FIELDIANA

Geology

NEW SERIES, NO. 42

New Interatheriines (Interatheriidae, Notoungulata) from the Paleogene of Central Chile and Southern Argentina

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New Interatheriines (Interatheriidae, Notoungulata) from the Paleogene of Central Chile and Southern Argentina

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PUBLISHED BY FIELD MUSEUM OF NATURAL HISTORY

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New Interatheriines (Interatheriidae, Notoungulata) from the Paleogene of Central Chile and Southern Argentina

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Abstract

Two new interatheriines (Interatheriidae, Notoungulata), *Santiagorothia chiliensis* and *Proargyrohyrax curanderensis*, are described from the transitional Eocene/Oligocene Tinguiririca Fauna, central Chile, and from roughly coeval localities in Chubut and Rio Negro provinces, Argentina. The former occurs in both central Chile and Argentina, whereas the latter occurs only in Argentina. Several Argentine specimens are referred to *Eopachyruchos*, an interatheriine for which an emended diagnosis is presented. The taxonomic status of *Argyrohyrax acuticostatus* is discussed and an emended description is provided. Additionally, we propose a phylogenetic taxonomic definition for the name Interatheriinae.

The transitional Eocene/Oligocene localities under consideration here occur within a poorly known interval of the South American Land Mammal Age (SALMA) sequence, intermediate between the Mustersan and Deseadan SALMAs. This temporal interval spans a transition in South American mammal evolution between older faunas dominated by various archaic, dentally conservative herbivores and younger faunas dominated by later diverging clades of more hypsodont forms. The Tinguiririca Fauna, the age of which is bracketed radioisotopically, records the first or last occurrence of seven subfamilial or higher level taxa. Although the Argentine localities are unconstrained geochronologically, similar faunal composition allows tentative correlation to the Tinguiririca Fauna. Not unexpectedly, therefore, *Santiagorothia chiliensis* and *Proargyrohyrax curanderensis* represent the earliest known interatheriines, a group previously restricted to Deseadan SALMA (Late Oligocene/Early Miocene) and younger faunas.

Santiagorothia chiliensis and *Proargyrohyrax curanderensis* are considered interatheriines based on their possession of the following diagnostic features of the clade thus named: deep parastyle/paracone groove on P2–4; very shallow parastyle/paracone groove on upper molars; smooth posterior ectoloph on upper molars; very high-crowned cheek teeth; distinctly bilobed p3–m3 with persistent labial and lingual sulci; auditory bulla lapping posteriorly onto the paraoccipital process; and maxilla excluded from the superior orbital border by a silver of anteriorly projecting frontal (although *Proargyrohyrax curanderensis* is known only from dental remains). *Santiagorothia chiliensis* and *Proargyrohyrax curanderensis* are most readily distinguished from other interatheriines in possessing cheek teeth with closed roots. Another distinction concerns the pattern of upper molar wear in *Santiagorothia chiliensis* and *Proargyrohyrax curanderensis*: as wear proceeds, a lingual sulcus closes to form an isolated fossette, whereas in other interatheriines this sulcus remains open.

Introduction

Herein we describe two new interatheriines, *Santiagorothia chiliensis* and *Proargyrohyrax curanderensis* (Interatheriidae, Notoungulata), from tran-sitional Eocene/Oligocene localities in central Chile and from Chubut and Rio Negro provinces of Argentina (Table 1). Also presented is an emended diagnosis of *Eopachyruchos* (formerly considered a hegetothere; Simpson, 1967), to which specimens

TABLE 1. Localities and references.

Locality	Reference
Portezuelo El Fierro, Tinguiririca River Valley, Chile (34°59'S; 70°26'W: town of Termas del Flaco)	Wyss et al., 1994
Lomas Blancas, Chubut, Argentina (44°11'S; 69°38'W)	This paper
Cañadón Blanco, Chubut, Argentina* (unknown coordinates)	Roth, 1901, 1903; Ameghino, 1906; Reguero, 1993
Laguana La Bombilla, Chubut, Argentina (44°16'S; 69°12'W)	Pascual, 1965b
Gran Barranca, Chubut, Argentina (45°42'S; 68°44'W)	Cifelli, 1985b
Rocas Bayas, Rio Negro, Argentina (69°02'S; 41°01'W)	Pascual et al., 1984

* The exact geographic position of this locality is unknown. Only Roth collected at Cañadón Blanco, and he left no information about the geographic provenance of the fossils from this locality. Ameghino (1906) showed the probable location of Cañadón Blanco. A map of this region, drawn by Mr. Fulgencio Domínguez in 1924 and copied by G. G. Simpson, exists in the Simpson Library at the Florida Museum of Natural History but is too imprecise to locate Cañadón Blanco.

from transitional Eocene/Oligocene localities in Chubut and Rio Negro provinces of Argentina are referred. The new interatheriine *Santiagorothia chiliensis* provides an important biostratigraphic tie between volcaniclastic deposits from the western slope of the Andean Main Range and classic mammal-bearing deposits of Patagonia.

Although the South American Cenozoic mammal record has been extensively studied for more than a century, some temporal intervals remain poorly known, most notably an approximately 15 million year hiatus between the Mustersan and Deseadan South American Land Mammal Ages (SALMAs) (Flynn & Swisher, 1995). The Tinguiririca Fauna (the first record of fossil mammals from the Andean Main Range of central Chile) occurs within this hiatus and provides valuable radioisotopic calibration points for this portion of the SALMA sequence (Flynn et al., 1991; Novacek et al., 1989; Wyss et al., 1990, 1992, 1993, 1994). The Tinguiririca Fauna thus represents a new, currently unnamed South American mammalian biochronologic unit (Wyss et al., 1994; Flynn & Swisher, 1995), which also helps constrain the age of a major Eocene–Oligocene faunal turnover event and the immigration of rodents to South America. Descriptions of taxa (like the interatheres in this paper) from the Tinguiririca Fauna and correlative units elsewhere will enable formal

erection and definition of a Tinguirirican SALMA in the future.

Several pre-Deseadan/post-Mustersan-age faunules are known from Chubut and Rio Negro provinces of Argentina (Table 1); together with the Chilean fauna these are critical to establishing the outlines of mammal evolution during the aforementioned hiatus. Although independent geochronologic information for the Argentine faunules is currently lacking, they show close taxonomic similarity to the Tinguiririca Fauna and are tentatively correlated to it on that basis (Wyss et al., 1994); see the systematic paleontology section for a more complete discussion.

Interatheres (Interatheriidae, Notoungulata), small to medium-sized herbivorous notoungulates, are well represented in most South American Cenozoic mammal faunas. The group first appeared in the ?Itaboraian SALMA (?Middle Paleocene) (Bond et al., 1995) and persisted into the Huayquerian SALMA (Late Miocene). A significant radiation of hypsodont forms occurred during the Oligocene (Cifelli, 1985a; Marshall & Cifelli, 1990). Interatheres are traditionally divided into two groups (Simpson, 1945), Notopithecinae (low-crowned Paleogene forms) and Interatheriinae (Late Oligocene and younger, hypsodont and hypselodont forms). Interatheriinae constitutes a monophyletic group (Cifelli, 1993; Hitz, 1994, 1995, 1997; Reguero et al., 1996), whereas taxa generally referred to the Notopithecinae probably form a paraphyletic assemblage (Hitz, 1994, 1995, 1997).

Santiagorothia chiliensis and *Proargyrohyrax curanderensis* represent the earliest known interatheriines (as that name is defined below), a group previously known from Deseadan and younger SALMAs (Cifelli, 1985a). This is consistent with the numerous other first and last occurrences of higher level taxa in the Tinguiririca Fauna, a fact reflecting its biostratigraphic distinctiveness (Wyss et al., 1994).

Below we present a systematic description of both new taxa and an emended diagnosis for *Eopachyruchos*. We also present an emended description of the taxon *Agyrohyrax acuticostatus*, which is represented by a single specimen that resembles both *Santiagrothia* and *Proargyrohyrax*. The material for *A. acuticostatus*, however, is insufficient to determine whether it is synonymous with either taxon. A reference collection of casts of all the Chilean material will be accessioned into the Field Museum collections. Material considered in this study is housed in the Los

Angeles County Museum of Natural History; the Florida Museum of Natural History; the Yale Peabody Museum; Servicio Geológico de Bolivia; Museo Nacional de Historia Natural, Bolivia; the Field Museum of Natural History; the American Museum of Natural History; the University of California Museum of Paleontology; Museo Nacional de Historia Natural, Santiago; Museo Argentino de Ciencias Naturales, Buenos Aires; and the Museo de La Plata.

Abbreviations

The following abbreviations are used in the text.

SGOPV   Museo Nacional de Historia Natural, Santiago

MACN   Museo Argentino de Ciencias Naturales, Buenos Aires

AMNH   American Museum of Natural History, New York

MLP   Museo de La Plata, La Plata

Systematic Paleontology

Notoungulata Roth, 1903
  Typotheria Zittel, 1893
    Interatheriidae Ameghino, 1887
      Interatheriinae Simpson, 1945

As a preamble, it bears mention that none of the taxonomic names listed above have previously been defined phylogenetically (*sensu* de Queiroz & Gauthier, 1990, 1992). Among its objectives, phylogenetic taxonomy (as this approach is termed) emphasizes the distinction between the naming of clades (definition) and the recognition of those clades in the first place (diagnosis). Here we consider only the name Interatheriinae. One of the many plausible ways to translate this name (as traditionally used, Simpson, 1945) into phylogenetic taxonomic terms would be to define Interatheriinae as the name referring to the clade stemming from the most recent ancestor of *Interatherium* and *Protypotherium*, plus all of its descendants. Such a definition describes a clade including all previously described interatheriines. Hitz (1997) demonstrated that *Santiagorothia chiliensis* is the nearest outgroup to this clade (Fig. 1). For reasons elaborated below and in Hitz

(1997), we chose a slightly more inclusive definition of Interatheriinae, namely as the clade stemming from the most recent ancestor of *Santiagorothia chiliensis* and *Interatherium*, plus all of its descendants (a node-based definition *sensu* de Queiroz & Gauthier, 1990, 1992).

