheniid humerus has dimensions of 28 and 22 mm for these respective regions).

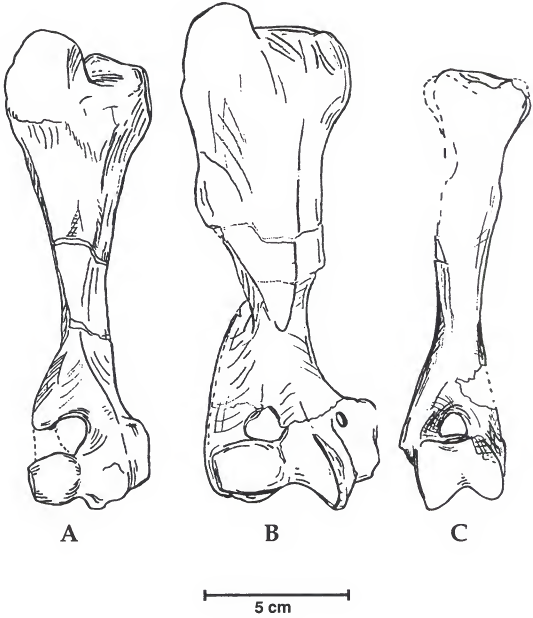

Figure 6.1. Ungulate humeri of Salla. A, Right humerus of Eurygenium sp. (MNHN-Bol-V-003644); B, left humerus (reversed) of Trachytherus spegazzinianus (UF 91933); and C, right humerus of cf. ?Coniopternium boliviensis (UF 149207).

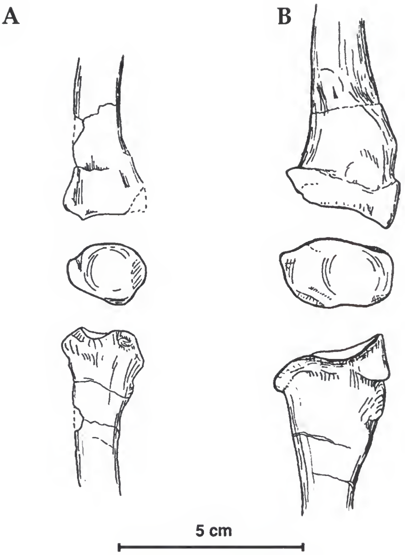

Figure 6.2. Proximal radii of two notoungulates. A, Right proximal radius of Eurygenium sp. (MNHN-Bol-V-003644) and B, left radius of Trachytherus spegazzinianus (UF 91933).

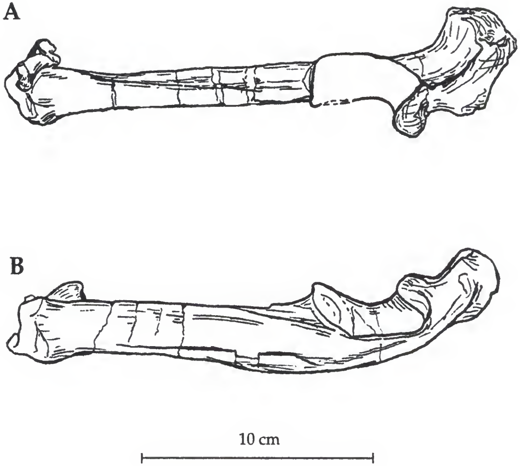

Figure 6.3. Left ulna of Trachytherus spegazzinianus (UF 91933). A, dorsal view; B , lateral view.

Table 6.1. Forelimb dimensions of Eurygenium sp., Trachytherus, and cf. ?Coniopternium of Salla. AP, anteroposterior; DV, dorsoventral; ML, mediolateral.

Humerus

Taxon/ID Nº	total L	distal W	midshaft	
		(biepicondylar)	(AP x	ML)
Eurygenium sp. MNHN-Bol-V-003644	156	41	26	16
Trachytherus sp.				
UF 91933	185(S)	66	34	27
UF 90960	158(S)	55	27	20
cf. ?Coniopternium	158	40	31	18

Antebrachium

	ulna	olecranon L	radius	radial head	
	(L_{Total})	(mid-sigmoidal notch to end)	(L_{Total})	(ML x	DV)
Eurygenium sp. MNHN-Bol-V-003644	166	41	126	21	15
Trachytherus sp.					
UF 91933	223(S)	60	167(S)	29	18
UF 90960	198(S)	51	138(S)	25	15

(S) Measures from Sydow, 1988.

Table 6.2. Limb proportions of a notohippid, mesotheriid, and macraucheniid of Salla.

	Eurygenium sp.	Trachytherus	cf. ?Coniopternium
Brachial Index 100(radius/humerus)	81	87-90(S)	---
Olecranon Indices			
100(olec/ulna)	25	26	---
100(olec/forearm)*	19	18(S)	---
Crural Index 100(tibia/femur)	93	94(S)	---
Metatarsal Index 100(Mt/femur)	25	33	44-49

(S) From Sydow, 1988.

* Index from Smith and Savage (1956). It is the ratio (expressed as a per cent) of the olecranon length (mid sigmoidal notch to end of olecranon) divided by the forearm length (mid sigmoidal notch to tip of longest digit)

The Trachytherus, Eurygenium, and ?Coniopternium humeri have deep olecranon and coronoid fossae, suggesting that they fully extended and flexed their forearms. The notohippid and macraucheniid have distinctive supratrochlear foramen. The status of this character is somewhat ambiguous in Trachytherus, but apparently it too has a supratroclear foramen (Sydow, 1988). The biepicondylar width is the greatest in Trachytherus (Table 6.1).

Antebrachium. The proximal radius of Eurygenium is ovoid whereas that of Trachytherus is more rectangular (Fig. 6.2 and table 6.1), suggesting greater forearm mobility for Eurygenium. Pronation was facilitate in Trachytherus by the morphology of the ulna (Fig. 6.3). The sigmoidal notch strides the lateral as well as the dorsal surface such that the when in anatomical position with the humerus the shaft of the ulna is rotated such that the dorsal surface is medially directed by about 45°. Little movement was required of the radius for complete pronation.

The ulnae of Eurygenium sp. and Trachytherus are robust and lack any significant distal reduction. They are bowed such that the proximal and distal ends are anteriorly directed (see Figs. 3.7A and 6.3). This bowing is opposite to that of the ulnae of many extant ungulates (e.g., Tapirus, Sus, Odocoelius, Hydrochaeris; see O'Leary and Rose, 1995: fig. 7). The ulna is unknown for the Salla macraucheniid, but that of the Coniopternium specimen of Cabeza Blanca has the conventional bowing in the sagittal plane (see Loomis, 1914: fig. 7).

The olecranon processes of Eurygenium and Trachytherus are distinctive, being about 25% the total ulnar length (Table 6.2). The olecranon processes of these ulnae curve medially in these two taxa, but more so in

Trachytherus. The olecranon process of Trachytherus is enlarged, flared, and medially directed. A medial curve of the olecranon is seen in arboreal and scansorial viverrids (Taylor, 1974; Laborde, 1987) and several mustelids (Gebo and Rose, 1993).

The radius of Eurygenium is shorter (relatively as well as absolutely) than that of Trachytherus. The brachial index (radial length/humeral length x 100) for Eurygenium is 81, whereas the brachial indices reported by Sydow (1988) were 87 for the "female" (UF 90960) and 90 for the "male" (UF 91933). See Tables 6.1 and 6.2.

The forearm of cf. ?Coniopternium is represented by only a distal portion of the radius (UF 173278). Two facets appear on the distal surface, presumably the articular surfaces for the scaphoid and lunar. This region appears to be a solid and single element, representing only the radius and not the ulna-radius as occurs in Theosodon (Scott, 1910). The ventral surface of the radius is grooved, perhaps an indication of the placement of a reduced ulna. The forearm appears to have been incapable of supination.

Manus. The manus of Trachytherus was pentadactyl, having a reduced first digit (Sydow, 1988), whereas the manus of Eurygenium sp. was tetradactyl, having a reduced fifth digit and no first digit (Chapter 3: Fig. 3.7B). The metacarpals Eurygenium sp. are shorter than those of Rhynchippus equinus and are not compacted as in R. equinus. The manus of the Salla macraucheniid is unknown.

Hindlimb.

Femur. The femora of Eurygenium sp. and Trachytherus are remarkably similar for two animals representing separated suborders (Fig. 6.4). Both have greater trochanters about as high as the head, their femoral heads lie at the end of obliquely oriented necks, and these elements have distinctive lesser and third trochanters. Differences between the two are few, but the femur of Eurygenium sp. has a more distal lesser trochanter and a rounder shaft in cross section (the shaft of Trachytherus is dorsoventrally flattened). The similarities in the femora of these taxa may represent a symplesiomorphic condition for the two suborders.

One femur referable to Trachytherus was fractured during life and healed (Fig. 6.4B). The animal lived for sometime after the accident despite the fact that it was a displaced fracture which reduced the total length of the limb to 80-90% its original length.

The femur of the macraucheniid, cf. ?Coniopternium primitivum, little resembles the notoungulate femora noted above (Fig. 6.4 and Table 6.3). The greater trochanter is higher than the head and more distant from it, giving the proximal femur a broad forked appearance. The neck is more distinct than that of the Coniopternium (=Notdiaphorus) (Loomis, 1914: fig. 8) and even the Santacrucian forms (Scott, 1910). Neither of two complete femora have a distinct lesser trochanter, but one has breakage that may be an indication of this. If so, it would appear to have extended to the mid-shaft level. A strong posterolateral ridge runs from the greater trochanter to the mid-shaft level where breakage suggest that a third trochanter projected. Both macraucheniid femora available show torsion of the distal region such that the knee would have had a slight lateral rotation.

A conspicuous pit for the plantaris muscle extends from the posterolateral mid-shaft level down to the lateral condyle. This depression occupies much of the distolateral quadrant of the posterior femoral shaft and is quite similar in form to the plantar pits of tapirids, equids, as well as Miocene macraucheniids and proterotheriids (see Scott, 1910).

The patellar groove is short and terminates proximally into a deep pit into which the patella could have slid. The distal wall of the patella pit is steep, unlike the graded wall of the suprapatellar fossa of Tapirus. The medial trochlear ridge appears higher than the lateral, but breakage of the lateral troclear ridge makes the comparison difficult. One specimen has a medial trochlear ridge that appears to be notched, but breakage in this region does not permit a definitive assessment of this feature. The deep patellar pit, however, would have permitted the patella to have become "locked" in place, thus providing a novel passive stay mechanism similar in principal to those of extant and some fossil horses (Hermanson and MacFadden, 1996).

Crux. The crux of Eurygenium sp., Trachytherus, and cf. ?Coniopternium all have unfused, articulating tibia-fibula. The Eurygenium skeleton preserves complete tibia and fibula. Trachytherus is represented by complete tibiae, but only distal fragments of the fibula. Only the distal tibia and fibula are preserved in the macraucheniid cf. ?Coniopternium.

The tibia of Eurygenium sp. and Trachytherus are relatively short. Crural indices ([tibial length/femoral length] x 100) for these animals are

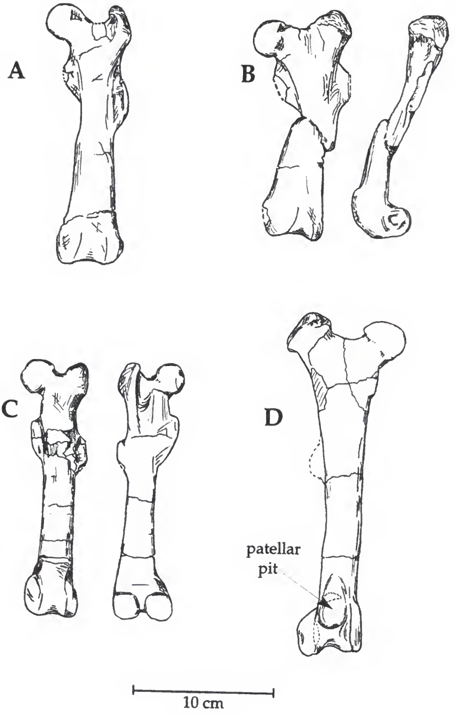

Figure 6.4. Femora of Salla ungulates. A, *Trachytherus spegazzinianus* (UF 90960); B, fractured and healed femur of *T. spegazzinianus* (MNHN-Bol-F-94-12); C, *Eurygenium* sp. (MNHN-Bol-003645) in dorsal (left) and ventral (right) view; D, cf. ?*Coniopternium boliviensis* (MNHN-Bol-94-30).