Compared to earlier diverging interatheres, interatheriines are typified by larger size and hypodont or hypselodont cheek teeth [although developed convergently in numerous other notoungulate clades as well (Cifelli, 1985a)]. Indeed, these are the characters typically associated with interatheriines by most workers (e.g., Cifelli, 1985a). The Tinguiririca Fauna is the earliest in South America, and globally, to be dominated by hypsodont herbivores (including, most notably, interatheres and archaeohyracids) (Wyss et al., 1994). It is fitting, then, that the earliest known large hypsodont interathere is a member of the clade here linked to the name Interatheriinae.

Members of this clade may be diagnosed by the following synapomorphies: deep parastyle/paracone groove on P2–4; very shallow parastyle/paracone groove on M1–3; smooth posterior ectoloph on M1–3; very high-crowned cheek teeth; distinctly bilobed p3–m3 with persistent labial and lingual sulci; auditory bulla lapped posteriorly onto the paraoccipital process; maxilla excluded from the superior orbital border by an anteriorly projecting sliver of frontal.

Finally, in our descriptions of the new interatheriines, Linnean taxonomic ranks are not recognized (*sensu* de Queiroz & Gauthier, 1990, 1992). Accordingly, the names of the new taxa should not be considered strict Linnean binomials, comprised of a genus name and a species name. Rather, they are simply two-part names referring to a single taxon. If readers strongly object to this approach, the names may be considered equivalent to Linnean binomials, but that is not the intent of the authors.

Argyrohyrax acuticostatus Ameghino 1901

1901   *Argyrohyrax acuticostatus*, Ameghino, p. 15.

TYPE—MACN A52-626, right dP3–4, M1–2.
TYPE LOCALITY—"Golfo de San Jorge," Chubut, Argentina.
KNOWN DISTRIBUTION—Known only from the type locality, "Golfo de San Jorge."
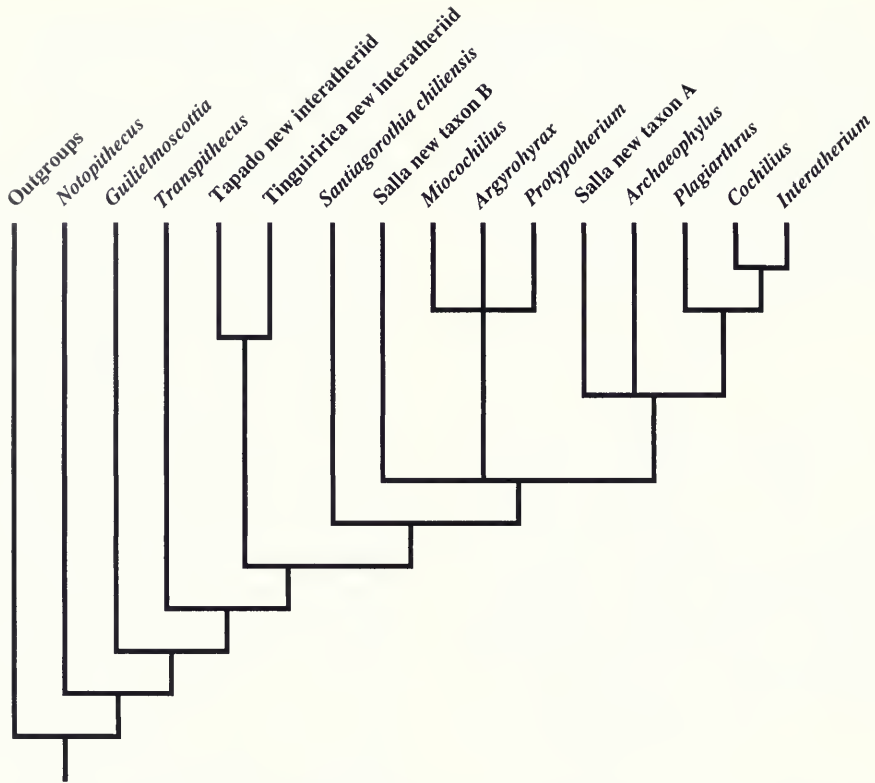REMARKS—Ameghino (1901) briefly described

Fig. 1. Interathere phylogeny after Hitz (1997). For a character matrix, tree statistics, and identification of synapomorphies for the various interathere clades recognized herein, refer to Hitz (1997). Several nomenclatural issues need highlighting. *Plagiarthrus* (as used here) is probably synonymous with *Argyrohyrax proavus* (for a discussion see Marshall et al., 1986), and *Argyrohyrax* (as used here) is probably synonymous with *Progaleopithecus tournoueri* (also see Marshall et al., 1986). Finally, several taxa are not yet formally described (but see Hitz, 1997, for informal descriptions), namely two interatheriines from the Upper Oligocene Salla beds of Bolivia and two non-interatheriine interatheriids from the Paleogene of central Chile.

(but did not figure) a single maxillary fragment (MACN A52-626), designating it the holotype of *Argyrohyrax acuticostatus*. A vague, handwritten provenance accompanies the specimen; it reads, "Golfo de San Jorge, Chubut." His description of the specimen is accurate, save for its reference to three molars (MACN A52-626 presently has only two molars, so M3 has evidently since been lost) and its failure to mention dP3–4. No other material in the MACN is catalogued as pertaining to *Argyrohyrax acuticostatus*.

The M1 and M2 of MACN A52-626 very closely resemble those of both *Santiagorothia chiliensis* and *Proargyrohyrax curanderensis* (treated below). In fact, upper molar morphology alone is insufficient to distinguish the latter two taxa, which are unmistakably distinct in other respects. This is a common problem for interatheriines; both upper and lower molar morphology tend to

be similar across many taxa, and sound identification often requires the preservation of additional anatomy. MACN A52-626 may indeed pertain to one of the interatheriine taxa described below, but its fragmentary condition prevents conclusive comparisons. Additionally, as mentioned above, the provenance of MACN A52-626 is exceedingly sketchy, making it highly unlikely that more complete material will be found to augment the type specimen.

Given the limited comparisons afforded by MACN A52-626, we believe the best course of action is to recognize two new taxa, both of which are known from significantly more complete material than MACN A52-626, rather than refer new additional specimens to *Agyrohyrax acuticostatus*. Although this approach introduces two new names to interatheriine nomenclature, the excellent material on which they are based will well
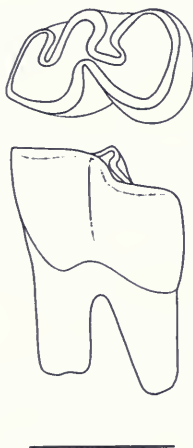
FIG. 2. **A.** MACN A52-626, *Argyrohyrax acuticostatus,* type (and only) specimen, RdP3–4, RM1–2. **B.** MACN A10908e, *Eohyrax platyodus,* occlusal and lateral views. Scale = 0.5 cm for all views.

Argyrohyrax proavus. Upper molars more compressed, trilobed lingually, and with the perpendicular anterior margin of the ectoloph turned outside forming a very salient perpendicular ridge. The three upper molars are 21 mm in length. Pyrotherium Beds."

Ameghino did not mention the deciduous premolars, a description of which follows.

Deciduous Upper Dentition (Fig. 2)—The deciduous P3–4 are quadrangular and broad, low-crowned, closed rooted, and molariform. The large parastyle is obliquely oriented and short. A deep parastyle/paracone groove is present on dP3, as is a shallower one on dP4. Paracone and metacone folds are well developed on both teeth, creating a sinuous ectoloph. Two labial fossettes are present (the posterior one being smaller), as is a small, bifid lingual sulcus. The hypocone is higher than the paracone and metacone and is separated from the short, straight metaloph by a deep lingual groove (mensural data are in Table 2).

Santiagorothia chiliensis, new taxon

HOLOTYPE—SGOPV 2914: cranium and mandibles, dentition complete except for L12–3, RI1–2, and Ri1–3, displaying moderate wear.

PARATYPES—SGOPV 2827: complete upper dentition and palate, anterior dentition poorly preserved, dP3–4 present. SGOPV 2861: RM1 (broken)–M3, lightly worn. SGOPV 2812: cranium with upper dentition, RI3–M3, LP1–2, LP4–M3, basicranium preserved. SGOPV 2821: complete skull and mandibles, atlas and axis, prepared upper dentition includes RI3–M3, prepared lower den-

serve future comparisons (e.g., the type for *Santiagorothia chiliensis* is a complete cranium).

We emphasize that, although *Agyrohyrax acuticostatus* may indeed be the senior synonym for one of the new taxa we describe below, the holotype (and only known specimen) is insufficient for such a determination. We strongly suggest that, in the future, recognition of new interatheriine taxa (and other notoungulate taxa as well) be limited to circumstances where relatively complete dentitions are known, thereby preventing the problem discussed above. A discussion regarding material needed for erecting new taxa is presented by Pascual (1965a).

EMENDED DESCRIPTION—Ameghino (1901, p. 15) briefly described the three upper permanent molars of *Argyrohyrax acuticostatus* as follows (translated from French): "A little smaller than

tition includes Ri3 (broken)–m3. Dentitions are little worn. SGOPV 2821 includes an unprepared postcranial skeleton.

REFERRED MATERIAL—SGOPV 2816: cranium and mandible, only the left side of which is prepared, posterior cranium missing. SGOPV 2826: mandibles, left side only prepared, Ri1–c, Li1–m3, highly worn. SGOPV 2862: right mandible, distorted, Rp3–m3, with light wear. SGOPV 2968: right mandible, Rp2–m3, moderate wear. The following specimens remain unprepared but are sufficiently observable that they can be referred to this taxon. SGOPV 2819: three maxillary teeth. SGOPV 2841: skull and partial skeleton. SGOPV 2845: mandible preserving two teeth. SGOPV 2846: partial skull and mandible. SGOPV 3016: partial palate. SGOPV 3034: lower jaw fragment. SGOPV 3040: maxilla with two teeth. SGOPV 3042: skull and partial skeleton. SGOPV 3048: maxilla with ?P4–M1. SGOPV 3079: rostrum. SGOPV 3098g: mandibular fragment. SGOPV 3125: mandibles preserving several crowns. SGOPV 3139: mandible with anterior dentition.