Table 6.3. Metatarsal/femoral ratios of selected Salla taxa.

Taxon/ ID Nº	**Mt III L**	**femoral L**	**Mt/femur**
Eurygenium sp. MNHN-Bol-V-003644	44.3	175	0.25
Trachytherus spegazzinianus UF 90960	60.7	179	0.33
cf. ?Coniopternium primitivum (femur a/UF 172425)	117.7	265	0.44
cf. ?Coniopternium primitivum (femur b/UF 172425))	117.7	238	0.49
Prohegetotherium sp. (composite UF 172502/UF 172445)	32.9	90	0.37

nearly identical (Table 6.2). Their crural indices are higher than those seen in fossorial carnivores, but at the low range of non-cursorial terrestrial carnivores (Gebo and Rose, 1993).

The fibula of the two notoungulates and the litoptern appear to be mobile. This is certain in the notohippid, Eurygenium sp., as demonstrated by the proximal and distal articular surface between the two crural elements. This distal fibula of Trachytherus and cf. ?Coniopternium articulates with the fibula, astragalus, and calcaneum.

Notoungulates and litopterns have a tricontact upper ankle joint (sensu Szalay, 1994); that is, calcaneal-fibular, astragalar-fibular, and astragalar-tibial articulation. The calcaneal-fibular contact in the Toxodontia and Litopterna is pronounced, giving the calcanea in these taxa broad fibular facets. These broad facets are the apparent source of the ordinal name for the litopterns, which means "smooth heel".

Upper Ankle Joint and Tarsals

Though the crux in the three families considered here is fundamentally similar, the tarsals are quite distinct. Compared to the Itaboraian notoungulate tarsals (Cifelli, 1983), the Trachytherus tarsals appear to be the least derived. The tarsals of the notohippid, as well as other Toxodontia (Scott, 1912), are distinct from the putative ancestral notoungulate form (Cifelli, 1983).

Upper ankle joint and tarsals of Trachytherus. The Trachytherus astragalus (Table 6.4 and Fig. 6.6A) has conspicuously asymmetric trochlear keels, with the lateral keel being much higher, and more acute, than the medial (see Fig.6.5 for tarsal terminology). The trochlear groove is shallow and most specimens lack a superior astragalar foreman. Several specimens have a shallow fossa at the distal termination of the trochlear groove to relieve the anterodistal tibial process during extreme dorsoflexion of the upper ankle joint. The groove for the tendon of the digital flexor is distinct from the trochlear groove. It forms a deep concavity in the superior plantar region of the bone. The astragalar neck is long, remarkably so in most specimens, and is obliquely oriented relative to the astragalar body. The diameter of the neck is conspicuously smaller than that of the head. The head is subspherical, essentially forming the "ball" of the astragalo-navicular "ball-and-socket" joint. The sustentacular facet lies along the proximoplantar portion of the neck and is convex in this region, but abruptly shifts to a concave surface just superior to the mid-body to form a deep notch for articulation with the posterior portion of the calcaneal sustentaculum. The ectal facet forms a smooth concavity that extends the entire length of astragalar body.

The dorsal prominence of the calcaneum is obliquely oriented with the dorsomedial surface providing an articular facet (ectal facet) for the astragalus and the dorsolateral surface forming a fibular facet (Fig. 6.8C). The ectal facet is convex and broad. The fibular facet is sharply convex in lateral view. The lateral calcaneal border has a groove for the tendon of the peroneus longus and one specimen (UF 172514) preserves a small peroneal process that is not directly adjacent to the distal region of the peroneal groove. There is a second fossa of unknown origin on the lateral side of the calcaneal body. The apex of

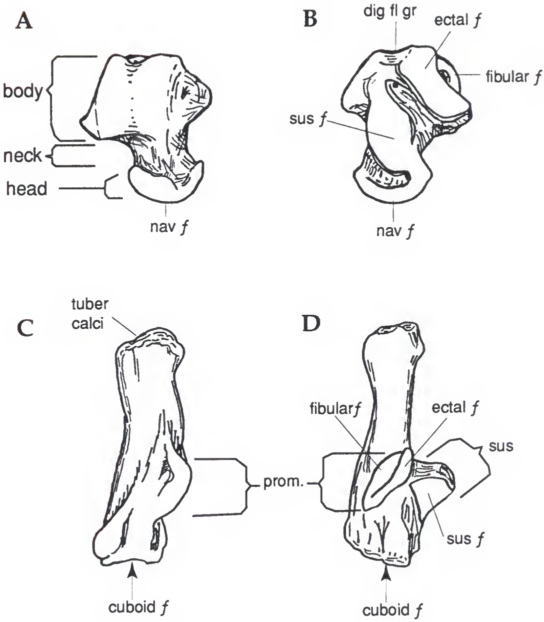

Figure 6.5. Proximal tarsals of a primitive notoungulate (Colbertia magellanica) indicating descriptive terms. A, dorsal astragalus; B, plantar view of astragalus; C, lateral view of calcaneum; D, dorsal calcaneum. Abbreviations: dig fl gr, digital flexor groove; *f*, facet; nav, navicular; prom, dorsal promiance; sus, sustentaculum. Adapted from Cifelli, 1993.

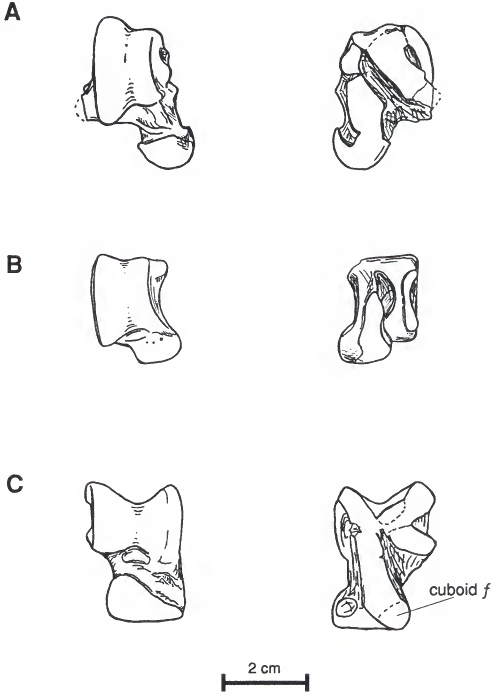

Figure 6.6. Ungulate astragali of Salla. Dorsal (left) and plantar (right) views of astragali of (A) *Trachytherus spegazzinianus* (Bol-F-94-02); B, *Eurygenium* sp. (UF 172431); and C, cf. *Coniopternium boliviensis* (UF 172426) (reversed).

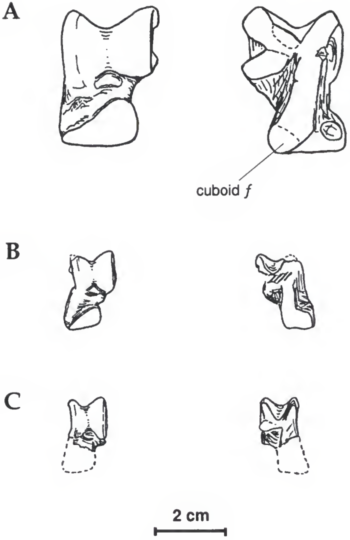

Figure 6.7. Left litoptern astragali. Dorsal (left) and plantar (right) views of astragali of A, cf. ?Coniopternium primitivum (UF 172426) and B and C, Tricoelodus boliviensis (MNHN-Bol-F-94-31 and UF 172455).

Table 6.4. Dimensions of notohippid, mesotheriid, and litoptern astragali (mm). Listed are measures of the total astragalar length (L_T), trochlear width (W_{troch}), and the transverse and dorsoventral lenghts of the astragalar head.

Taxon	**ID Nº**	L_T	W_{troch}	**head**	
				(trans)	(dorsovent)
NOTOHIPPIDAE					
Eurygenium sp.	Bol-V-5305	---	14.2	---	---
Eurygenium sp.	UF 172432	31.8	14.4	---	---
Eurygenium sp.	UF 172431	29.1	16.1	15.9	11.0
Eurygenium sp.	Bol-V-4077	26.3	15.0	14.9	11.7
cf. gen. nov.	UF 172410	37.3	17.8	16.3	16.5
MESOTHERIIDAE					
Trachytherus	Bol-F-94-01	37.5	14.7	15.6	13.9
Trachytherus	Bol-F-94-02	40.7	16.5	16.7	13.5
Trachytherus	UF 172437	35.0	15.4	14.2	12.3
Trachytherus	Bol-F-94-10	35.0	15.1	---	---
Trachytherus	UF 90960	34.6	14.8	13.9	13.8
LITOPTERNA					
cf. ?Coniopternium	UF 172426	38.4	25.5	21.8	13.6
cf. ?Coniopternium	UF 172424	42.5	26.8	21.0	13.8
Tricoelodus	Bol-F-94-31	21.5	11.6	9.8	6.2
Tricoelodus	UF 172455	---	10.0	---	---

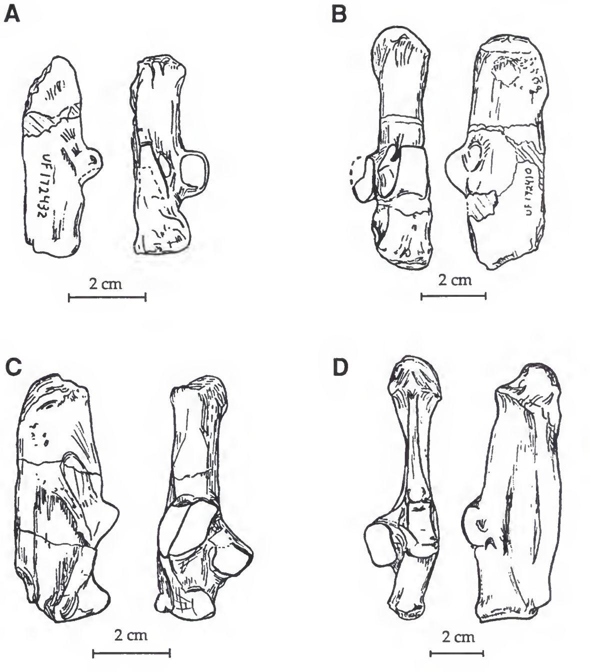

Figure 6.8. Calcanea of Salla ungulates. A, Eurygenium sp. (UF 172432), right calcaneum, lateral and dorsal views; B, Toxodontia indeterminant (cf. new notohippid genus, left calcaneum, dorsal and lateral views; C, Trachytherus spegazzinianus (UF 172514), right calcaneum, lateral and dorsal views; D, cf. ?Coniopternium boliviensis (MNHN-Bol-V-005305), left calcaneum, dorsal and lateral views.

Table 6.5. Calcaneal dimensions for notohippids, mesotheriids, and litopterns. Listed are measures for the total calcaneal length (L_T), greatest width, including the sustentaculum (W_{sus}), and the transverse width of the shaft measured midway between the sustentaculum and the tip of the tuber calci (W_{shaft}).

Taxon	**ID Nº**	L_T	W_{sus}	W_{shaft}
NOTOHIPPIDAE				
Eurygenium sp.	Bol-003644	54.0	22.4	11.3
Eurygenium sp.	UF 172432	54.6	20.0	11.8
cf. gen. nov.	UF 172410	75.4	---	14.5
MESOTHERIIDAE				
Trachytherus	UF 172514	66.7	26.5	15.2
Trachytherus	UF 90960	61.0	24.6	13.0
LITOPTERNA				
cf. ?Coniopternium	UF 172426	88.5	27.6	11.5
cf. ?Coniopternium	Bol-V-5305	99.4	32.0	11.0

the tuber calci is rugose, lacking a distinctive groove for the Achilles tendon. The sustentacular process is modestly large having a nearly planar facet. A groove for the flexor hallucis longus is present on the plantar surface of the sustentaculum. The distal region of the plantar surface has a large rugose region for attachments of the plantar ligaments. The cuboid facet is ovoid, being laterally compressed, and convex, gaining depth in the dorsomedial direction.

The cuboid of Trachytherus is roughly trapezoidal in dorsal view, with the medial edge being higher than the lateral. A peroneal groove extends from the lateral border and crosses the plantar surface where it is shielded by a rugose tuberosity. The medial surface has a semicircular navicular facet proximally and a distal lambdoidal ectocuneiform facet. The cuboid did not articulate with the astragalus.

In superior aspect, the navicular has a rounded concavity for articulation with the spherical astragalar head. The lateral surface is devoted almost entirely to the cuboid facet. The pear-shaped ectocuneiform facet is the most prominent feature in distal view. The mesocuneiform facet is about two-thirds the size of the ectocuneiform facet and it lies in a plane that is slightly oblique to that of the ectocuneiform mesocuneiform. The entocuneiform facet is the smallest of the navicular's distal facets and it lies medioplantar to the other cuneiform facets. It is subhemispherical whereas the other cuneiform facets of the navicular are essentially planar.

The entocuneiform is laterally compressed and appears as a medioplantar plate that buttresses the Mt II. The proximal surface is notched to articulate with the protruding hemispherical facet of the navicular. No metatarsals have been found articulating with this element, but the distal surface is smooth and concave in three specimens, indicating that they articulated with a somewhat reduced Mt I. One specimen (UF 172444), however, has a rugose distal surface suggesting that a functional entocuneiform-Mt I joint was absent on this individual. Thus, the presence of an Mt I may have varied in the population.

The mesocuneiform is nearly as broad as the ectocuneiform, but is proximodistally shorter, such that the Mt II had a more proximal origination than the other metatarsals.

The ectocuneiform is the most robust of the tarsal cuneiforms. It is I-beam to teardrop shaped in when viewed either proximally or distally and has a pronounced plantar process. It articulates distally only with the Mt III.

The cuboid has a broad articulation with Mt IV, but lacks a separate facet for articulation with Mt V. The presence of a reduced Mt V is inferred from its impression in the matrix lying against the Mt V facet of Mt IV of MNHN-Bol-F-94-10.

Upper ankle joint and tarsals of Eurygenium sp. The fibula of Eurygenium sp. is not fused with the tibia. The most distal portion articulates with the calcaneum and the mediodistal portion articulates with the lateral wall of the lateral trochlear keel of the astragalus. The astragalus of Eurygenium (Fig. 6.6B and Table 6.4) is dissimilar to that of Trachytherus in several ways. The neck of the Eurygenium sp. astragalus is conspicuously short, almost nonexistent, and the head is ovoid, rather than a subspherical structure, being longer transversely than dorsoventrally. The plane of the ectal facet faces lateroplantar, and is essentially parallel with the sustentacular facet, having an anteroposterior rather than oblique orientation. This facet does not project beyond the inferior border of the body. Both calcaneal facets are flatter than those of Trachytherus, and whereas these lie on about the same plane in Trachytherus, the ectal fact of Eurygenium lies much deeper in the astragalar body than the sustentacular facet. Also, the medial wall of the astragalar body is nearly vertical. In essence, the two proximal tarsals lie transverse to one another, rather than dorsoventral.

The total lengths of the calcanea of Eurygenium are shorter than those of Trachytherus (see Table 6.5 and Fig. 6.8). The sustentaculum projects from the level of the ectal prominence and contains a groove for the tendon of the deep flexor muscle. The sustentacular facet of the calcaneum is planar. The ectal facet on the calcaneum of both specimens is abraded, but it is clearly small and facing dorsomedially, and is ventromedial to the ectal prominence. The tibial facet runs anteroposteriorly, is fairly broad, becoming broader distally, and occupies the dorsal surface of the ectal prominence. The tuber calci is of moderate length and has a broad, rugose termination, lacking a groove for the Achilles tendon. The lateral calcaneal surface has a shallow peroneal groove in the distal region, but lacks a peroneal process. The dorsal and plantar surfaces of the calcaneal neck are parallel, lacking a distodorsal projection as seen in the Trachytherus calcaneum. The cuboid facet is much longer transversely than dorsoventrally. The area for attachment of the plantar ligaments is shallow.

The navicular has a sub rectangular-to-ovoid astragalar facet suggesting that the astragalonavicular joint facilitated parasagittal rotation and inhibited transverse movement. There is a facet for articulation with the cuboid on the lateral surface, but not with the calcaneum as occurred in the cf. ?new notohippid genus specimen below. Considerable distance remains between the astragalus and cuboid with no possible contact between these elements.

The cubocalcaneal articulation of Eurygenium sp. is proximal to the navicular-ectocuneiform articulation. This is distinct from Rhynchippus pumilus (Chaffee, 1952), the notohippid described below, and the toxodontids Adinotherium and Nesodon (Scott, 1912) . In these taxa, the calcaneal-cuboid articulation is at the same level as the navicular-ectocuneiform joint.

Eurygenium sp. appears to have been functionally tridactyl, with Mt II, III, and IV being of similar size. Metatarsal V was not recovered but the cuboid has a small articular surface for this element. There was no Mt I.

The metatarsals were not very long in Eurygenium sp. (see Table 3.4). Indeed, it had the lowest metatarsal to femoral ratio among the ungulates of Salla for which these could be determined (Table 6.3).

Tarsals of cf. new notohippid genus. This tarsus (UF 172410) is tentatively referred to the new notohippid genus described in Chapter 3. It should, however, be noted that it could also be a tarsus of Proadinotherium sp. The tarsus of Proadinotherium is unknown and thus cannot be compared. As will be shown below, this tarsus has the distal calcaneal-astragalar articulation seen in toxodontids, and calcaneal-cuboid articulation at the level of the navicular-ectocuneiform articulation as occurs in early toxodontids (Scott, 1912) and the notohippid Rhynchippus pumilus (Chaffee, 1952). These characters suggest that the tarsals are on an animal closely related to the Toxodontidae, but, as noted elsewhere (Chapters 3 and 7), this new notohippid may be the sister taxon to the toxodontids.

The molar fragment associated with this partial pes is a talonid of a heavily worn left m2. The tooth and tarsals were found at the same locality as UF 149221 (see Fig. 3.5B), which is the heavily worn dentition of the new notohippid genus. Both specimens have the same preservation. It is quite possible that the tooth associated with the tarsals (UF 172410) and UF 149221 are of the same individual. The possibility that they are of different animals is accented by the fact that a distal calcaneal tuber associated with these tarsal elements fit perfectly on the calcaneum of a Coniopternium specimen (UF 172426) collected two years previous to the collection of the tarsal elements at hand.

Only the most distal portion of the fibula of UF 172410 is preserved. It is a rather robust element with a broad semicircular astragalar facet at the medial malleous and a shallow, convex calcaneal facet on the distal surface. The region proximal to the astragalar facet of the fibula is not preserved, so it is impossible to determine the extent of contact, if any, with the tibia.

Although the proximomedial trochlear keel of the astragalus is missing, it is evident that the trochlea is relatively deep compared to those of Trachytherus and Eurygenium sp. The neck is obliquely oriented as is the navicular facet. There is a slight constriction behind the head. The plantar surface is distinct in that the calcaneal facets are shifted laterally and are facing in that direction. As in Eurygenium, the ectal facet is set deeper in the astragalar body than the sustentacular facet. Also, like the previously described proximal tarsals, the astragalus and calcaneum are transversely oriented to one another.

The calcaneum is fairly robust (Fig. 6.8B). The ectal facet of the calcaneum is nearly vertical, lying deep to the ectal prominence. The fibular facet is nearly as wide as the body of the calcaneum. The maximum width of the fibular facet of the calcaneum is 11.7 mm whereas the width of the tuber calci is only about 13 mm. The apex of the tuber calci has a groove for the Achilles tendon. The lateral surface lacks a distinctive peroneal groove, but a groove for the deep flexors underlies the sustentaculum on the medial surface. A narrow, ovoid, convex navicular facet lies distal to the sustentaculum, just proximomedial to the cuboid facet. This is nearly identical to the form seen on the calcaneum of Adinotherium ovinum (Scott, 1912: plate XXI.5). As in Adinotherium, Nesodon, and Rhynchippus pumilus, the calcaneal-cuboid joint is as the same level as the navicular-ectocuneiform articulation.

The navicular has a damaged ovoid facet for the astragalar head. The lateral surface of the navicular has a concave facet for articulation with the distinctive navicular facet of calcaneum. Just distal and plantar to the calcaneal facet of the navicular lies a smaller cuboid facet. The distal navicular surface contains a large teardrop-shaped ectocuneiform facet that is transversely concave but convex in its anteroposterior dimension. The mesocuneiform facet is damaged, as is the medial border of the navicular.

The cuboid and ectocuneiform are cemented together by matrix. The proximal and distal surfaces of these elements lie on nearly the same plane, except for the apex of the strongly convex proximal surface of the cuboid which forms the surface for calcaneal articulation. The plantar cuboid surface has a large rugose process for protecting the peroneal tendon. The distal surface has a large Mt IV facet, but unfortunately the lateral corner is damaged such that it is impossible to determine if there was an articulation with Mt V.

The ectocuneiform is narrow and dorsoventrally deep, having a pronounced, broad plantar process. The facet for the Mt III is damaged as is the medial surface. A facet for the mesocuneiform is discerned at the mediodistal surface, adjacent to the mesocuneiform facet of the navicular. Associated metapodal remains are fragmentary and can not certainly be determined to be either metatarsals or metacarpals. The presence of Mt III and IV can be confidently inferred from the large facets of the ectocuneifrom and cuboid. The mesocuneiform and entocuneiform were not preserved.

Tarsals of the macraucheniid of Salla (cf. ?Coniopternium). Cifelli and Soria (1983b) tentatively referred the Salla macraucheniid to Coniopternium. Postcranial elements were not available to them so their description of ?C. primitivum was based soly on isolated teeth. Since then, additional collections have been made that have produced the postcranial elements listed below. Unfortunately, none are associated with teeth.

Sufficient material is present to permit a comparison of Salla hind foot elements with those of Coniopternium andinum from the Loomis Collection (described as Notodiaphorus crassus by Loomis, 1914; see Cifelli and Soria, 1983b). The Salla specimens are all slightly smaller than the Amherst specimens. UF 172426 represents the most complete hind foot in the UF collection and is described here in some detail.

The distal tibia and fibula of UF 172426 demonstrate the tricontact nature of the upper ankle joint; that is, the tibioastragular, fibularastragalar, and fibularcalcaneal contact (see Szalay, 1994).

The astragalus (Fig. 6.7A) has a spool-shaped body, moderately notched, subequal medial and lateral crest, with the lateral crest being a little broader. There is no superior astragalar foremen, though a pit along a crack may appear as such. (I examined this portion of the specimen before gluing the fragments together. It is merely a defect and not a foremen, which is also lacking in UF 172424.) The trochlear surface does not extend as far into the plantar surface as in the adianthid specimen described below. There is no distinct groove for the deep digital flexor tendon. The trochlear groove terminates dorsodistally in a fossa for the ventral projection of the tibia. The astragalar neck is broader than the gracile neck of the adianthid astragalus noted below. The head is convex and ovoid with the major axis oriented transversely. The navicular facet extends anteriorly on the ventrolateral surface such that it nearly reaches the lateral margin of the tibial fossa. The navicular facet on the dorsal surface extends to the sustentacular facet and to a notch shaped medial facet that also occurs on the adjacent part of the navicular. An indistinct cuboid facet grades into the sustentacular facet separated by a barely palpable ridge (cuboastragalar contact is confirmed by the presence of an astragalar facet on the cuboid). Examination of these elements in anatomical position suggests that the cuboastragalar contact occurred only during the loaded portion of the locomotion cycle. The long sustentacular facet is essentially continuous with the cuboid facet and extends proximally to the level of the ectal facet.

The calcaneum (Fig. 6.8D) is laterally compressed with the neck appearing to bend medially. The fibular facet is convex, semicircular when viewed laterally. The surface just distal to the fibular facet is smooth, demonstrating that the fibula contacted the body of the calcaneum during extreme flexion. The MNHN specimen has a dorsal fossa for calcaneal-fibular contact during extension, a character which is lacking on the UF calcaneum. The ectal facet of the calcaneum is wedged shaped, having an angle of approximately 90° for snug fit into the notch-like ectal facet of the astragalus. The sustentaculum is not conspicuously long and its facet is slightly concave. The calcaneal neck is directed medially and has a ventrodistal rugose surface demonstrating the attachments for the astragalocalcaneal ligament and extensor muscles (m. brevis and retinaculus). The dorsal rugosity for the plantar ligaments is less pronounced. The cuboid facet forms an oblique notch becoming deeper dorsally and medially, almost touching the sustentaculum.