A number of specimens from post-Mustersan/pre-Deseadan SALMA localities in Argentina are also referred to this taxon. MLP 91-IX-5-15, left maxilla with P1 (root), P2–3 (broken), P4–M3, and anterior portion of the left zygoma. MLP 61-VIII-3-314, left M1. MLP 83-I-12-1, maxillary fragment with broken left P2–M2. MLP 91-IX-5-14a, mandibular fragment with left p4 (roots), m1–2. MLP 91-IX-5-14b, mandibular fragment with left m1–2. MLP 93-XI-25-8, left M1 or M2 (broken). The following specimens are also tentatively referred to this taxon: MACN A10908a, left m3 (paralectotype of ?*Eohyrax platyodus*); MACN A10908b and c, two isolated p3.

ETYMOLOGY—*Santiagorothia* after Santiago Roth, in honor of his contributions to South American mammalian paleontology, and *chiliensis* for Chile, where the majority of the specimens were recovered.

DIAGNOSIS—Synapomorphies outlined earlier that are diagnostic of the Interatheriinae serve to identify *Santiagorothia chiliensis* as a member of this clade.

Santiagorothia chiliensis is most easily distinguished from other interatheriines (except *Proargyrohyrax curanderensis*) in possessing cheek teeth with closed roots, whereas the cheek teeth are hypselodont in other interatheriines. During wear, the upper cheek teeth of *Santiagorothia chiliensis*, which are initially longer than wide, become equidimensional, and the lingual sulcus on

the upper molars closes. In other interatheriines (except *Proargyrohyrax curanderensis*), the upper molars retain a more rectangular (longer than wide) form throughout their ontogeny, and the lingual sulcus remains open throughout wear. The labial fossettes of the upper molars are more persistent in *Santiagorothia chiliensis* than in other interatheriines (again, save *Proargyrohyrax curanderensis*).

Compared to *Proargyrohyrax curanderensis*, *Santiagorothia chiliensis* has upper and lower premolars that are significantly smaller than the molars (less molarized), a significantly narrower (anteroposteriorly) anterior zygomatic root, and is slightly smaller (best seen in the lower dentition).

TYPE LOCALITY—Portezuelo El Fierro, Abanico (= Coya Machalí) Formation, Tinguiririca River Valley, central Chile (see Wyss et al., 1994).

KNOWN DISTRIBUTION—Known from the type locality (all SGOPV specimens) [radioisotopic determinations bracket its age between approximately 37.5 and 31.5 Ma (Wyss et al., 1994)] and several localities in Patagonia, Argentina. These post-Mustersan/pre-Deseadan SALMA (but isotopically undated) faunules from Chubut and Rio Negro provinces are probably roughly temporally equivalent to the Tinguiririca Fauna and include "Astraponotéen plus supérieure" level at Gran Barranca (south of the Lake Colhué Huapí) (Bond et al., 1996), Puesto Almendra, Departamento Sarmiento, Chubut province (MACN A10908a,b,c); Lomas Blancas, La Curandera, Chubut province (MLP 93-XI-25-8); Rocas Bayas, Departamento 25 de Mayo, Rió Negro province (MLP 91-IX-5-15, MLP 83-I-12-1, MLP 91-IX-5-14a, MLP 91-IX-5-14b); and Laguna La Bombilla, Departamento Paso de Indios, Chubut province (MLP 61-VIII-3-314).

REMARKS—**Systematic**—Wyss et al. (1994) reported the presence of a second smaller interatheriine, "Tinguiririca interatheriine new taxon B," represented by a single specimen, SGOPV 3065. More detailed examination of this specimen reveals it to probably represent an archaeohyracid, possibly referable to "*Bryanpattersonia sulcidens*," a taxon currently being revised by one of us (M.R.).

There is considerable variation within the sample from the Tinguiririca Fauna, most of it having no taxonomic significance. Three mandibles, SGOPV 2862, SGOPV 3032, and SGOPV 2868, seem to have been compressed during deposition or subsequent tectonic activity. All three are compressed transversely, lending the teeth a narrow

and somewhat distorted morphology. A second source of variation is the high degree of hypsodonty in this taxon, with both the shape and dimensions of the teeth changing significantly with wear. A few specimens display minor differences (noted in the description) not attributable to wear or geologic deformation. However, because of the small size of our sample, which limits a thorough assessment of variation, it seems appropriate to provisionally refer them to a·single taxon.

Stratigraphic—In his original studies of fossil mammals from the Gran Barranca, Florentino Ameghino (1901, 1902) recognized two stratigraphic intervals within his "Couches à *Astraponotus*" (now termed the Mustersan SALMA), the upper of which he called "Partie supérieure des couches à *Astraponotus*." In works published after 1906, however, he ceased recognizing the two intervals as distinct. Recent evidence suggests that the "Partie supérieure des couches à *Astraponotus*" level is indeed distinct, corresponding to a level recognized by Simpson in his field notes from the Scarritt Patagonian expeditions (Profile M, p. 40; this information is also presented in Cifelli, 1985b: section V, sites 16 and 17, fig. 5, p. 11).

In 1996 one of the authors (M.R. and colleagues) collected fossil mammals from the "upper channel level" in Simpson's Profile M (sites 16 and 17 of Cifelli, 1985b) at the Gran Barranca. This work confirms the existence of a stratigraphic level containing the same taxa as described by F. Ameghino in 1901 (*Pseudopachyrucos fóliformis*) and 1902 (*Interhippus deflexus*), with the provenance of "Partie supérieure des couches à *Astraponotus*" (or "Astraponotéen plus supérieure," as termed by Bond et al., 1996). Other taxa from this level [listed in Cifelli (1985b) as recovered from sites 16 and 17] are *Eomorphippus obscurus*, ?*E. pascuali*, *Anisotemnus distentus*, and *Pleurostylodon* sp. indet. Most of these taxa are regarded as Mustersan in age except for *Pleurostylodon* and *Anisotemnus*, which are Casamayoran. Of special note is that *Eomorphippus obscurus* is found only in the latest Mustersan deposits and is not known from typical Mustersan deposits that have been well sampled (Wyss et al., 1994; Bond, pers. comm.). In addition, *E. obscurus* is known from Cañadón Blanco and the Tinguiririca Fauna. Both faunas are regarded as post-Mustersan/pre-Deseadan in age (Wyss et al., 1994). The Tinguiririca Fauna also contains a specimen of *Eomorphippus. cf. pascuali*, likely further extending its biostratigraphic range (Wyss et al., 1994).

Recent work by Goin and Candela (1997) reveals a diverse marsupial fauna from the "Astraponotéen plus supérieure" level. Goin and Candela report that these specimens appear morphologically intermediate Mustersan and Deseadan taxa. Moreover, they identify an argyrolagid that strikingly resembles ?argyrolagid specimens from the Tinguiririca Fauna.

Finally, the "Astraponotéen plus supérieure" level has produced several interathere specimens (MACN A10908a,b,c) that are tentatively referred to *Santiagorothia chiliensis*, the most common taxon in the Tinguiririca Fauna.

In sum, the "Astraponotéen plus supérieure" level and its associated fauna (including both the recent collections and Ameghino's original specimens) suggests the presence of a post-Mustersan/pre-Deseadan SALMA temporal interval in Argentina which, based on faunal similarity, is likely correlative with the Tinguiririca Fauna (Bond et al., 1996). Like the Tinguiririca Fauna, the "Astraponotéen plus supérieure" level displays an odd mix of "archaic" taxa and clearly younger forms. We suggest here that the several other Argentine localities listed in the *Known Distribution* section above may correlate to the "Astraponotéen plus supérieure" level at the Gran Barranca (and thus also to the Tinguiririca Fauna) as well. Such a temporal correlation is least secure for the Rocas Bayas locality, which is faunally distinctive. Our suggested correlations are summarized in Figure 3.

DESCRIPTION—**Material**—*Santiagorothia chiliensis* (Figs. 4–11) is known from superb dental and cranial material. Several nearly complete skulls are known, as are several complete palates and mandibles (mensural data are in Tables 3–5. Postcranial material is also known from Chile, but it remains unprepared due to the tenacity of the volcaniclastic matrix.

Upper Dentition—The anterior upper dentition shows minor variation between specimens. I1 is the largest incisor in all specimens examined. Although I2 is not preserved, in SGOPV 2914 the alveoli of I2 and I3 are subequal, indicating that the teeth were probably similar in size. The upper canine in SGOPV 2914 is considerably larger than I2–I3 (as inferred from alveoli), whereas in SGOPV 2812 and SGOPV 2821, it is only slightly larger. I1, I3 (and I2 presumably as well), and C are laterally compressed. I3 displays a distinct anteroexternal vertical ridge in SGOPV 2812 and SGOPV 2821, whereas in SGOPV 2914 it does not. A similar ridge occurs on the upper canine. I1 and I3 lack enamel
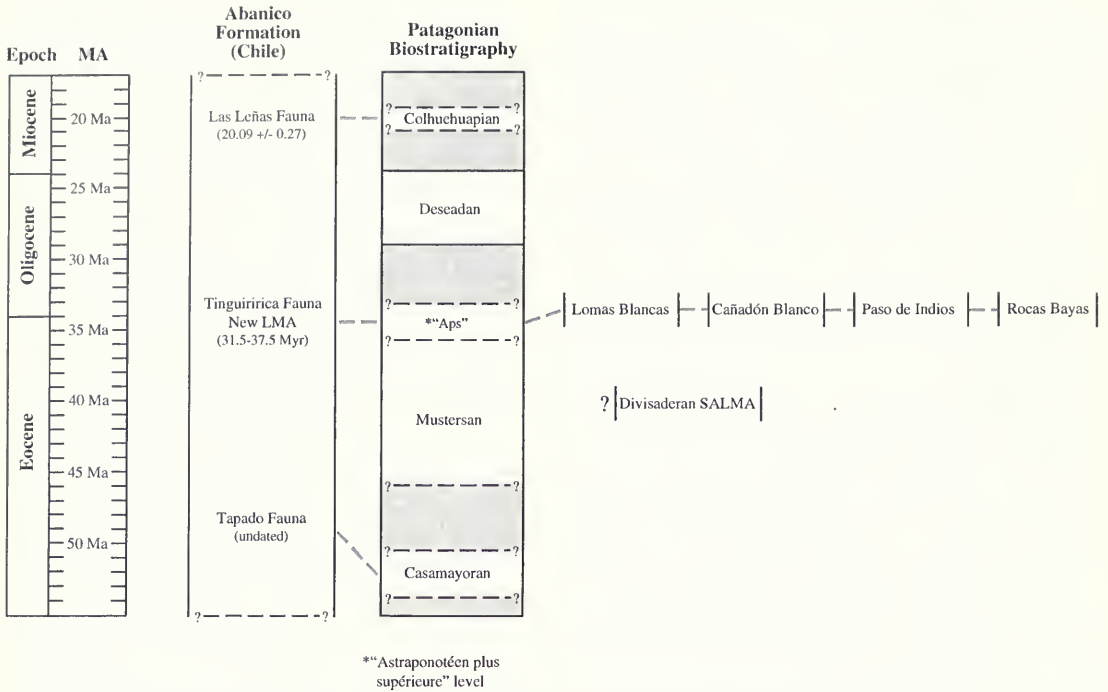
*"Astraponotéen plus
supérieure" level