The apex of the cuboid ascends proximally and medially such that it makes the slightest contact with the distoplantar surface of the astragalus; perhaps only in the loaded portion of the locomotion cycle. The astragalar facet is small and is just ventral to the larger superior navicular facet. In the midst of the medial cuboidal surface lies a prominence of which the proximal part is devoted to the inferior navicular facet and the distal portion to the ectocuneiform facet. The groove for the peroneus tendon is seen on the lateral and distal surfaces of the cuboid. The distal surface for articulation with the Mt IV is roughly teardrop shaped and concave. A small lateral notch for a much reduced Mt V is visible on the cuboid of MNHN-Bol-V-005305, but this region is damaged on UF 172426.

The navicular is moderately wide, but short in the anterioposterior dimension. The astragalar facet is deeply concave on UF 172426, but somewhat shallower on UF 172425. The distal surface of UF 172426 is somewhat eroded but is well preserved on UF 172425 which shows a cloverleaf pattern of three facets; a large central facet for the ectocuneiform flanked on the lateral side by a small cuboid facet and on the medial side by the mesocuneiform facet. Dorsal to the mesocuneiform facet is a small ectocuneiform facet, sloping anteriorly along the dorsal navicular surface. A process from this dorsal surface is broken on both specimens.

MNHN-Bol-V-005305 preserves the right ectocuneiform and the associated proximal Mt II and III. The ectocuneiform is nearly square in dorsal view, with the anteroposterior dimension being slightly greater than the lateral. The proximal surface articulates primarily with the navicular, but has a small cuboid facet sloping over the lateral surface. There are three small circular facets on the medial surface, one centrally placed at the proximomedial surface (the mesocuneiform facet) and the other two distally placed at the dorsal and ventral corners (Mt II facets). The distal ectocuneiform surface is strongly concave in lateral view, but convex when viewed dorsally. It articulates only with the Mt III.

The Mt III of UF 172425 is complete except for the plantar process. It is gracile and 117.7 mm long. MNHN-Bol-005305 is about the same size, but lacks the most distal articulating surface. Unassociated femurs having lengths of 238 and 265 mm permit a first order estimation of the metatarsal/femur ratio (Table 6.3). These have the highest values of taxa of Salla, suggesting that this litoptern was more cursorial than the notoungulates.

Adianthid astragalus. A small astragalus (Fig. 6.7B) found in close proximity to lower molar and premolar fragments that are referable to the adianthid Tricoelodus boliviensis Cifelli and Soria 1983a. The astragalus is certainly that of a litoptern and, given the scarcity of litopterns within the fauna, it is likely that the astragalus and teeth represent a single taxon, likely one individual. The astragalus is therefore tentatively referred to T. boliviensis.

The most conspicuous difference between this and the proceeding astragalus is size. In addition to being smaller than the cf ?Coniopternium primitivium astragalus, it is relatively narrower, giving it a more gracile appearance. The neck is relatively long.

Otherwise this element is fundamentally similar to the macraucheniid astragalus. The trochlear surface of the Tricoelodus astragalus extends further over the dorsal surface, reaching toward the midline of the plantar surface of the body, providing a space in which the tendon of the digital flexor likely occupied. The neck is nearly as long as the body is obliquely oriented. The neck lacks any conspicuous constriction. The navicular facet covers the head and extends halfway up the neck on the ventrolateral surface. There is no evidence of a cuboid facet on the astragalus, however, there is some damage to the lateroplantar region of the astragalar neck that may obscure such a feature. The plantar surface of the navicular facet grades into the sustentacular facet which extends nearly the length of the astragalus. The ectal region is somewhat abraded in the uncataloged MNHN-Bol, but is preserved in UF 172455 (Fig. 6.7C) which demonstrates the deep V-shaped laterally oriented facet typical of most litopterns.

Functional Significance

Theoretical and empirical means may be used to infer function of fossil structures. One may predict function by way of understanding some basic principal (e.g., levers in biomechanical systems) or by comparing the functional unit of extinct taxa with those of modern forms whose function is known. The former method is sometimes called the paradigm method (Rudwick, 1964; Van Valkenburgh, 1994), whereas the latter may be referred to as an analog method. The two approaches may yield different conclusions, as exemplified below.

The the high greater tuberosity seen in the notohippid and mesotheriid above may be interpreted as an indication of strength, not speed, by use of the paradigm method, but the analog method would show it as an indication of speed.

By applying the principals of levers one may note the greater mechanical advantage of the high greater tuberosity of the humerus. The tall tuberosity allows for muscle insertion to be further removed from the axis of rotation of the humerus. This would permit a greater output force which is expressed as torque = (force) x (length from the axis of rotation). Muscle insertions close to the axis of rotation would have less force in the output but would move the lever through a larger arc of rotation, giving it greater velocity.

Applying these principals to the notoungulate humeri described here one may conclude that they were adapted for strength at the expense of speed.

Examination of extant cursorial taxa, however, shows that they tend to have tall greater tuberosities (O'Leary and Rose, 1995). So, by analogy, one might conversely consider a tall greater tuberosity as an indication of cursorial mode of locomotion rather than strength.

Such conflicts should provoke further inquiry. In this case, limited electromyographic observations do not support the assumption that the m. supraspinatus protracts the humerus during ambulation in quadrupeds (Larson and Stern, 1989). O'Leary and Rose (1995) interpret the tall greater tuberosity as functioning to limit humeral abduction and thus restricting humeral movements to the parasagittal plane.

In taxa that are phylogenetically distant from the modern analogs (such as notoungulates and litopterns) our confidence that they function like the extant taxa may be diminished. When possible, both paradigm and analog methods should be employed.

Lomotor function of Salla ungulates.

Paradigm and analog methods provide insights regarding means of locomotion in the taxa described above. The macraucheniid litoptern is unambiguously interpreted as being a cursor, whereas the interpretation of the notoungulates is more complex.

Macraucheniid locomotion. Evidence of a cursorial mode of locomotion in the macraucheniid of Salla includes restriction of movements to the parasagittal plane, a non-supinating antebrachium, and elongated metatarsals.

The parasagittal movements are inferred from the deep trochlear grooves of the humerus and astragalus, the transversely long astragalonavicular articulation, and the precise astragalocancaneal articulation. These joints restricted transverse movements while allowing considerable parasagittal motion.

Unfortunately, no complete antebrachium is preserved but its obligate prone position is inferred from the lack of a capitulum. Also, closely related species are known to have contacting and obligately prone antebrachia.

The macraucheniid of Salla appears to have had a passive stay mechanism for its hind limb. This is quite unlike that of horses, which lock the patella in the superior position by means of an enlarged, notched median ridge of the patellar trochlea (Hermanson and MacFadden, 1996). In this macraucheniid, a deep fossa lies just distal to the short patellar groove. During extension of the lower leg the patella slides proximally in the short patellar groove. Upon hyper-extension, it would have slid into the suprapatellar fossa where the acute distal wall would have prevented it from being easily dislodged (Fig. 6.9). This acute edge could support the patella, thus preventing flexion of the lower limb with little or no muscular activity from the quadriceps. Thus, it likely provided the animal with an energy-saving means of standing for long periods of time.

No patella is known of the Salla macraucheniid, but those of the Santacrucian are narrow ovoids lacking pronounced lateral projections. This would not have been required in a patellar pit stay mechanism since this system did not involve the use of the medial patellar ligament being wrapped around the medial trochlear ridge.

Scott (1910) noted a deep "suprapatellar fossa" on the femora of Diadiaphorus and Thoatherium, both proterotheriid litopterns. He did not mention this feature on the macraucheniid Theosodon. I failed to find where Scott (or anyone else) discuss the significance of this deep patellar pit. He described and figured patellae of proterotheriids which had a V-shaped articulating surface in lateral view, the distal angle being more acute than the proximal.

I constructed a model of a patella (from Magicsculpt®) and attached cloth "ligaments". The shape of the patella was based on the morphology of Santacrucian proterotheriids (which also have the deep patellar pit) and on the contours of the suprapatellar fossa of the Salla specimens. Manipulation of the model illustrates that the patella would have been "locked" during hyperextension, thus it would have maintained the extension of the crux. Tension on the intermediate patellar ligament alone does not dislodge the patella as long as the proximal end is prevented from swinging either too high or too low.

Unlocking could have occurred by a pull from the quadriceps, which would have applied tension to the proximal patella rocked the it on the acute angle of its articular surface. The result of these actions would be to raise the distal end of the patella, permitting it to be pulled over the lip of the distal border of the patellar pit.

Fixing of the crux by the knee-joint passive stay mechanism could have also resulted in passive extension of the ankle joint as well if the extensors and flexors of the extremities of the macraucheniid were tendinous, as in horses (Rooney, 1974; Hermanson and MacFadden, 1996).

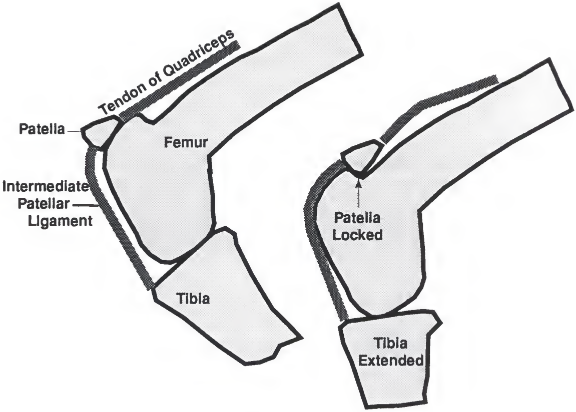

Figure 6.9. Knee joint of cf. ?Coniopternium boliviensis. When the knee is flexed (left), the patella slides along within the patellar groove. When extended (right), the patella may be drawn into the patellar pit where it would become wedged and prevent flexion.

The tarsals have a dynamic arrangement and cannot be fairly characterized as either serial or overlapping. They were both. They apparently functioned in series during passive stance. For example, all the forces traveling from Mt IV through the distal tarsals would have gone up through only the cuboid and not the navicular. When forces on the cuboid were heavy, it slid medially and proximally such that its apex came into contact with the astragalus where some of the energy would have been transferred through the astragalus. This is evident from the cuboid facet on the plantar surface of the astragalus and the corresponding astragalar facet of the cuboid.

To summarize, the macraucheniid of Salla was specialized for speed in open country, rather than for mobility or strength. Though its tarsals were serial in stance, some overlap during times of the heaviest mechanical stress may have served to dissipate the forces somewhat, though not as efficiently as in taxa having fully overlapping tarsals (e.g., equids). The novel passive stay of the knee would have reduced muscle fatigue. This indicates that the animal was capable of standing for long periods of time, possibly approaching the amount of time that horses stand, an excess of 20 hours a day (Hermanson and MacFadden, 1996 and referenced within). Like horses, it likely lived in open habitats, but the low crowned teeth of the Salla macraucheniid indicate that it could not have tolerated much abrasives in its diet. The need for browse and an open habitat locomotory morphology suggest that it preferred a savanna habitat.

Trachythere locomotion. Based on the wide angle of femoral head to acetabulum, low greater trochanter, long distally placed lesser trochanter, and uncoossified tibia-fibula, Sydow (1988) categorized the hindlimb of Trachytherus as being unspecialized. She noted that the pronounced crests of the humerus and enlarged pisiform were similar to forms seen in "scratch diggers" (sensu Hildebrand, 1974) and suggested similar habits for Trachytherus.

More complete tarsals have been found since her work and these do not conflict with Sydow's interpretation of an unspecialized hind limb. Certainly, Trachytherus was not a cursorial ungulate, as its pes lacked modifications for limiting lateral movements. Indeed, the pes appears to have been quite mobile as evidenced by its spherical astragalar head and obliquely oriented astragalar neck. Trachytherus likely could have ambulated on uneven substrate (eg., hillsides, boulders, logs, branches).

Curiously, the remarkably strong forelimb of Trachytherus shows some tendency for reduction of supination of the antebrachium. This is evident in the rectangular radial head and the rotation of the ulna such that it facilitated pronation.