FIG. 3. Tentative correlation of the Abanico (= Coya Machalí) Formation in central Chile (and the faunas preserved in it) and middle Cenozoic Patagonian mammalian biostratigraphy [after Flynn & Swisher (1995)]. The Abanico Formation is 1,000–2,000 m thick and appears to lack unconformities through its ?Paleogene–?early Neogene span, although as yet, mammal remains are known only from three localities (Flynn et al., 1995; Wyss et al., 1994). Dashed boundaries with accompanying questions indicate lack of radioisotopic and paleomagnetic information, and gray regions represent hiatuses. The Las Leñas Fauna (Flynn et al., 1995), located about 60 km NNE of the Tinguiririca Fauna (Wyss et al., 1994), has an associated Ar^{40}/Ar^{39} determination of 20.09 ± 0.27 Ma, arguing for its approximate tie to the Colhuehuapian SALMA [which is bracketed by the Santacruzian SALMA (above) and the Deseadan SALMA (below), both of which are dated (Flynn & Swisher, 1995)]. As discussed in the text, we tentatively correlate the Tinguiririca Fauna (and an as yet unnamed land mammal age based on it) to the "Astraponotéen plus supérieure" level recognized by Ameghino (1901) and Bond et al. (1996). Traditionally this level was considered uppermost (latest) Mustersan, including by Ameghino himself (1906), but Bond et al. (1996) argued that it is faunally distinct and warrants recognition as a new temporal interval. We tentatively correlate several post-Mustersan/pre-Deseadan Patagonian localities to the "Astraponotéen plus supérieure" level as well (see Table 1 for references to these localities). Correlation of the radioisotopically dated Tinguiririca Fauna with the "Astraponotéen plus supérieure" level potentially moves at least part of the Mustersan SALMA (that directly underlying the "Astraponotéen plus supérieure" level) into the Late Eocene, further complicating temporal placement of the problematic Divisaderan SALMA. The Divisaderan has been considered earliest Deseadan or latest pre-Deseadan (MacFadden et al., 1985; Marshall et al., 1986) based on several taxa common to the two SALMAs. Bond (1991), however, argues the Divisaderan to be considerably older than the Deseadan, and Wyss et al. (1994) argue that it predates the Tinguiririca faunal interval. If a post-Mustersan pre-Tinguiririca Fauna age for the Divisaderan is accepted and the "Astraponotéen plus supérieure" level (which superposes Patagonian Mustersan deposits) is considered temporally equivalent to the Tinguiririca Fauna (as suggested here), then there is no room in which to place the Divisaderan within the Patagonian SALMA sequence (hence, its ambiguous placement). The oldest biostratigraphic interval in the Andean sequence identified to date is the Tapado Fauna, located about 12 km NW of the Tinguiririca Fauna; an approximate Casamayoran age has been suggested for it (Wyss et al., 1994), but detailed taxonomic description and radioisotopic calibration are pending.

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FIG. 4. **A.** SGOPV 2914, *Santiagorothia chiliensis*, holotype, complete dentition except for LI1–2, RI1–2, Ri1–3, lateral view. **B.** SGOPV 2914, dorsal view. **C.** SGOPV 2914, posterior view. Scale = 1.0 cm.
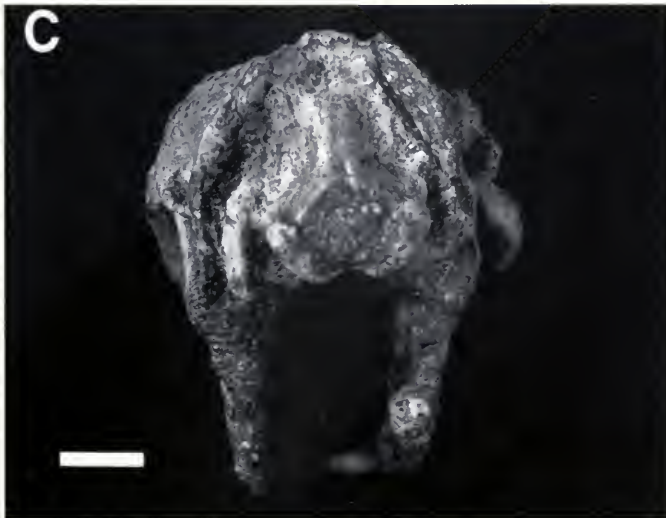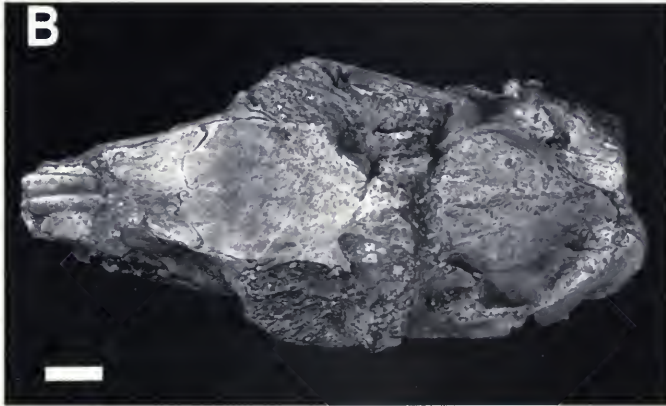
FIG. 5. **A.** SGOPV 2812, *Santiagorothia chiliensis,* cranium with RI3–M3, LP1–2, P4–M3, heavy wear. **B.** SGOPV 2812, occlusal outline of RP3–M1. Scale = 1.0 cm.

on their lingual faces. I3 and C are imbricate, the posterior margin of I3 laying labial to the anterior margin of C.

The first premolar does not appear to be replaced, which is inferred from its extreme state of wear in most specimens. SGOPV 2827 is an exception, however, and the P1 bears a distinct paracone and is broader transversely than the preceding teeth.

The deciduous premolars (dP2–4) have not yet been replaced in SGOPV 2827 and are heavily worn. dP2 has a well-developed paracone and metacone with correspondingly strong undulations on the ectoloph. It also displays an anteriorly projecting parastyle and a single central fossette. The crown is roughly rectangular in outline save

for the anterior projection of the parastyle. dP3 and dP4 resemble one another as well as the permanent molars: the paracone and metacone are distinct and the parastyle is salient. The ectoloph resembles that of dP2, with distinct undulations corresponding to the cusps. A fossette forms from a lingual sulcus between the protocone and the hypocone after heavy wear. The crowns are roughly rectangular (but more elongate than dP2) except for the strong, anteriorly projecting parastyle.

P2–4 are known only from moderately worn examples. The P2–4 sequence increases gradually in size posteriorly. The paracone and parastyle are expanded anteriorly, with a deep groove dividing the two. This parastylar expansion produces a
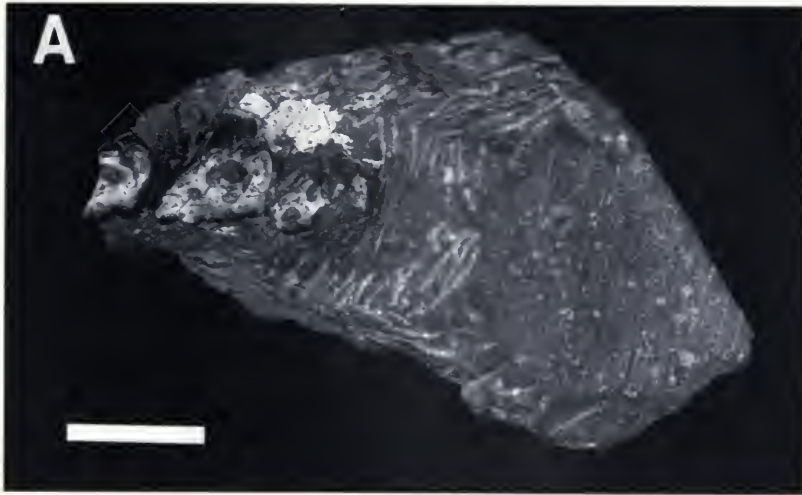
FIG. 6. **A.** SGOPV 2861, *Santiagorothia chiliensis*, RM1 (broken)–M3, light wear. **B.** SGOPV 2861, occlusal outline of RM2. Scale bar = 1.0 cm.

tooth that is longer than wide during early wear stages but later becomes roughly equidimensional. The ectoloph is relatively smooth, the metacone column being very low. The paracone column is low on SGOPV 2914 but is slightly more distinct on SGOPV 2812 and SGOPV 2821. A bifid lingual sulcus is short-lived; it rapidly closes off to become a persistent U-shaped internal fossette, the bend of which points lingually. An anteroexternal fossette is present on P3–4; it persists until late wear stages but ultimately disappears. A high posterior cingulum merges early in wear with the remainder of the crown. Other cingulae are lacking. P2–4 are hypsodont but form closed roots.

The five specimens listed below form a fairly complete wear series from relatively light to heavy wear (light—SGOPV 2827 > SGOPV 2861 > SGOPV 2821 > SGOPV 2914 > SGOPV 2816 > SGOPV 2812—heavy). This series provides a fairly complete record of the transformations of molar crown morphology throughout wear. M1–3 all bear a very smooth ectoloph with a shallow paracone/parastyle groove and only slight undulations corresponding to the paracone and metacone. A bifid lingual sulcus between the protocone and hypocone persists until moderate wear stages, at which point it closes off to become a U-shaped lingual fossette, as on the premolars; this structure persists throughout the remaining wear stages. An anteroexternal fossette and a smaller posteroexternal one are present initially but disappear after moderate wear, the posterior one being obliterated first. A high, very broad posterior cingulum is distinct from the hypocone early in wear but rapidly merges with the rest of the crown as wear proceeds. A transverse fossette is created upon merging of the posterior cingulum with the metaloph, but it rapidly disappears with wear. Other cingula are lacking. The occlusal surface is considerably longer than wide in little-worn teeth, with the

FIG. 7. **A.** SGOPV 2821, *Santiagorothia chiliensis,* Ri3–m3, light wear, lateral view. **B.** SGOPV 2821, occlusal view. **C.** SGOPV 2821, occlusal outline of RP1–M3. Scale bar = 1.0 cm.