Notohippid locomotion. Previous knowledge of postcranial elements of notohippids was limited to a manus, partial fore and hindlimbs of Rhynchippus equinus (Loomis, 1914) and the pes of R. pumilus (Chaffee, 1952). The elongated, compacted metacarpals and elongated limbs of R. equinus suggested a cursorial mode of locomotion.

A number of skeletal characters of Eurygenium sp. suggest that it was not cursorial and may be better described more appropriately as subcursorial or ambulatory. In most available limb proportions, Eurygenium sp. had ratios nearly identical to Trachytherus. Eurygenium did however have a lower brachial index and a lower Mt/femur ratio suggesting that it was even slower (low-geared) than Trachytherus.

Postcranial characters suggesting generalized ambulatory locomotion include short, splayed metacarpals, mobile antebrachium, well developed humeral crests, pronounced olecranon process, unspecialized femur, and short metatarsals. Some features of the tarsal, however, indicate a trend toward incipient cursoraliaty.

The tarsals of Eurygenium sp. have less lateral mobility than that seen in Trachytherus. The astragalar head of the Eurygenium sp. is distinctly longer in the transverse axis than that of Trachytherus which is subspherical. This astagalonavicular joint of the notohippid would have permitted only parasagittal movements, whereas this joint was unrestrictive in the trachythere. Another cursorial feature was the humeral head. Like many cursors (O'Leary and Rose, 1995), it is off-set from the shaft. This condition is seen in both Eurygenium sp. and Trachytherus.

Eurygenium sp. is judged to have been relatively unspecialized in its locomotor behavior. Its hind foot morphology is suggestive of a trend toward a subcursorial lifestyle while the strong, dexterous forelimb was probably useful for prehension as well as locomotion.

Chapter Summary

Ungulates from three families of two extinct, endemic South American orders were examined and described in terms of their postcranial morphology. The postcrania elements of Eurygenium sp. is found to be about as unspecialized as that of Trachytherus spegazzinianus. Both species showed a mosaic of primitive and advanced characters with Eurygenium sp. having reduced digits, and a tarsus that restricted lateral movements; whereas Trachytherus had a specialized antebrachium.

The litoptern, cf. ?Coniopternium boliviensis, has many morphological features associated with cursorial habits. These include elongated metatarsals, fixed and prone antebrachium, and joints that prohibit lateral movement (e.g., humeral-antebrachial and astragalonavicular joints). Though their tarsals were serial in passive stance, some cuboastragalar contact occurred during intervals of heavy stress.

A distinctive suprapatellar fossa indicates that this macraucheniid stood for long periods with little fatigue. This would represent an ancient passive stay apparatus, predating the analogous passive knee-extension of horses and rhinos by 10 million years (see Hermanson and MacFadden, 1996).

CHAPTER 7
SYSTEMATICS OF ADVANCED TOXODONTIA

Introduction

The new information gained from the study of the Toxodontia of Salla can improve our understanding of the phylogenetic relationships within this group of notoungulates. Indeed, several of the findings of the previous chapter conflict with expectations of the most recent phylogenetic analysis of this group (Cifelli, 1993). For example, Cifelli (1993) suspected that a tridactyl manus would be a synapomorphy for notohippids and toxodontids. Discovery of a primitive tetradactyl manus in Eurygenium sp. (Chapter 3) clearly falsifies this hypothesis and suggests that the true relationships between notohippids and toxodontids are more complex than expected.

Cifelli (1993) performed a cladistic analysis of advanced Toxodontia. His findings suggest that the leontiniids were sister taxa to the notohippids and toxodontids (Fig. 7.1). The notohippids appeared as a paraphyletic group whereas the toxodontids were holophyletic and monophyletic. Eomorphippus appeared as a sister taxon to the rest of the Notohippidae in Cifelli's analysis. Otherwise, the Notohippidae would have appeared as a holophyletic-monophyletic group.

Cifelli (1994) also found a close relationship between Rhynchippus and Morphippus. The synapomorphies uniting these taxa, however, are

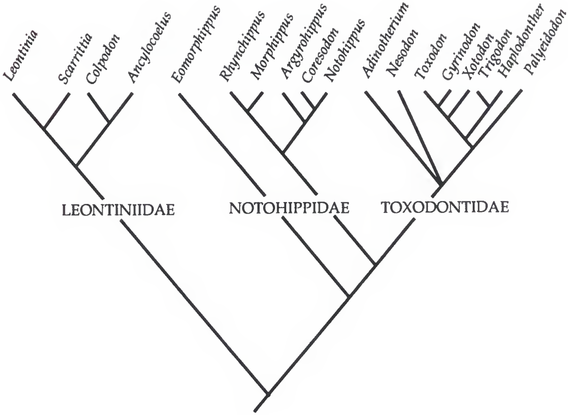

Figure 7.1. Cladogram of advanced Toxodontia. A strict consensus of 25 trees. Adapted from Cifelli, 1993.

tautological since they include characters of the upper teeth of the type of M. imbricatus which was shown in Chapter 3 to be a specimen of R. equinus (see discussion in Chapter 3).

The new findings of Salla are included in a new phylogenetic analysis. Although cladistic techniques are used, conventional family names are retained for the sake of convenience. "Good classification is conservative" (Simpson, 1945: p. 13) and though the results of the following and recent analyses suggest that notohippids are paraphyletic, the present nomenclature should be retained until a consensus regarding the phylogenetic relationships is obtained.

Methods

General Procedures

Cladistic analysis is used as a tool to generate hypotheses regarding the phylogeny of the Toxodontia of Salla and their relationship with other advanced Toxodontia (i.e., notohippids, leontiniids, and toxodontids). Because no lower jaws of the leontiniids of Salla are known, these taxa are excluded from this study, but are presumed to be closely related to Leontinia and Scarrittia (see Chapter 3). Some primitive, isotemnid-like taxa referred to Notohippidae by Bond and Lopez (1993) are included in the phylogenetic analysis.

Character states were determined and scored for morphological features in advanced Toxodontia (Table 7.1). Specimens of all taxa in this analysis were directly examined for character state determination except Argyrohippus praecox. Character states for this taxon were obtained from the original description by Patterson (1935). Other literature consulted for character assessment include: Simpson (1967) for Pleurostylodon modicus, Plexotemnus complicatissimus, Puelia coarctatus, and Eomorphippus obscurus; Bond and Lopez (1963) for Pampahippus arenalesi; Ameghino (1897) for E. latirostris; Ameghino (1897) and Loomis (1914) for Rhynchippus equinus; Simpson (1932) and Patterson (1934a) for R. pumilus; Loomis (1914) for Proadinotherium leptognathum and Patterson (1934a) for P. muensteri; Scott (1914) for Adinotherium ovinum and Nesodon imbricatus; Loomis (1914) and Patterson (1934a) for Leontinia gaudryi; and Chaffee (1952) for Scarrittia canquelensis. Some of the characters and character states used were based upon the work of Cifelli (1993). Dental characters were used almost exclusively, since most of the taxa are known only from teeth. The well known isotemnid Pleurostylodon modicus Ameghino, 1897 provided information regarding dental characters regarded as ancestral (Simpson, 1967; Cifelli, 1993). The data matrix (29 morphological characters; 18 taxa) was analyzed, using the Branch-and-Bound algorithm of PAUP (Swofford, 1989). The taxa consisted of 12 species of notohippids, two genera of leontiniids, and three genera of toxodontids plus the outgroup. The polarity established for the 29 character states assumes that the isotemnid condition (Pleurostylodon) represents the plesiomorphic condition.

Table 7.1. Taxon-character matix of Toxodontia.

Pleurostylodon modicus	00000	0?000	00000	00000	0?000	0000
Pampahippus arenalesi	00000	0?100	00010	00000	0?000	0000
Plexotemnus complicatissimus	?????	?????	00010	00000	0?001	1??1
Puelia coarctatus	?????	?????	00010	00000	0?001	1???
Eomorphippus obscurus	00001	11100	10010	00111	0?000	0110
new notohippid genus of Salla	00000	11101	20010	01011	1?000	0121
Rhynchippus equinus	00000	01101	20010	01111	12000	0110
Rhynchippus pumilus	00000	01101	20010	01111	1?000	0110
Rhynchippus brasiliensis	00000	01101	20010	01111	1?000	0110
Eurygenium pacegnum	00000	01101	20010	11111	01000	0111
Eurygenium latirostris	00000	0?101	21010	11111	0?000	0111
Argyrohippus praecox	00000	01111	20111	11111	1?010	0??0
Argyrohippus fraterculus	00000	01121	30111	11111	1?010	0110
Nesodon imbricatus	11010	1?1?1	20000	01111	12100	0110
Proadinotherium leptognathum	11010	1?1?1	20000	01111	1?100	011?
Adinotherium ovinum	11010	1?1?1	20000	01111	12100	0110
Leontinia gaudryi	00100	00100	00010	0?011	1?000	0001
Scarrittia canquelensis	00100	00100	00010	0?011	11000	0000

Character Diagnosis

Convention. The 29 character states are defined below. The number given is that used in the taxon-character matrix. Some character states are also represented by a bracketed number which represents character states derived from Cifelli, 1993. The number within the bracket represents the character number in the matrix of Cifelli, 1993.

Characters. 1, [19]. Caniniform or incisiform I1s are regarded as plesiomorphic (0); whereas the chisel-like form, as seen in Nesodon, is considered derived (1).

2, [23]. Rooted anterior dentition is typical and plesiomorphic (0); whereas ever-growing, unrooted anterior teeth, as seen in toxodontids, are regarded as derived (1).

3. Incisiform I1-2, as in Pleurostylodon (Simpson, 1967) or notohippids (e.g., Chapter 3) (0); I1 or I2 rounded in cross section and enlarged is the derived condition (1). Such a caniniform incisor occurs in the I1 of Leontinia (Loomis, 1914) and the I2 of Scarrittia (Chaffee, 1952).

4, [20]. Toxodontids have the derived condition of I2 being triangular in cross section (1) (Scott, 1912; Cifelli, 1993). The plesiomorphic condition of this character is an incisiform or caniniform I2 (0).

5. Eomorphippus obscurus has procumbent upper incisors which are regarded as being derived (1). Upper incisors oriented dorsoventrally are regarded as the plesiomorphic state (0).

6. Transversely oriented premaxillary dental arcades (e.g., the new notohippid genus [Chapter 3], toxodontids [Scott, 1912], and E. obscurus

[Simpson, 1967]) are considered to be derived (1). U-shaped to V-shaped forms are scored as plesiomorphic (0). It is unclear if the form of E. obscurus and that of toxodontids and the new notohippid are homologous. In E. obscurus, all three incisors form the leading edge, whereas in the new notohippid and toxodontids the third incisor lies posterior to the second.

7 [6]. Several notohippids are known to have horse-like fossettes ("infundibula") of the upper incisors (Ameghino, 1897), derived from the internal cingulum (1). The absence of this fossette is scored as plesiomorphic (0). Its condition is unknown in several taxa.

8. Only the out-group isotemnids have caniniform canines (0). The canine is reduced and incisiform in the rest of the taxa examined (1).

9. Closed tooth row, without a diastema is scored as plesiomorphic (0). (The small gap surrounding the isotemnid incisor is not regarded as being a diastema.) Of the taxa examined, only Argyrohippus has a true diastema. The diastema of A. praecox only occurs between upper canine and incisors (1); whereas a diastema separates the upper canine from the incisors and premolars of A. fraterculus (2) (Patterson, 1935).

10. Conspicuously curved upper molars are regarded as derived (1); whereas molars less curved are considered primitive (0).

11. Cheekteeth crown heights are scored as a transition series from low-crowned to very high crowned. These are defined and scored as follows: brachydont [HI of M1 < 1] (0); cheekteeth mesodont [HI M1 ≈ 1] (1); cheekteeth hypsodont [1 < HI M1 < 2] (2); cheek teeth euhypsodont [HI M1>2](3).

12. The conspicuously broad palate of Eurygenium latirostris is scored as derived (1); whereas the typical narrower morphotype is plesiomorphic (0).

13. Absence of thick layer of cement on cheek teeth is regarded as plesiomorphic (0). Trace amounts are also scored as plesiomorphic, whereas a thick, conspicuous coating of cement on cheekteeth is scored as derived (1).