FIG. 8. **A.** SGOPV 2826, *Santiagorothia chiliensis,* Ri1–c, Li1–m3, heavy wear. **B.** SGOPV 2826, occlusal outline of Lp3–m3. Scale bar = 1.0 cm.

paracone and parastyle expanded anteriorly and the protoloph running posterolingually from the anteroexternal corner. These dimensions become approximately equidimensional after moderate wear as the crown approaches the roots. The crown of RM1 of SGOPV 2827 is exposed along its entire length, clearly showing the anteroposterior narrowing of the crown rootward. All molars are hypsodont and form closed roots.

M3 resembles the other molars strongly despite its considerably smaller size. In contrast to the anterior molars, M3 has a posteriorly projecting metastyle. Some aspects of M3 vary considerably between specimens. In particular, the M3 of SGOPV 2821 and MLP 91-XI-5-15 have anterior and pos-

terior labial fossettes that are less persistent than in the other specimens; they disappear after light wear, leaving a featureless occlusal surface. In addition, the lingual sulcus of these two specimens is not bifid and the tooth thus lacks a "median lobe."

Lower Dentition—The i1 is slightly smaller than i2, whereas i3 is considerably larger than both. Although i1 and i2 are too worn or obscured in presently available specimens to reveal details of crown morphology, i1 appears nearly cylindrical, whereas i2 is broader and more incisiform. The i3 has a shallow central vertical lingual groove dividing the tooth into two portions, the posterior of which is slightly larger. The canine is
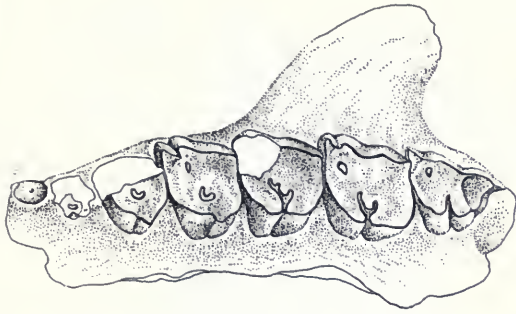
A

B
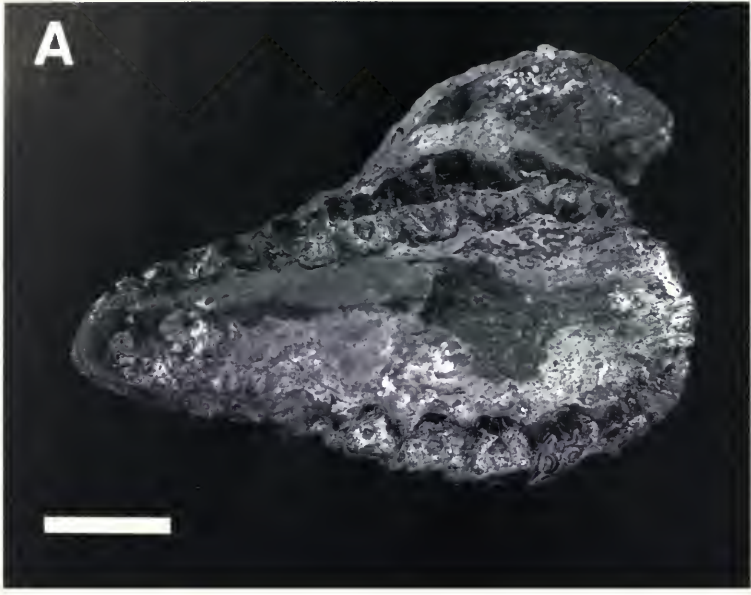
C

FIG. 10. MLP 91-IX-5-15, *Santiagorothia chiliensis*, LP1–M3, moderate wear. Scale bar = 1.0 cm.

larger than i3; it likewise consists of two portions, but it also has a small posterior heel. The i3 and c are imbricate, the posterior portion of each tooth lying labial to the anterior portion of the succeeding tooth.

The p1 is long and narrow; two vertical lingual grooves, an anteriorly positioned one and a less deeply incised posterior one, divide the tooth into three portions. The external face is smoothly convex except for a very shallow labial, vertically oriented groove occurring opposite the posterior lingual one. No diastemata are present in the anterior tooth row.

The p2 is similar to p1 except that a metaconid is clearly differentiated and the posterior lingual groove is accompanied by a distinct labial one and so defines a very small talonid.

The third and fourth lower premolars are similar, both possessing a large trigonid and a distinctly smaller but well-developed talonid. The trigonids are roughly triangular in outline and the talonids are round. The trigonid and talonid are separated by strong labial and lingual sulci, lending a bilobed appearance to the teeth. On p3 the labial sulcus is positioned slightly anterior to the lingual sulcus, whereas on p4 they are opposite one another. On both teeth a vertical groove separates the anterior margin of the trigonid from the metaconid. The metaconid is robust and swings posteriorly along its lingual margin. Extreme wear (SGOPV 2826) obliterates the anterointernal groove

and lingual sulcus, but the labial sulcus persists. The p4 has approximately the same dimensions as the molars. The p3 is about the same length anteroposteriorly as p4 but is distinctly narrower transversely.

The molar trigonids are square in outline and are separated from the rounded talonids by strong labial and lingual sulci, again producing a bilobed appearance. On the molar trigonids there is a shallow groove between the anterior margin of the tooth and the metaconid, which disappears with wear. The metaconid extends nearly transversely without swinging posteriorly at the lingual margin as it does on the posterior premolars. No hypoconulid is observed on m1 or m2, but completely unworn specimens are not presently known, and this feature may simply be highly transitory. The talonids and trigonids are subequal on m1 and m2, but on m3 the talonid is considerably larger. The m3 talonid is roughly elliptical, its outline interrupted by a shallow posterolingual groove separating a hypoconulid from the remainder of the talonid. All lower cheek teeth are hypsodont and form closed roots.

Cranium—The skull roughly resembles a larger version of *Notophithecus,* a Casamayoran non-interatheriine interatheriid described in detail by Simpson (1967). General differences seen in *Santiagorothia chiliensis* (apart from its much larger size) include a longer rostrum, a slightly more laterally expanded braincase, less extreme postorbital constriction (although still quite marked), and a less laterally expanded occipital region.

The premaxilla, moderately well preserved in several specimens, shows considerable variation. On the facial region of SGOPV 2821 the suture between premaxilla and maxilla slopes posteriorly and a small process of the premaxilla projects into the maxilla posterodorsally. On SGOPV 2812 and SGOPV 2914 the premaxilla/maxilla suture is oriented nearly vertically (the posterodorsal region is not preserved so no process may be discerned). On the palate the premaxilla/maxilla suture occurs immediately posterior to I3.

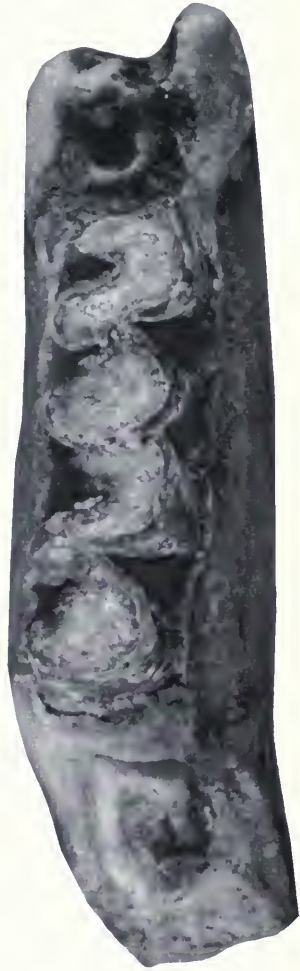The palatine/premaxilla suture is discernible only in its extreme anterior portion where it reaches about as far anteriorly as the posterior margin of P4. The internal choanae are not preserved but

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FIG. 9. **A.** SGOPV 2827, *Santiagorothia chiliensis,* palate and permanent upper dentition save dP3–4, very light wear, occlusal view. **B.** SGOPV 2827, lateral view. **C.** SGOPV 2827, occlusal outline of RM2. Scale bar = 1.0 cm.

Tooth	SGOPV 2821	SGOPV 2861	SGOPV 2812	SGOPV 2827	SGOPV 2826	MLP 83-I-12-1	MLP 91-IX-5-15	MLP 61-VIII-3-314	MLP 93-XI-25-8
I1 AP	—	—	—	—	—	—	—	—	—
I1 TR	—	—	—	—	—	—	—	—	—
I2 AP	—	—	—	—	—	—	—	—	—
I2 TR	—	—	—	—	—	—	—	—	—
I3 AP	5.19	—	—	—	4.73	—	—	—	—
I3 TR	2.73	—	—	—	1.85	—	—	—	—
C AP	5.27	—	5.66	—	5.19	—	—	—	—
C TR	3.00	—	—	—	2.00	—	—	—	—
P1 AP	5.85	—	—	5.34	—	—	—	—	—
P1 TR	3.18	—	—	3.00	—	—	—	—	—
P2 AP	—	—	5.77	d5.74	—	—	—	—	—
P2 TR	—	—	5.13	d4.79	—	—	—	—	—
P3 AP	7.09	—	7.02	d7.35	6.16	—	5.5*	—	—
P3 TR	4.92	—	6.24	d5.41	4.91	—	6.0*	—	—
P4 AP	7.45	—	6.89	d7.60	6.58	6.3*	6.6	—	—
P4 TR	5.66	—	6.99	d5.38	5.94	5.5*	5.6	—	—
M1 AP	6.29	—	6.47	7.95	6.41	7.1	5.8	—	—
M1 TR	5.76	—	7.06	4.33	5.72	5.4	5.6	—	—
M2 AP	7.54	8.70	7.18	7.76	7.00	7.0	6.8	7.2	7.7
M2 TR	5.68	5.61	6.82	3.64	5.45	5.2	4.7	4.9	4.8
M3 AP	6.47	7.85	7.40	—	6.24	—	6.4	—	—
M3 TR	4.88	4.42	5.73	—	4.28	—	4.1	—	—

* Estimated.

must have had a relatively posterior position, well beyond the posterior part of M3. The palantine notches are narrow and short anteroposteriorly, extending anteriorly to the posterior part of M3.