14. Absent or deeply notched protoloph on unworn upper premolars was regarded by Simpson (1967) as a derived diagnostic character for notohippids (1). This character is also observed in unworn leontiniid premolars (Patterson, 1934a). The outgroup has a complete protoloph (0) as do toxodontids.

15. Patterson (1935) noted a second posterior, cup-shaped cingulum on upper premolars of species of Argyrohippus. This character appears to be a synapomorphy for Argyrohippus and is scored as being derived. A single upper premolar posterior cingulum is scored as plesiomorphic (0).

16. Upper premolars of the out-group Pleurostylodon have an anterolingual cingulum (0). This character is lost in a few later taxa (e.g., Eurygenium, Argyrohippus spp.). The absence of an upper premolar anterolingual cingulum is considered derived (1).

17. M2 of the out-group has an anterolingual cingulum (0). The loss of anterolingual cingula of molars is regarded as derived (1).

18. As with the M2 above, loss of the anterolingual cingulum of the M1 is derived (1) and its retention is considered derived (1).

19. Isotemnids have an accessory trigonid cusp on lower molars (0). The absence of this cusp is presumed to be derived (1). None of the taxa in the sample had this cusp except the out-group, Pleurostylodon.

20. Short talonids, that is those that extend but a short distance past the entolophid, are regarded as primitive (0); whereas talonids extending well past the entolophid are considered derived (1).

21. Many notohippids, toxodontids, and all known leontiniids have an early formed fossettid in the entolophid (1). Unworn specimens of Rhynchippus pumilus (MACN A 52-68; FMNH P14673), and Leontinia gaudryi (FMNH P13285) demonstrate that this fossettid is formed within the entolophid and is not a result of closure of the hypolophid with the entolophid (contra Chaffee, 1952). Presence of the fossettid is scored as derived (1) and its absence is scored as primitive (0), though it is lost in younger taxa of toxodontids (e.g., Toxodon) and its absence in probably Eurygenium represent a reversal rather than the primitive state.

22. The transformation series of the manus is presumed to have gone from pentadactyl (0), tetradactyl (1), to tridactyl (2). The manus of Pleurostylodon is unknown. The only known isotemnid manus is that of Thomashuxleya externa, which is pentadactyl (Simpson, 1967).

23 [26]. In the out-group, leontiniids, and notohippids, the crochet of the upper molars originates near the mid-point of the metaloph (0). The crochet of early toxodontids, however, originates lingually, at anterior edge of hypocone (1).

24 [15]. The coronal pattern of most of the taxa, including Pleurostylodon, is superficial and is obscured with little wear (0). The coronal pattern of some taxa (e.g., toxodontids, Argyrohippus) is deep and persists in well worn teeth (1).

25. Most taxa, including the out-group, have no more than two well-developed cristae originating from the ectoloph of the upper molars (0). Supernumerary cristae are present (1) in taxa formerly regarded by Simpson (1967) as belonging to "Acoelohyrax" (see Chapter 3).

26. Simpson regarded the posterolingually projecting posterior cingulum of upper premolars or molars as diagnostic for "Acoelohyrax" (1). Taxa lacking this character were scored as having the plesiomorphic trait (0).

27. Pleurostylodon has a relatively narrow I1 (0). Taxa having a relatively broad I1 (I1 > I3) were scored as being derived (1).

28. As above, narrow I2 narrow was scored as plesiomorphic (0); I2 broad, having greater width than I3 (but less than I1) was considered derived (1); whereas the most derived condition is when I2 is the broadest incisor (I2 > I1>I3) (2).

29. The premolars of Eurygenium are conspicuously small compared to their molars. This premolar abbreviation is considered derived and is defined as when the anteroposterior length of P4 is less than one-third the length of M1 [P4/M1<1/3] (1). The primitive state is scored when the anteroposterior length of P4 is subequal to M1 [P4/M1>1/3] (0).

Results and Discussion

A strict consensus of 74 trees is shown in Figure 7.2. Each of these shortest trees had a length of 41 and a consistency index of 0.805.

The results of this phylogenetic analysis using parsimony (PAUP) suggests that Family Notohippidae, as conceptualized by Ameghino (1897) and Simpson (1967), is paraphyletic (see Fig. 7.1). Toxodontids are nested within taxa traditionally regarded as being notohippids. This finding is similar to the results of Cifelli (1993); however, in his analysis, Deseadan and younger notohippids formed a monophyletic and holophyletic clade. The presence of the tetradactyl manus of Eurygenium sp. of Salla, however, does not lend support to Cifelli's results since the notohippid Rhynchippus equinus and toxodontids share the derived character of tetradactyl manus; whereas, Eurygenium sp. has the plesiomorphic tetradactyl manus. Rhynchippus equinus and early toxodontids also have more distally placed third trochanters, whereas it is more proximal on Eurygenium sp. The toxodontid-like muzzle of the new notohippid genus of Salla provides further evidence of the paraphyletic state of Deseadan and younger notohippids. It suggests that the new notohippid genus and the Toxodontidae had a common ancestor not shared with other notohippids.

Loss of molar entolophid fossettids and shortening of the anteroposterior dimensions of the upper premolars with loss of anterolingual cingula are regarded as synapomorphies for Eurygenium sp. of Salla and E. latirostris (see revised generic diagnosis in Chapter 3). Reduction or loss of lower internal incisive cingula occurs in Eurygenium sp. of Salla and M. imbricatus, which, along with the loss of entolophid fossettids, suggests that M. imbricatus belongs within the Eurygenium clade. The anterior lower dentition of E. latirostris is unknown.

No shared derived characters were found uniting the three species of Rhynchippus. Synapomorphies uniting the two species of Argyrohippus include thick cement covering teeth, diastema, accessory cup-shaped posterior cingulum of upper premolars (Patterson, 1935), and a deep coronal pattern preserving crown pattern into advanced wear (Cifelli, 1993). Not evident in this analysis is the possibility that Argyrohippus gave rise to the poorly known Santacrucian Notohippus, which also had cement. These two genera form the subfamily Notohippinae (Simpson, 1945), which is likely monopheletic. The remaining notohippids would not comprise a single, monophyletic subfamily.

The family Leontiniidae is also nested among the Notohippidae when isotemnid-like taxa (i.e., Pampahippus, Plexotemnus, and Puelia) are included in Notohippidae (sensu Bond and Lopez, 1993). The isotemnid-like taxa appear to be sister taxa to leontiniids and traditional notohippids (sensu Simpson, 1967) (see Fig. 7.2).

Though the cladogram of Figure 7.2 represents the strict consensus of the most parsimonious trees, alternative hypotheses should also be considered. The assumption that the simplest explanation is the best explanation may not be true in every case. In this case, a number of taxa are united at node 4 (Fig. 7.2) by their hypsodonty, loss of molar cingula, and curved molars. These characters occur in hypsodont notoungulates and could have been achieved independently in the Toxodontia taxa examined such as occurred in the Typotheria (see Cifelli, 1993). A more trustworthy analysis will need to await corroborative evidence from more postcranial elements and/or auditory regions. These regions are currently poorly represented in most Toxodontia taxa.

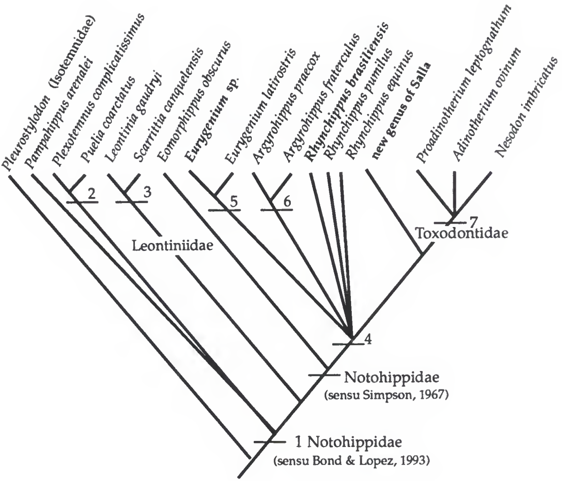

Figure 7.2. Strict consensus of 74 trees of advanced Toxodontia (tree length = 41, consistency index = 0.805). Synapomorphies for the labeled nodes are: 1) reduction of canine, incomplete premolar protoloph; 2) supernumerary upper molar cristae, upper premolar-molar projection of posterior cingulum; 3) caniniform incisor; 4) hypsodont and strongly curved molars; 5) reduced anteroposterior dimension of premolars, loss of entolophid fossettids of molars; 6) thick cement covering of teeth, diastema, accessory cup-shaped posterior cingulum of upper premolars; 7) hypselodont anterior incisors, crochet of upper cheek teeth oringinating on lingual side of tooth, anterior to the "hypocone".

Chapter Summary

The Toxodontia of Salla challenge current concepts regarding the phylogeny of the advanced Toxodontia (leontiniids, notohippids, and toxodontids). One notohippid of Salla (the new genus and species) appears to share a muzzle morphology with toxodontids whereas another (Eurygenium sp.) lacks the derived tridactyl manus shared with the notohippid Rhynchippus equinus and toxodontids. These findings suggest that some notohippids and toxodontids had a common ancestor not shared with other notohippids. This implies that the familial designations as currently recognized are over-simplified. Revisions of nomenclature should await fuller evidence from phylogenetic analyses that incorporate auditory regions and postcranial skeletons of these taxa since their dentition is so prone to homoplasy.

The inclusion of primitive isotemnid-like taxa in the Notohippidae is instructive in regard the possible ancestry of the family, but this analysis shows it has the undesired effect of making the family "doubly" paraphyletic. That is, the inclusion of these taxa in Notohippidae appears to make the family paraphyletic to both the leontiniids and toxodontids (see Fig. 7.2). Simpson (1967) had opted for retaining these taxa in the isotemnids, but noted that "the difference between the two interpretations is rather formal and not very important" (Simpson, 1967: p. 179).

Probably it is more important to note the diversity of both the morphology and phylogeny of the advanced Toxodontia. In the Deseadan, these included robust browsers (leontiniids) and animals that appeared to be able to consume abrasive grasses. The surprise at Salla is that the most common notohippid, Eurygenium sp., lacked the cursorial adaptations seen in Rhynchippus equinus, the most common notohippid of Patagonia. This suggests both phylogenetic and ecological differences between these taxa, indicating a greater diversity of the Notohippidae than previously appreciated.

CHAPTER 8
FAUNA OF SALLA

The last faunal list of Salla was published by MacFadden et al. (1985). Since that time, additional collecting and study of specimens from Salla prompt a revision of this list (Table 8.1).

The herpetofauna remains unstudied. A number of anuran specimens have been collected, including a partial skeleton, but these have yet to be described. Reptiles are uncommon, there being but a few fragmentary remains referable to Squamata.

The avifauna is currently under study by Robert Chandler of Georgia College and State University. The avifauna presented in Table 8.1 is based on his work in progress. These include three orders of birds that likely occupied a variety of ecological niches, including carnivory (a falcon and phorusrachid) and a probable gramnivore (rheid).

The metathere fauna is quite diverse, despite their lack of abundance in terms of individual specimens. The marsupials represented a group that was well studied and the alpha taxonomy appears to have been stable by the time the last faunal list was published. The metathere fauna includes several presumably carnivorous taxa (borhyaenids) and a possible saltatory rodent-like herbivore Proargyrolagus bolivianus (Wolff, 1984). Sanchez and Kay (1995) recently described some of the cranial anatomy of Proargyolagus and noted that it was more primitive than Plio-Pleistocene argyrolagids.

Table 8.1. Revised Faunal List of Salla.

- Class Aves
    - Order Rheiformes
        - Family Rheidae

    - Order Ralliformes
        - Family Cariamidae
            - cf. *Cariama* sp.
        - Family Phorusrhacidae

    - Order Falconiformes
        - Family Falconidae

- Class Mammalia
    - Order Metatheria
        - Family Borhyaenidae
            - *Paraborhyaena* *boliviana* Petter and Hoffstetter, 1983
            - *Pharsophorus* *lacerans* Ameghino, 1897
            - *Notogale* *mitis* (Ameghino, 1897)
            - *Sallacyon* *hoffstetteri* Villarroel and Marshall, 1982
            - borhyaenine, gen. et sp. indet.
        - Family Caenolestidae
            - *Palaeothentes* *boliviensis* Patterson and Marshall, 1978
        - Family Polydolopidae or Caenolestidae
            - ?*Polydolops* sp. or ?Paleaeothentine, gen. et sp. indet.
        - Family Argyrolagidae
            - *Proargyrolagus* *bolivianus* Wolff, 1984

    - Order Xenarthra
        - Family Dasypodidae
            - Euphractini "sp. A"
            - Euphractini "sp. B"
        - Family Peltephilidae
            - cf. *Peltephilus* sp.
        - Family Glyptodontidae
            - Glyptalenae
        - Family Paleopeltidae
        - Family Orophodontidae

Table 8.1. (continued)

- Order Primate
  - Family Incertae Sedis
    - *Branisella boliviana* Hoffstetter, 1969
    - *Szalatavus attricuspis* Rosenberger et al., 1991

- Order Rodentia
  - Family Echimyidae
    - *Sallamys pascuali* Hoffsetter and Lavocat, 1970
  - Family Dasyproctidae
    - *Incamys bolivianus* Hoffstetter and Lavocat, 1970
    - *Cephalomys bolivianus* Lavocat, 1976
    - *Neoreomys* sp.
  - Family Dinomyidae
    - *Branisamys luribayensis* Hoffstetter and Lavocat, 1970
  - Family Octodontidae
    - *Migraveramus beatus* Patterson and Wood, 1982

- Order Condylarthra or Litopterna
  - Family ?Didolodontidae or Protolitopternidae
    - *Salladolodus deuterotheroides* Soria and Hoffstetter, 1983

- Order Litopterna
  - Family Macraucheniidae
    - ?*Coniopternium primitivum* Cifelli and Soria, 1983
  - Family Adianthidae
    - *Thadanius hoffstetteri* Cifelli and Soria, 1983
    - *Tricoelodus boliviensis* Cifelli and Soria, 1983

- Order Notoungulata
  - Suborder Typotheria
    - Family Interatheriidae
      - Interatheriinae sp. nov. A Hitz, in prep.
      - Interatheriinae sp. nov. B Hitz, in prep.
    - Family Archaeohyracidae
      - *Archaeohyrax* sp. nov. Reguelo and Cifelli, in prep.
      - *Eohegetotherium* sp. nov. Reguelo and Cifelli, in prep.
    - Family Mesotheriidae
      - *Trachytherus spegazzinianus* Ameghino, 1889
    - Family Hegetotheriidae
      - *Prohegetotherium* sp. nov. Reguelo and Madden, in prep.
      - Unnamed gen. nov. Reguelo and Madden, in prep.

Table 8.1. (continued)

Suborder Toxodontia
Family Leontiniidae
Leontinia sp. nov. (small) Shockey, in prep.
Leontinia sp. nov. (medium) Shockey, in prep.
Family Notohippidae
Eurygenium sp. nov. Shockey, in press
Rhynchippus cf. R. brasiliensis Soria and
gen. nov. Shockey, in press
Family Toxodontidae
Proadinotherium sp.

Order Astrapotheria
astrapotheriid, indet.

Order Pyrotheria
Pyrotheriidae
Pyrotherium sp. nov.

Order and Family Incertae Sedis
cf. Acamana Simpson et al. 1962 sp.

With the exception of dasypodids, xenarthrans are uncommon and have yet to be studied in detail. Freddie Carlini, of the Museo la Plata, has examined the xenarthran collection at UF and provided the revisions presented in the revised faunal list. In particular, these include the subfamilial placement of dasypodids species, which remain undescribed.

The primates of Salla are currently being studied by Richard Kay of Duke University and M. Takai of Koyoto University. Though primate specimens are uncommon at Salla, these have been studied quite intensely. To date, these are only known to have come from the Branisella Level, the portion of Unit 5 just above the El Planimiento, though the exact stratigraphic level from which the holotype of Branisella came is unknown. Two genera have been described.

Rodents have also been well-studied (Hoffstetter and Lavocat, 1970; Lavocat, 1976; Patterson and Wood, 1982). The rodent fauna given in Table 8.1 is unchanged form MacFadden et al. (1985).

The litopterns of Salla were described by Cifelli and Soria (1983a and 1983b). The taxa listed here is unmodified from MacFadden et al., (1985) except that the misprinted spellings have been corrected.

Until recently, the notoungulates have not been closely examined. Numerous additions and changes to the faunal list are given below.

Sydow (1988) described the postcranials of two individuals of Trachytherus, one large and one small, and regarded these as male and female. She recognized but one species at Salla, T. spegazzinianus, attributing the variation in morphology to sexual dimorphism and the significant change in tooth appearance with wear. Trachytherus spegazzinianus is conspecific with the Patagonian trachythere (Patterson [1934b] had regarded all named species of the Deseadan to be synonyms of T. spegazzinianus). This, incidentally, represents the only ungulate of Salla known that is conspecific with a any from the classic Deseadan localities of Patagonia.

Ralph Hitz of the University of California, Santa Barbara, has completed studies of the interatheriids of Salla. He recognizes two new species which will likely be placed in two new genera.

Marcelo Reguelo of the Museo de la Plata and Richard Cifelli, University of Oklahoma, have studied the remaining typotheres. Reguelo recognizes two genera each of archaeohyracids and hegetotheriids, with but one species in each genus. He considers all four of these species to be endemic to Salla, that is, none are referable to known species from the Deseadan of Patagonia.

The Toxodontia have been described in this work (see Chapter 3). The two species of leontiniids and two of the three species of notohippids are new. Eurygenium sp., though a new species, is the same species that had been referred to cf. Rhynchippus sp. from the Petaca Formation in Southern Bolivia (Senjinés and Jiménez, 1976). The only notohippid possibly referable to a named species is Rhynchippus cf. brasiliensis, a taxon otherwise known only from the type locality near São Paulo, Brasil (Soria and Alvarenga, 1989). The toxodontid is only referable to Proadinotherium sp.

Of the Astrapotheria, nothing can be added to the poor state of knowledge of the Salla taxon. There is but a tusk fragment in the UF collection and an incisor in the MNHN-Bol collection that are referable to this order.

Choosing the Persian deity of confusion as the namesake for Acamana (Simpson et al., 1962) still seems appropriate, as there is virtually nothing to add to the knowledge of the fragments referred to cf. Acamana.

Pyrotherium had served as the most important diagnostic Deseadan taxon, indeed it was the namesake, for Ameghino's "couches a Pyrotherium". Therefore, the presence of this genus at Salla served to support the Deseadan age given to this Bolivian locality. The closeness of Salla to Patagonian Deseadan localities is implied by the assessment that the Salla pyrothere is conspecific with that of Patagonia (MacFadden and Frailey, 1984). All Deseadan species of Pyrotherium were regarded by Patterson (1977) to be synonyms of P. romeroi (the correct spelling is "romeroi" [Ameghino, 1889], a patronym for Capt. Antonio Romero; not "romeri", contra Loomis [1914], Patterson [1977] and MacFadden and Frailey [1984]).

MacFadden and Frailey (1984) qualitatively noted the smaller size of the Salla pyrothere from those of Patagonia, but did not consider this to be of taxonomic significance. This size difference between the Patagonian and Bolivian specimens was likely understated. For example, the mean of length of p3-m3 of four Salla specimens is 188 mm, whereas, AMNH 11725 from Patagonia has a p3-m3 length of 293 mm. There is no overlap of any of the dental measurements (Fig. 8.1, Table 8.2). The Patagonian pyrotheres have linear dimensions 1.5 times greater than those of Salla. The coefficients of variation (CV) of the teeth (P4-M2 and p4-m2) of 4 Patagonian specimens ranged from 1.8 - 13.7 and those of the p4-m2 of four Salla specimens were 1.8-12.0 (Table 8.2); a range that one may find in extant species. However, when these measures of Patagonian and Salla specimens were combined, the

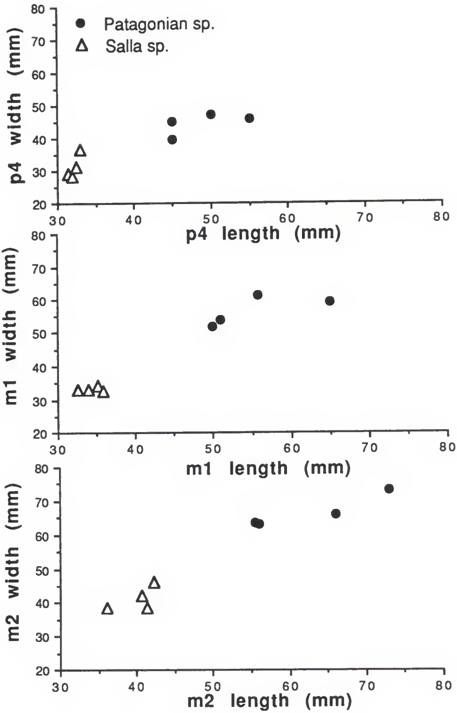

Figure 8.1. Lengths and widths of cheek teeth of pyrotheres from Patagonia (filled circles) and Salla (open triangles).

Table 8.2. Morphometrics of Pyrotherium from Patagonia and Salla.

Specimen	**Locality**	**P4** (a-p)	**P4** (tvw)	**M1** (a-p)	**M1** (tvw)	**M2** (a-p)	**M2** (tvw)
AM 3207	Cabeza Blanca	47	63	55	68	68	85
AM 3250	Cabeza Blanca	51	64	55	69	77	93
Ameghino, 1897	Patagonia	46	58	57	61	70	75
Gaudry DATE	"Deseado"	43	57	55	61	57	68
PU 20693	Salla	33	36.7	35.2	38.4	42.3	46
mean of all		44.0	55.7	51.4	59.5	62.9	73.4
s of all		6.78	11.07	9.12	12.37	13.52	18.04
CV all		15.41	19.86	17.73	20.80	21.55	24.57
mean Patagonia		46.7	60.5	55.5	64.7	68.0	80.2
s Patagonia		3.30	3.51	1.0	4.35	8.29	11.0
CV Patagonia		7.07	5.80	1.80	6.71	12.19	13.70

Specimen	**Locality**	**p4** (a-p)	**p4** (tvw)	**m1** (a-p)	**m1** (tvw)	**m2** (a-p)	**m2** (tvw)	**p3-m3**
AM 3207	Cabeza Blanca	55	46	65	59	73	73	---
Ameghino, 1897	Patagonia	45	45	50	52	56	63	---
Gaudry, 1906	"Deseado"	50	47	51	54	66	66	---
AM(NH) 11725	Patagonia	45	39.4	55.8	61.4	55.6	63.5	293
PU 20684	Salla	32.5	31.4	34.0	33.0	40.6	42.0	195.3
PU 20692	Salla	32.0	28.2	35.8	32.8	41.3	38.6	189.6
PU 20694	Salla	31.4	29.3	32.6	33.2	36.1	38.7	172.8
PU 20693	Salla	33.0	36.7	35.2	34.2	42.3	46.0	192.8
mean (all)		40.5	37.9	44.9	44.9	51.4	53.8	208.7
s (all)		9.38	7.68	12.15	12.78	13.38	13.91	47.9
CV (all)		23.18	20.28	27.04	28.47	26.06	25.84	22.97
mean(Patagonia)		48.75	44.35	55.45	56.6	62.65	66.37	293
s (Patagonia)		4.79	3.40	6.85	4.35	8.41	4.61	---
CV (Patagonia)		9.82	7.66	12.36	7.68	13.43	6.95	---
mean (Salla)		32.2	31.4	34.4	33.3	40.1	41.3	187.6
s (Salla)		0.68	3.77	1.41	0.62	2.74	3.49	10.15
CV (Salla)		2.12	12.02	4.11	1.87	6.84	8.45	5.41
Ratio (Patonian /Salla)		1.51	1.41	1.61	1.70	1.56	1.61	1.56

range of CV increased to 15.4 - 28.4, demonstrating a greater variation in morphology than expected to occur in a living natural population (Simpson et al., 1960; Gingerich, 1974). Given this vast difference in body size, the Pyrotherium of Salla is considered to be a species distinct from P. romeroi.