The rostral portion of the maxilla is quadrate and mildly excavated anterior to the orbit. The infraorbital foramen is large and positioned above P4. The orbital rim is preserved completely only in SGOPV 2914. This specimen shows that a posteriorly projecting maxillary process is excluded from the rim of the orbit by a very thin sliver of frontal, which projects anteriorly to contact the lacrimal.

The lacrimal is poorly preserved in all specimens but is apparently positioned largely within the orbit, only a very small portion extending onto the orbital rim and slightly beyond. The lacrimal foramen cannot be discerned.

The nasals are narrow and elongate, broadening posteriorly. They are confined to the superior part of the rostrum and are slightly convex mediolaterally. SGOPV 2821 shows the nasal and frontal suture to be roughly transverse, undulating slightly with two mild excursions. On SGOPV 2812 and SGOPV 2914 the suture is different. From the junction of the nasal and nasal-frontal sutures it runs a short distance anteriorly then sharply posteriorly, forming a strong posteriorly projecting process on the lateral margin.

The zygoma displays the hallmark interathere pattern: a jugal which both excludes the maxilla and extends posteriorly between the maxilla and squamosal (Riggs and Patterson, 1935). The maxilla extends along the ventral margin of the zygoma nearly to its posterior root. The squamosal extends anteriorly about as far as the level of the supraorbital process. The anterior root of the zygoma projects posteriorly and transversely away from the skull at about 60°. The remainder of the zygoma nearly parallels the braincase. The position of the anterior root of the zygoma on the rostrum varies between specimens, reaching from mid-M3 to anterior M1 on SGOPV 17-89-12 and SGOPV 2914 and from anterior M3 to posterior M1

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FIG. 11.   **A.** MLP 91-IX-5-14b, *Santiagorothia chiliensis*, Lm1–2. **B.** MLP 91-IX-5-14a, *Santiagorothia chiliensis*, Lm1–2. **C.** MLP 61-VIII-3-314, *Santiagorothia chiliensis*, ?M1 or M2, occlusal view. **D.** MLP 61-VIII-3-314, anterior view. Scale bar = 0.5 cm.

TABLE 4. Dental measurements for the lower dentition of *Santiagorothia chiliensis* (mm).

Tooth	SGOPV 2821	SGOPV 2826	MLP 91-IX-5-14a	MLP 91-IX-5-14b	MACN 10908a	MACN 10908b	MACN 10908c
i1 AP	—	—	—	—	—	—	—
i1 TR	—	—	—	—	—	—	—
i2 AP	—	—	—	—	—	—	—
i2 TR	—	—	—	—	—	—	—
i3 AP	—	4.23	—	—	—	—	—
i3 TR	—	1.95	—	—	—	—	—
c AP	5.57	5.10	—	—	—	—	—
c TR	1.94	1.80	—	—	—	—	—
p1 AP	5.57	—	—	—	—	—	—
p1 TR	2.79	—	—	—	—	—	—
p2 AP	5.94	5.46	—	—	—	—	—
p2 TR	2.66	2.34	—	—	—	—	—
p3 AP	6.24	6.30	—	—	—	6.2	6.0
p3 TR	3.14	3.32	—	—	—	3.4	3.5
p4 AP	6.71	6.47	6.4	—	—	—	—
p4 TR	3.70	3.73	4.1	—	—	—	—
m1 AP	6.93	5.79	6.7	6.7	—	—	—
m1 TR	4.05	3.59	3.5	4.1	—	—	—
m2 AP	7.34	5.99	—	6.2	6.2	—	—
m2 TR	3.67	4.12	—	3.7	4.0	—	—
m3 AP	8.22	8.22	—	—	—	—	—
m3 TR	3.53	3.81	—	—	—	—	—

on SGOPV 2821. A small but distinct descending process is present on the anterior zygomatic root in SGOPV 2821 but is more weakly expressed in the other specimens. This process is continuous with a very low, laterally projecting blade that runs posteriorly on the lateral zygomatic margin.

The rectangular frontal is considerably elongate anteroposteriorly. The nasal-frontal suture is positioned well anterior of the orbit. A moderately sized supraorbital process projects posteriorly. The anterior orbital rim is sharp and bears a large supraorbital foramen about midway along its length.

The parietal narrows posteriorly and bears a low sagittal crest. The squamosal region is moderately inflated, the pars epitympanicus forming a flattened triangular region with sharp dorsal and posterior borders. The occiput contains greatly enlarged epitympanic sinuses and is very broad. The moderately inflated, fully ossified bullae form the dominant feature of the basicranium.

The glenoid fossa is anteroposteriorly narrow and deep, its posterior border being very steep and slightly excavated. The postglenoid process forms a short, transverse ridge extending medially to the bulla. A probable postglenoid foramen lies near the bulla on the postglenoid process. This basicranial region is compressed anteroposteriorly, with the meatus and postglenoid process tightly fused. The meatus itself is short and projects posterodorsally. A transversely compressed paraoccipital process arises directly posterior to the

TABLE 5. Check tooth crown height for a sample of *Santiagorothia chiliensis* (mm).

	Upper jaw			Lower jaw	
Tooth	SGOPV 2827 (unworn, crown completely exposed)	SGOPV 2861 (slightly worn, crown incompletely exposed)	Tooth	SGOPV 2862 (light wear, crown incompletely exposed)	SGOPV 2821 (moderate wear, crown incompletely exposed)
P4	—	—	p4	—	5.90
M1	11.60	11.70	m1	7.80	5.00
M2	12.50	—	m2	10.10	—
M3	—	—	m3	—	—

bulla, such that the bulla abuts its anterior border. The posterior lacerate foramen lies medial and adjacent to the paraoccipital process. Posteromedial to the posterior lacerate foramen occurs a condylar foramen. No foramina occur along the bulla's medial border, but two occur anteriorly; in these respects the bulla closely resembles *Protypotherium* (Patterson, 1936). The foramen ovale is large and lies in the fissure between the bulla and alisphenoid. Ventral and slightly lateral to the foramen ovale lies the external eustachian opening, the two being separated by a thin sliver of bone. Ventral to the eustachian foramen lies a shelf of bone which Patterson (1936), in describing *Protypotherium*, termed a styliform process, acknowledging, however, its uncertain homology. The medial margin of the foramen ovale contains a septum, perhaps demarcating an additional foramen. Simpson (1967) noted a similar septum in what he interpreted as the medial lacerate foramen of *Notopithecus*, suggesting that it may have subdivided the foramen in two, thereby demarcating also the anterior lacerate foramen. A canal appears to run immediately lateral to the foramen ovale, along the fissure of the tympanic/alisphenoid suture; poor preservation of this canal precludes further interpretation.

Patterson (1936) described two additional, very small foramina medial and ventral to the foramen ovale in *Protypotherium*, interpreting one of these as the anterior carotid foramen. Patterson (1936) thus regarded the course of the carotid artery as being intrabulla. The similarity between *Santiagorothia chiliensis* and *Protypotherium*, with respect to position of the basicranial foramina, suggests a similar pattern of carotid circulation in the two taxa.

Proargyrohyrax curanderensis, new taxon

HOLOTYPE—MLP 61-VIII-3-27, left maxillary fragment with P4–M3, preserving anterior root of the left zygoma.

PARATYPES—MLP 61-IV-14-1, left mandible with p3–m3; MLP 61-VIII-3-24, left mandible with p2–m3.

REFERRED MATERIAL—MLP 93-XI-25-19, right m1; MLP 93-XI-25-3, right p3–4.

ETYMOLOGY—*Proargyrohyrax* for its similarity to the interathere taxon *Argyrohyrax* (although no strict phylogenetic relationship is implied) and *curanderensis* for the geographic location near which the fossils were recovered.

TYPE LOCALITY—Lomas Blancas, near La Curandera, Departamento Paso de Indios, Chubut province, Argentina.

KNOWN DISTRIBUTION—Known only from the type locality. This locality is probably biostratigraphically correlative to the "Astraponotéen plus supérieure" level at Gran Barranca, Chubut, and the Tinguiririca Fauna of central Chile.

DIAGNOSIS—Synapomorphies outlined earlier that are diagnostic of the Interatheriinae serve to identify *Proargyrohyrax curanderensis* as a member of this clade.

Proargyrohyrax curanderensis has the following attributes, distuinguishing it from other interatheriines except *Santiagorothia chiliensis*: cheek teeth that form closed roots, upper cheek teeth that become more equidimensional with wear, and persistent labial fossettes on the upper molars. Like *Santiagorothia chiliensis*, the parastyle on M1–2 in *Proargyrohyrax curanderensis* curves and projects labially and p3 has a strong postmetastylid crest projecting posteriorly.

Proargyrohyrax curanderensis can be distinguished from *Santiagorothia chiliensis* by the following features in *Proargyrohyrax curanderensis*: larger overall (the absolute size difference varies considerably from between teeth and specimens, but a difference of 10% may serve as an approximation), upper and lower premolars (particularly the posterior premolars) more molariform (close in dimensions to the molars), labial fossettes on the upper molars more persistent, trigonids on p3–4 squarer in occlusal outline, and anterior root of the zygomatic arch well expanded anteroposteriorly and laterally, much more so than in *Santiagorothia chiliensis*.

REMARKS—Although there is no direct association of upper and lower dentitions, the specimens referred to *Proargyrohyrax curanderensis* are taken to represent the same taxon, given compatibility in size. In addition, the maxilla (MLP 61-VIII-3-27) occludes well with the mandibles (MLP 61-VIII-3-24 and MLP 61-IV-14-1).

DESCRIPTION—**Material**—*Proargyrohyrax curanderensis* is represented by cheek teeth and a portion of the maxilla (Fig. 12). Given the less complete material from which it is known, *Proargyrohyrax curanderensis* can be described in much less detail than *Santiagorothia chiliensis* (for example, a complete wear series for the cheek teeth is unavailable for the former). Mensural data are presented in Tables 6 and 7.