At least 20 taxa of ungulates (Condylarthra, Litopterna, Notoungulata, Astrapotheria, Pyrotheria, and Incertae Sedis) are known from Salla. Of these 17 are known well enough to be discerned at the species level. Fourteen (82%) are endemic to Salla. An additional two species are known from other low latitude localities, but not from Patagonia. Thus, 16 of 17 (94%) of the ungulate species of Salla are unknown in Patagonia. A significant majority (70%), however, can be referred to known genera from the classical Deseadan localities of Patagonia. Six of the 20 (30%) are distinct at the generic level.

The ungulate fauna of Salla may be described as generically similar to, but specifically distinct from, Deseadan faunas of Patagonia. The high degree of endemism suggests either temporal and/or ecological differences between the Deseadan of Salla versus the Deseadan of Patagonia. The generic similarities suggest that these differences, whether temporal and/or geographic, are not great.

Since the lower faunal strata of Salla overlap temporally with the younger faunas of Patagonia (see Chapter 1 and Flynn and Swisher, 1995) it is possible to make a general determination as to whether the faunal differences between Salla and the Patagonian localities are temporal or geographic. Units 1 and 2 have an estimated age range of 28.0 to 27.8 Ma., yet the taxa from these horizons are largely unknown in Patagonia. Of the Toxodontia, all that have been collected from these lower regions of Salla are unknown in

Patagonia. Eurygenium sp. is known from Unit 1 and the type locality for the new notohippid genus and the larger new leontiniid is within Unit 2.

The Toxodontia of Salla suggest that the faunal differences between Salla and Patagonia represent geographic rather than temporal effects. Other taxa should be studied in terms of their stratigraphic positions at Salla to determine any changes over time.

CHAPTER 9
SUMMARY

Summary of Past UF Work at Salla

The Salla Beds of Bolivia preserve a rich and diverse sample of fossil mammals that lived during the "Splendid Isolation" of South America. The Deseadan is of considerable interest because it represents a period of time when the endemic ungulate fauna became dominated by hypsodont taxa (Pascual and Ortiz Juareguizar, 1990), developed advanced locomotor adaptations (Chapter 6), and obtained one of its peak diversities (Cifelli, 1985). Also, the rodents had their initial radiation during this time and the oldest primates known from South America are Deseadan.

Salla is an important Deseadan locality because it is relatively large and fossiliferous and because it is at a considerably lower latitude than the classical Deseadan localities of Patagonia.

Teams from the University of Florida have investigated Salla since the late 1970s and have acquired one of the largest collections of Deseadan fossils housed in North America. An important fruit of this labor was the demonstration that the Deseadan SALMA occurred in the late, not early, Oligocene (MacFadden et al., 1985). Other contributions of UF studies of Salla include the discovery and description of the oldest argyrolagid (Wolff, 1984), additional primate specimens (Wolff, 1984; Rosenburger et al., 1991), and the skeleton of Trachytherus (Sydow, 1988).

Summary of Present Findings

The present study examined some of the ungulates of Salla and provided the alpha taxonomy of Toxodontia, descriptions of deciduous dentitions of a notohippid and mesotheriid, an ecomorphological study of the feeding ecology of the Toxodontia, and a comparative study of locomotion in three of the endemic ungulates.

The results of the alpha taxonomy indicate that most of the Toxodontia of Salla represent new species (Chapter 3). Two leontiniid species are new and likely represent a new genus. Two notohippids are new, one at the generic level, and a third is tentatively referred to Rhynchippus brasiliensis, which is otherwise known only from the Tremembé Formation in Brasil. The toxodontid of Salla is tentatively referred to Proadinotherium sp. and appears to be smaller than P. leptognathum. The guide fossil Pyrotherium is judged to be a distinctly smaller species than that of Patagonia (Chapter 7).

The study of juvenile specimens (Chapter 4) aids in determining tooth homologies of deciduous teeth of notoungulates. The deciduous teeth of Eurygenium sp. provide evidence for a more parsimonious interpretation of cusp homologies than that offered by Patterson (1934a). The unworn deciduous teeth of the typothere Trachytherus recorded its evolutionary history by showing the "face" topology of primitive typotheres. It also showed the origin of the median loph, a feature characteristic of mesotheriids.

A multivariate analysis of the feeding structures of extant ungulates clearly delineated browsing ungulates from those that consumed mostly grasses (Chapter 5). Eigenvalues were determined for the Eurygenium sp. and this extinct animal was compared with taxa of known diets. Specifically, this analysis suggested that Eurygenium sp. was a mixed feeder that consumed large quantities of grasses. More generally, it demonstrates a method of applying multivariate techniques to determine the diets of extinct animals.

The notohippid Eurygenium sp. is represented by a virtually complete, articulated skeleton and represents the only known reasonably complete notohippid skeleton. Eurygenium sp. appears to have been less cursorial and less derived than Rhynchippus spp. (see Chapters 3 and 6). The postcranial elements of Eurygenium sp. was compared to the mesotheriid notoungulate, Trachytherus, and a litoptern, cf. ?Coniopternium (Chapter 6). The litoptern demonstrated numerous cursorial adaptations. These include elongated metapodials, a dynamic tarsus which overlapped during periods of stress, and a novel knee-locking mechanism that would have facilitated standing for long periods of time. This knee locking mechanism predates that of horses and rhinos by over ten million years.

The phylogenetic analysis using parsimony (PAUP) of the advanced Toxodontia supports the notion that the Notohippidae are a paraphyletic group (Chapter 6). The inclusion of primitive, isotemnid-like taxa (e.g., Pampahippus, Puelia) in the Notohippidae complicates matters further since these taxa also appear as sister taxa to the Leontiniidae. The Deseadan notohippids are poorly resolved in this analysis. Greater resolution of the phylogenetic relationships of these taxa may be accomplished with increased knowledge of notohippid postcranial elements and/or auditory regions.

The ungulate fauna of Salla is generically similar to, but specifically different from, Deseadan faunas of Patagonia (Chapter 7). Also, large animals are uncommon at Salla, but relatively common in Patagonia. These differences are regarded here as being more likely a geographic/ecological effect rather than a temporal one. The Toxodontia from the lower (i.e. older) horizons of Salla are distinct from Patagonian taxa of similar ages. The notohippids of Salla have no conspecifics in Patagonia but two are known from other low latitude Deseadan localities (Eurygenium sp. is known from Petaca Formation in southern Bolivia and Rhynchippus brasiliensis is found in Brasil).

An incidental, but perhaps instructive, finding was a pathologic Trachytherus femur. The femur had a displaced fracture in life which overlapped and healed such that the length of the femur was reduced by perhaps 10 - 20%. The survival of this animal sufficiently long after the fracture so that it healed suggests a forgiving environment at Salla. Though the animal no doubt suffered locomotor impairment, it continued to forage and was not eaten, at least long enough for the bone to mend. One might speculate that food was plentiful and predators were few for such a crippled animal to survive. Indeed, taxa considered to be carnivorous (borhyaenids and phorusrhacids) are quite uncommon.

In short, this contribution describes five new species of ungulates, offers a parsimonious explanation of tooth homologies of juvenile notoungulates, reveals the origin of the mesotheriid median loph, offers a new method of determining the hypothetical diet of extinct animals, describes the only known notohippid skeleton, and presents the most ancient example of a knee-lock mechanism, one distinct from that of horses and rhinos.

Appendix A. Uncataloged specimens of MNHN-Bol with temporary identification numbers.

ID Nº	Taxon	Locality/Unit	Material	Collector/Date
F-93-10	Small Leontiniid species A	Tapial Pampa Unit 5, below El Planimiento	Palate with upper teeth minus right I1-2 & left P4	Ruben Andrade 2 Oct. 1993
F-94-01	Trachytherus spegazzinianus	Poco Poconi, Northwest Unit 5 Branisella	left astragalus	Marcelo Sanchez 8 June 1994
F-94-02	Trachytherus spegazzinianus	Calaboza Pata Unit 4 Prinicpal Guide	right astragalus	Marcelo Sanchez 24 May 1994
F-94-10	Trachytherus spegazzinianus	Poco Poconi, Northwest Unit 5 Branisella	left tarsals, proximal Mt III & IV, & distal tibia and fibula	Richard Kay 8 June 1994
F-94-11	Trachytherus spegazzinianus	Irupata Loma Unit 6 "Upper White"	left tarsals, proximal Mt III & IV, & left tibia	Blythe Williams 9 June 1994
F-94-12	Trachytherus spegazzinianus	Willa Kkollu	left femur (fractured and healed)	Richard Kay & Alex Van Nievelt 3 June 1994
94-30	cf. ?Coniopternium sp.	Quebrada Kollpajahuira (NE of Poco Poconi) Unit 3	right femur, left distal femur, right astragalus, left cuboid, two vertebrae	Bruce J. Shockey 13 June 1994
94-31	Tricoelodus boliviensis	Toloma	left astragalus	Nick Czplewski 13 June 1994

Appendix B. Morphometrics of structures associated with feeding in perissodactyls.

Taxon/ID Nº	**MW/PW**	**i3/i1**	**hi**
Equus grevyi UF 14239	57.9/68.6 = 0.84	12.2/12.7 = 0.96	---
Equus asinus UF 156889	51.4/61.2 = 0.84	14.5/11.6 = 1.25	---
Tapirus terrestris UF 8127	45.7/62.5 = 0.73	6.5/9.5 = 0.68	14.0/24.8=0.56
Tapirus bairdii UF 24112	48.1/70.8 = 0.68	6.2/10.0 = 0.62	--heavy wear--

Appendix C. Masses of ungulates and their source denoted below. Rounded mean masses of each sex were used for sexually dimorphic species.

GRAZERS

Equus burchelli[1]	250	Equus grevyi[B]	360
Ceratotherium simum[1]	2950	Damaliscus lunatus[D]	140
Connochaetes taurinus[1]	212	Alcelaphus buslaphus[D]	175
Hippotragulus equinnus[D]	270	Hippotragulus niger[D]	230
Bison bison[1]	668		

BROWSERS

Rhinoceros sodaicus[2]	2000	Diceros bicornis[1]	1490
Dicerorhinus sumatrensis	800	Tapiris terreststris[1]	263
Madoqua kirki[1]	5.1	Neotragus moschatus[C]	9
Tragelaphus imberbis[1]	77.5	Tragelaphus scriptus[1]	52.3
Mazama mazama	18	Pudu pudu	9
Odocoelius virginianus[1]	50	Odocoelius hemionus	74
Rangifer tarandus[1]	95	Alces alces[1]	447
Ammodorcas clarkei	30	Litocranius walleri[D]	43.5
Giraffa camelopardalis[1]	1115	Okapia johnstoni[2]	225
Cephalophus silvicutor[C]	60	Cepalophus monticola[C]	7
Silvicapra grimmia[C]	19		

MIXED FEEDERS

Rhinocerus unicornis[2]	3000	Aepyceros melampus[D]	55
Tetraceras quadricornis[2]	19	Syncerus caffer[C]	270
Ovis canadensis[1]	61.4	Oryx gazella[D]	170
Gazella thomsoni[D]	20	Gazella granti[D]	80
Ourebia ourebi[C]	17	Oreotragus oreotragus[C]	15
Reduncia arundinum[C]	58	Reduncia fulvorufula[C]	30
Raphicerus campestris[C]	10.5	Kobis kob[C]	86
Taurotragus oryx[1]	570	Antilocapra americana[1]	38

[1] Janis and Moreno, 1992
[2] Walker (Nowak and Paradiso [eds.]), 1983
[B] Kingdon, 1979
[C] Kingdon, 1982a
[D] Kingdon, 1982b

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BIOGRAPHICAL SKETCH

Bruce J. Shockey initially trained and worked as a mental health counselor, having received a Bachelor or Arts in psychology from the University of Florida and a Master of Arts, Education in guidance and counseling from Western Carolina University. He worked as a clinical social worker before returning to academia to study zoology and paleontology.

During his graduate studies, Shockey served as laboratory instructor for Core Biology, Animal Physiology, and Functional Vertebrate Morphology. He also worked as a research assistant to his major advisor, Bruce J. MacFadden. Shockey received a Master of Science Teaching degree in 1993.

For his postdoctoral studies, Shockey plans to continue work in Bolivia. He has received a National Science Foundation International Research Fellowship to support this work.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Bruce J MacFadden

Bruce J. MacFadden, Chair
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

S. David Webb

S. David Webb
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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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Ronald Wolff

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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