Upper Dentition—P4 is molariform and quadrangular. A well-developed parastyle curves labi-

A

B

FIG. 12. **A.** MLP 61-VIII-3-27, *Proargyrohyrax curanderensis,* holotype, L maxillary fragment with P4–M1, moderate wear. **B.** MLP 61-IV-14-1, *Proargyrohyrax curanderensis,* left mandible with p3–m3, light wear. Scale bar = 1.0 cm.

ally and connects to a moderately developed paracone column. The paracone and parastyle are separated by a deep groove. Small anteroexternal and posteroexternal fossettes are present, the anterior of which is larger. The protoloph contacts the extreme lingual margin of the metaloph but is not fully united with it. Together, the protoloph and metaloph demarcate a central, heart-shaped fossette. The anterior portion of this fossette approaches but does not contact the anteroexternal fossette. A lingual sulcus is absent, although it is probable that the lingual fossette represents a sulcus that closed through wear. The posterior cingulum is moderately distinct and is lower than the metaloph. It joins the metaloph labially and lingually, forming a posterior fossette that is transversely elongate.

The molars are longer than wide and are interrupted lingually by a deeply bifid sulcus. They are generally similar in morphology except as noted below.

M1, the largest tooth of the series, is elongate and bears a large anteroexternal fossette near the paracone. A small posteroexternal fossette lies close to the metacone. The parastyle is salient and projects labially. The lingual sulcus is narrower and the median lobe smaller than on M2. The transverse dimension becomes greater as wear approaches the roots. M1 has a thick internal root and two fused external roots.

M2 is narrower transversely than M1. Although the parastyle is smaller than on M1, it still curves labially. The parastyle/paracone groove is larger than on M1 but still shallow. The well-developed paracone is more prominent than the metacone. The short protoloph is oriented obliquely, its lingual margin being free. The lingual sulcus is narrow. A small medial lobe occurs internally and with significant wear merges with the internal face of the protoloph. Anteroexternal and posteroexternal fossettes are present as is a transverse fossette between the metaloph and the posterior cingulum. M2 has three roots.

M3 is the smallest molar. Its lingual sulcus is

TABLE 6. Measurements of the upper cheek teeth of *Proargyrohyrax curanderensis* (mm).

Tooth	MLP 61-VIII-3-27
dM3 AP	—
dM3 TR	—
dM4 AP	—
dM4 TR	—
P4 AP	7.7
P4 TR	6.4
M1 AP	8.1
M1 TR	6.7
M2 AP	7.9
M2 TR	5.6
M3 AP	6.8
M3 TR	4.0

TABLE 7. Measurements of the lower cheek teeth of *Proargyrohyrax curanderensis* (mm).

Tooth	MLP 61-VIII-3-24	MLP 61-IV-14-1	MLP 93-XI-25-3	MLP 93-XI-25-19
p2 AP	7.1	—	—	—
p2 TR	3.5	—	—	—
p3 AP	7.5	7.2	7.4	—
p3 TR	4.4	3.9	4.3	—
p4 AP	7.7	7.1	7.6	—
p4 TR	4.5	4.0	4.4	—
m1 AP	7.6	7.3	—	7.4
m1 TR	5.0	4.4	—	4.5
m2 AP	8.1	7.4	—	—
m2 TR	4.8	4.1	—	—
m3 AP	7.7	8.8	—	—
m3 TR	3.6	3.5	—	—

bifid but has a very small posterior limb. Like the other upper molars, M3 bears a posteriorly projecting metastyle.

Lower Dentition—The lower dentition is not known anterior to p3 for *Proargyrohyrax curanderensis*. The p3 is molariform, the trigonid and talonid being enlarged, equidimensional, and close in size to the molars. The trigonid is square in outline and open lingually (anterointernal groove). The protoconid and metaconid, the former of which is more distinct, are joined by a short, straight metacristid. A crest, termed a postmetastylid by Marshall et al. (1983), extends posteriorly from the metaconid. The trigonid and talonid are unconnected during initial wear stages, but an isthmus quickly forms thereafter. A narrow, deep labial sulcus separates the trigonid and talonid. A low cristid obliqua extends posterolabially from the medial part of the metacristid. The groove on the posterointernal margin of the talonid is a weak.

The p4 resembles p3, the main difference being that the postmetastylid on p4 is less developed and projects less posteriorly. The labial sulcus between the trigonid and talonid is wider than on p3.

The m1 and m2 are similar, although m1 displays a broader anterointernal groove. They resemble p4 except that the trigonid is relatively larger and rounder. In addition, m1–2 lack the postmetastylid of the premolars.

On m3 the metacristid is shorter than on m1–2 and the talonid is considerably larger than the trigonid. The wide, transverse entolophid is flanked by two moderately deep sulci, the posterior deeper than the anterior.

Cranium—The anterior root of the zygoma is the only part of the cranium of *Proargyrohyrax curanderensis* known. It is broad both laterally and anteroposteriorly. Its anterior margin is even with the anterior margin of P4 (the anterior border of the orbit is in line with the anterior margin of P4 as well). The maxilla forms the anterior and anteroventral portion of the orbit. The zygomatic root bears a small descending process. Judging from preserved sutures, the jugal lay lateral to the zygomatic process of the maxilla. The infraorbital foramen is large, arising from the base of the orbit and situated adjacent to P3.

Eopachyrucos, Ameghino 1901

1901   *Eopachyrucos,* Ameghino, p. 370.
1906   *Eupachyrucos* [lapsus], Ameghino, p. 469.

TYPE—*Eopachyrucos pliciferus* Ameghino, 1901.

EMENDED DIAGNOSIS—"Upper molar hypsodont; tapering rapidly from roots to apex; wear surface near apex longer than wide; labial surface of ectoloph with strong, subequal paracone and metacone ridges; two circular, equal labial fossettes retained to late wear stage; deep bifid groove between protocone and hypocone retained (open and not as fossa) to late wear stage" (Simpson, 1967, p. 116). Lower premolars and molars high crowned but have very long roots; anterointernal groove of the trigonid persistent. The p3 trigonid with paracristid reduced and metacristid well developed and straight. Talonid of the premolars and molars shorter and less rounded than those of *Proargyrohyrax curanderensis* and *Santiagorothia chiliensis*.

KNOWN DISTRIBUTION—Patagonia: Gran Barranca, Departamento Sarmiento, Chubut province; Cañadón Blanco, Chubut province, Argentina; Rocas Bayas, Departamento 25 de Mayo, Río Negro province, Argentina.

REMARKS—Florentino Ameghino referred *Eopachyrucos pliciferus* to the Hegetotheriidae (1901, 1906) believing its occlusal morphology to closely resemble the Santacrucian *Pachyrukhos* (Hegetotheriidae, Pachyrukhinae) of Patagonia. *Eopachyrucos pliciferus* was included by Simpson (1967) as ?Hegetotheria incertae sedis. According to Ameghino's handwritten label that accompanies the fossil ("*Eoprotypotherium*" souche *Protypotherium* Astraponoth) this specimen was collected by Carlos Ameghino in rocks of Mustersan (*Astraponotus* beds) age. "*Eoprotypotherium*" is an unpublished name that Ameghino used in an informal phylogenetic sense, to emphasize his notion of the ancestry of this form with respect to *Protypotherium* (eventually Ameghino decided to use the name *Eopachyrucos*). As Simpson realized, however, the provenance of several specimens in the Ameghino Collection, for various reasons, was confused or lost and should be treated with caution.

In his description of the type species of *Eopachyrucos*, Ameghino (1901) mentioned various lower teeth and mandibular fragments (MACN A55-12) although the type, as catalogued in the MACN, is an upper molar. The latter is very similar to the unworn upper molar of *Argyrohyrax acuticostatus*, but much smaller. The upper molar of *Eopachyrucos* is also similar to the molars of *Guilielmoscottia* (a Mustersan SALMA non-interatheriine interathere) but is more hypsodont. *Eopa-*

chyrucos is an interathere, its inclusion in the Interatheriinae being based mainly on its hypsodonty. MACN A55-12 also displays a very shallow parastyle/paracone groove, which is additional evidence for its interatheriine affinities (see diagnosis of *Santiagorothia chiliensis*, including the list of tentative interatheriine synapomorphies).

Eopachyrucos pliciferus Ameghino 1901

1901   *Eopachyrucos pliciferus*, Ameghino, p. 370.
1967   *Eopachyrucos pliciformis*, Simpson, p. 116, lapsus pro pliciferus.

TYPE—MACN A55-12, isolated left M1 or M2.

PARATYPES—MLP 12-1529, incomplete mandibular fragment with alveoli of right i1–2, and left p1–4, and four isolated cheek teeth: right p4, m1 and m3, and left m1, apparently of the same individual; MLP 91-IX-5-17, an isolated right p2.

TYPE LOCALITY—?Gran Barranca, Chubut province, Argentina.

KNOWN DISTRIBUTION—Known from Patagonia, Argentina. The type, MACN A55-12, was likely collected at the "Astraponotéen plus supérieure" level (Bond et al., 1996), Gran Barranca (south of Colhué-Huapi Lake), Departamento Sarmiento, Chubut province; MLP 12-1529 comes from Cañadón Blanco, Chubut province; MLP 91-IX-5-17 is from Rocas Bayas, Departamento 25 de Mayo, Río Negro province.

DIAGNOSIS—Small with high-crowned cheek teeth. Anterior lower premolars are similar to *Cochilius*. Similar also to *Guilielmoscottia* but higher crowned and with well-developed metacristid on the lower molars. The m3 entoconid more expanded than in *Santiagorothia chiliensis* and *Proargyrohyrax curanderensis*.

REMARKS—Ameghino's holotype consists of an isolated upper molar, the principal diagnostic characters of which are listed above in the diagnosis. The Cañadón Blanco and Rocas Bayas specimens are similar in size to the holotype and occlude well with it; on this basis we refer these specimens to this taxon.

Ameghino's original description (1901 p. 123) of the molars of *E. pliciferus* is excerpted as follows: ". . . presentan el mismo contorno que los de *Pachyrukhos*, pero poco arqueados, de corona más corta y provistos de raíces separadas aunque muy cortas," [has the same outline as *Pachyrukhos* but has a shorter crown and stocky, but separate roots]. Other features mentioned by Ameghino include (1) "ectolofo sinuoso terminando . . . en dos cúspides en forma de V" [ectoloph sinuous, terminating . . . in two cuspids which have the form of a V], (2) "cara lingual dividida en dos lóbulos por . . . un surco que se ensancha hacia abajo y penetra en la corona formando un pliegue de esmalte" [the lingual face is divided into two lobes . . . a groove which broadens and penetrates the crown forming a fold of enamel], and (3) "presencia de dos fosetas de esmalte, una anterior y otra posterior" [presence of two fossettes, an anterior and posterior].

DESCRIPTION—**Material**—*Eopachyrucos pliciferus* is known from isolated upper and lower cheek teeth (Fig. 13). Mensural data are provided in Table 8.

Upper Dentition—The type (M1 or M2) is similar to the molars of *Argyrohyrax acuticostatus, Santiagorothia chiliensis*, and *Proargyrohyrax curanderensis* but is much smaller, narrower, and slightly more elongate. It is decidedly hypsodont and lacks a deep paracone/parastyle groove. An anterior labial fossette and a smaller medial labial fossette are present. A third smaller, lingually positioned fossette is present, likely forming from the merger of the postcingulum and metaloph (measurements of MACN A52-12: interoposterior, 3.9 mm; transverse, 2.6 mm). The crown height is 6.1 mm.

Lower Dentition—The lower dentition is similar to that of *Cochilius*, but the molar trigonids of *E. pliciferus* generally have a broader anterointernal groove and a much larger metacristid, the overall outline thus markedly more square.
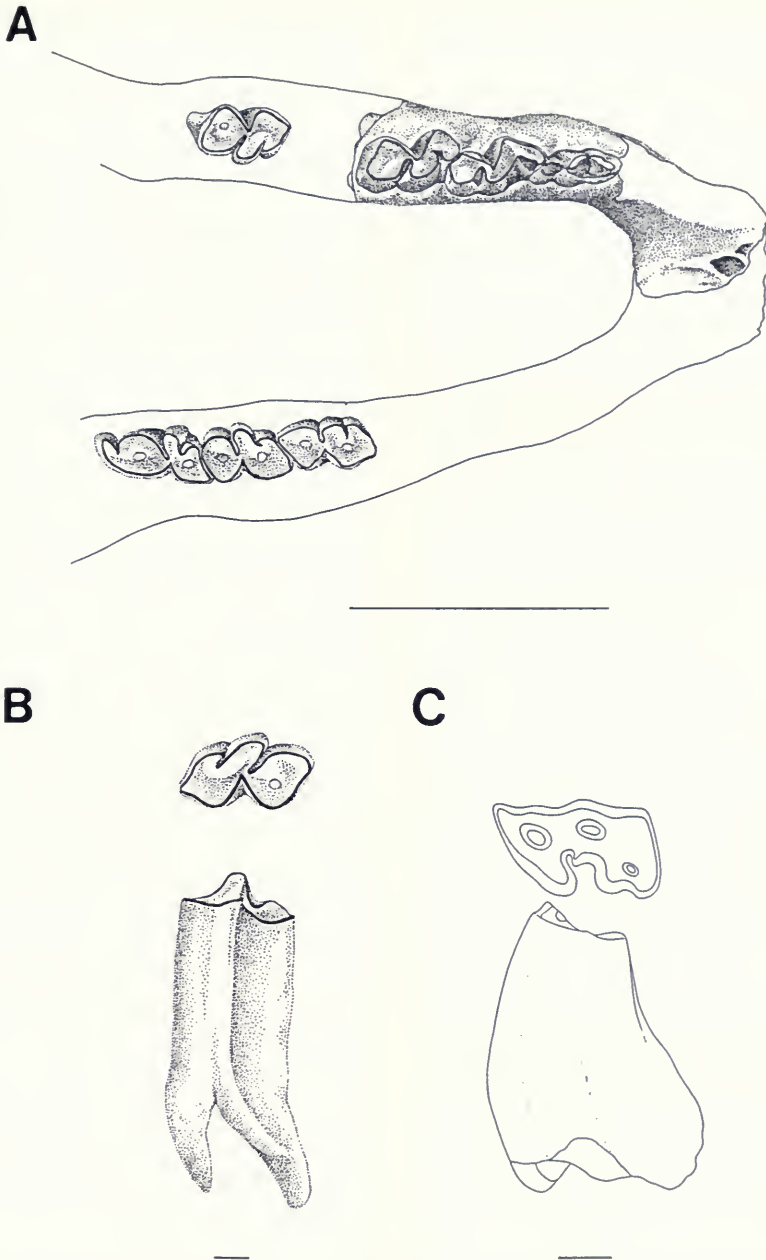
The p2 is narrow, displaying a well-developed

TABLE 8. Measurements of the lower cheek teeth of *Eopachyrucos pliciferus* (mm).

Tooth	MLP 12-1529	MLP 91-IX-5-17
p1 AP	4.1	—
p1 TR	1.6	—
p2 AP	4.1	3.9
p2 TR	1.9	1.6
p3 AP	4.4	—
p3 TR	2.4	—
p4 AP	4.0	—
p4 TR	2.4	—
m1 AP	4.1	—
m1 TR	2.5	—
m2 AP	—	—
m2 TR	—	—
m3 AP	5.3	—
m3 TR	2.5	—

Fig. 13. **A.** MLP 12-1529, *Eopachyruchos pliciferus,* partial left mandible and associated teeth, Lp2–p4, Lm1, Rm1–3, light to moderate wear, scale = 1.0 cm. **B.** MLP 12-1529, *Eopachyruchos pliciferus,* Lm2, light to moderate wear, scale = 0.1 cm. **C.** MACN A55-12, *Eopachyruchos pliciferus,* holotype, LM1 or LM2, light wear. Scale bar = 0.1 cm.

trigonid with a distinct protoconid and raised anteroexternal margin, a lingually projecting metaconid, and a transversely oriented metacristid connecting protoconid and metaconid. A small rounded talonid connects directly to a wide metaconid by a narrow isthmus and is bounded on either side by two sulci.

The p3 is molariform with the trigonid being slightly more triangular in outline than the square outline of m1–2. In contrast to the molars, the

paracristid is reduced. The first and second molars display a transverse metacristid with a lingually projecting metaconid, the latter of which is much larger on m2. Both teeth are distinctly bilobed with persistent lingual and labial sulci; the trigonid and talonid are connected by a narrow isthmus. The talonid on both is square in occlusal view. The m3 trigonid is square in outline and smaller than on m1 and m2. The hypoconulid is well developed on m3, and a distinct persistent groove separates it from the entoconid. The m3 talonid forms an elongate oval outline and is more than twice as large as the trigonid.

Interatheriidae incertae sedis

"?*Eohyrax*" *platyodus* Ameghino 1904

1904a   *Eohyrax platyodus*, Ameghino, p. 200.
1967   ?*Eohyrax platyodus*, Simpson, p. 108.

LECTOTYPE—?*Eohyrax platyodus*: The left m1 (MACN A10908e), upon which Ameghino (1904) based most of his observations, was taken by Simpson (1967) as a lectotype (Fig. 2).

TYPE LOCALITY—?Gran Barranca, Departamento Sarmiento, Chubut province, Argentina (although the provenance is not reliable).

REMARKS—According to Simpson (1967, p. 108) ?*Eohyrax platyodus* is an archaeohyracid more primitive than *Eohyrax rusticus* from the Casamayoran of Patagonia, and "[i]ts presence in the Mustersan would be anomalous." Simpson designated an interatheriine lower molar (MACN A10908e: left m1) as lectotype. This tooth is lower crowned than the other interatheriine teeth from the sample.

The material supposedly pertaining to ?*Eohyrax platyodus* evidently represents a mixture of several individuals assignable to at least three different taxa. Six teeth (MACN A10908a–f) represent the syntypes of ?*Eohyrax platyodus*. Five of these are referable to the Interatheriinae and the sixth to the Archaeohyracidae. MACN A10908a,b,c are tentatively referred to *Santiagorothia chiliensis*, and MACN A10908d is referred to Archaehyracidae cf. *Pseudhyrax*.

Interathere Phylogeny

Apart from one numerical cladistic study based largely on dental characters (Cifelli, 1993), there has been little phylogenetic study of the Interatheriidae. Cifelli identified rampant homoplasy in this group, the only resolved node in his study being a clade distinguishing the Interatheriinae (all hypsodont forms) from *Notopithecus* (a low-crowned Casamayoran taxon). As in previous studies (Cifelli, 1985a; MacFadden et al., 1985; Marshall et al., 1986), Cifelli (1993) suggested the probable existence (although not borne out by his analysis) of two monophyletic groups within the Interatheriinae: an *Interatherium* and allies clade and a *Protypotherium* and allies clade. Results from more recent phylogenetic analyses of interatheres (Hitz, 1994, 1995, 1997; Reguero et al., 1996) support the monophyly of the Interatheriinae and suggest that "Notopithecinae" represents a paraphyletic assemblage (see the diagnosis of *Santiagorothia chiliensis* for a tentative list of interatheriine synapomorphies). In Hitz's analyses (1994, 1995, 1997) *Santiagorothia chiliensis* (referred to in Hitz (1997) as Tinguiririca New Taxon A) is placed as the nearest outgroup to all taxa previously included in the Interatheriinae (Fig. 1).

Conclusions

The taxa discussed above are derived from a very poorly known temporal interval in the South American mammalian fossil record. This interval (between the Mustersan and Deseadan SALMAs) spans a transition in South American mammal evolution between older faunas, with lineages generally characterized by primitive features, and younger faunas whose members display more progressive attributes such as hypsodonty (Pascual et al., 1985). By far the best represented of the faunas treated here is the Tinguiririca Fauna from Chile, which contains a biostratigraphically novel assemblage of taxa including the first or last appearances of at least seven subfamilial or higher taxa. The Patagonian faunules are less diverse but may well show a similar pattern when better known. The new interatheriines described here are exemplary in illustrating the transitional nature of these newly recognized post-Mustersan/pre-Deseadan-age faunal horizons; although they represent the earliest known interatheriines, they are plesiomorphic in important features compared to later forms (e.g., in possessing cheek teeth with closed roots).

The occurrence of *Santiagorothia chiliensis* in geographically disparate localities (central Chile

and Patagonia) supports their temporal correlation and strengthens the case for recognition of a new land mammal age encompassing at least a portion of the post-Mustersan/pre-Deseadan hiatus within the South American land mammal sequence (Wyss et al., 1994; Flynn & Swisher, 1995).

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