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Small Archaeohyracids (Typotheria, Notoungulata) from Chubut Province, Argentina, and Central Chile: Implications for Trans-Andean Temporal Correlation

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November 26, 2003
Publication 1526

PUBLISHED BY FIELD MUSEUM OF NATURAL HISTORY

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Accepted May 7, 2003
Published November 26, 2003
Publication 1526

PUBLISHED BY FIELD MUSEUM OF NATURAL HISTORY

ISSN 0096-2651
PRINTED IN THE UNITED STATES OF AMERICA

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John J. Flynn **André R. Wyss**

Abstract

We describe small-bodied archaeohyracids of transitional Eocene-Oligocene age from Chubut, Argentina, including two from Santiago Roth's important but poorly known Cañadón Blanco locality and two occurring in the Tinguiririca Fauna of the Andean Main Range of central Chile. Three taxa are recognized. We refer specimens from both Patagonia and the central Andes to one of these taxa, initially named *Arachaeohyrax gracilis* by Roth (1903) but receiving a new generic designation here. A diminutive form from Cañadón Blanco and an intermediate-sized form from Chile are each recognized as new species. These taxa help to clarify the temporal correlation of lithostratigraphic units currently located on opposite sides of the Andean divide, and aid in the recognition of a biochronologic interval, the early Oligocene (to possibly late Eocene)-aged Tinguirirican, interposed between the classical Mustersan and Deseadan "ages" of the South American land mammal succession.

Introduction

Archaeohyracids are among the most poorly known of South America's early Cenozoic mammals. In view of the group's typical rarity elsewhere on the continent (apart from the Deseadan of Bolivia), the abundance and diversity of archaeohyracids in the transitional Eocene-Oligocene-aged Tinguiririca Fauna of central Chile (Wyss et al., 1994) are remarkable. Equally noteworthy is a previously poorly understood, roughly contemporaneous faunule from Chubut, Argentina—Roth's Cañadón Blanco assemblage (Roth, 1901, 1903). Two small archaeohyracid taxa are known from Cañadón Blanco. One was previously undescribed, and the other occurs also in the Tinguiririca Fauna; both are named or renamed below.

Chilean Fauna

The Tinguiririca Fauna (Wyss et al., 1990, 1994; Wyss, Flynn, et al., 1993) is derived from the dominantly volcanic and volcaniclastic Abanico (= Coya-Machalí) Formation (see Charrier et al., 1996). Attaining a stratigraphic thickness of up to 2000–3000 m, the Abanico Formation represents the geographically most widespread lithostratigraphic unit on the western (Chilean) slope of the central Andean Main Range. The Tinguiririca Fauna, documenting a pre-Deseadan (South American Land Mammal "Age;" SALMA), post-Mustersan (SALMA) biochronologic interval (Tinguirirican SALMA) recently added to the South American fossil mammal succession (Wyss et al., 1994; Flynn & Swisher, 1995; Bond et al., 1996; Flynn et al., 2003), is the first of a series of Cenozoic mammal faunas discovered within this formation during the past decade (Flynn et al., 1995; Wyss et al., 1996; Charrier et al., 1997; Wyss et al., 1999). Radioisotopic determinations place the age of the Tinguiririca Fauna at ~31.5 Ma (see Flynn et al., 2003), based on direct dating of several fossiliferous horizons (see Charrier et al., 1996; Flynn & Wyss, 1999). The Tinguirirican SALMA is certainly earliest Oligocene in age and

possibly quite short in duration (~31–33 Ma), but may extend into the late Eocene (Flynn et al., 2003).

Among numerous taxonomic peculiarities, the Tinguiririca Fauna contains by far the most diverse archaeohyracid fauna known to date (Wyss, Norell, et al., 1993; Wyss et al., 1994; Croft, 1998, 2000; Croft et al., 2003). Indeed, archaeohyracids, represented by at least six taxa, are a dominant element of the Tinguiririca Fauna both in numerical abundance and in taxonomic diversity. Uncertainty about the number of taxa stems from the unknown association of upper and lower dentitions—a problem compounded by the similar size of several of the taxa and the time-consuming preparation of specimens from extraordinarily hard matrix.

Several archaeohyracids from the Tinguiririca Fauna are referable to forms known from Argentina (Wyss et al., 1994); many such references could previously be made only informally, owing to the tangled nomenclature of many of the forms from Patagonia. Here we seek to update and stabilize the nomenclature of a small archaeohyracid common to the Cañadón Blanco and Tinguiririca faunas, and describe two new, closely related forms. The other archaeohyracids from the Tinguiririca Fauna are described formally elsewhere (Croft et al., 2003). A minimum of three archaeohyracid skulls are known from the Tinguiririca Fauna (skulls of this group were previously limited to a single specimen of *Archaeohyrax patagonicus* from Argentina and undescribed specimens from Salla, Bolivia). In addition, the Tinguiririca Fauna provides associated postcranial and dental material for the group.

Argentine Fauna

The fossil assemblage from Cañadón Blanco is among the most enigmatic in the South American land mammal succession. Collected by Roth, probably during 1897 and 1898, the locale (known to occur within Chubut Province) has not been relocated definitively. (A manuscript in preparation by one of us, M.R., seeks to clarify the locations of Santiago Roth's collecting efforts, including Cañadón Blanco.) Roth's specimens from Cañadón Blanco were long considered to represent a temporally mixed assemblage, representing the Casamayoran, Mustersan, and Deseadan SALMAs (Simpson, 1967; Patterson, unpublished manuscript; Patterson et al., in prep.). Discoveries in Chile and elsewhere in Argentina have revealed, however, that the bulk of the Cañadón Blanco assemblage likely pertains to a single fauna, approximately contemporaneous with the Tinguiririca Fauna and Ameghino's "Astraponotéen plus supérieur" horizon from the Gran Barranca south of Lake Colhué Huapi (Wyss et al., 1994; Bond et al., 1996; Reguero, 1998).

Among its archaeohyracids, the Cañadón Blanco fauna includes two small forms, of which only *Archaeohyrax gracilis* (whose subsequent nomenclatural history is discussed below) has previously been named (Roth, 1903). Herein we provide a new generic designation for this species; we also place within this genus two new diminutive species, one from Cañadón Blanco and one from the Tinguiririca Fauna.

Abbreviations

APS, Astraponotéen plus supérieur; MLP, Museo de La Plata; SGOPV, Museo Nacional de Historia Natural, Santiago, vertebrate paleontology collections; MACN, Museo Argentino de Ciencias Naturales, "Bernardino Rivadavia"; SALMA, South American Land Mammal "Age."

Nomenclatural Note

Because the early phase of study of South American fossil mammals produced a plethora of dubiously founded names, "whoever thinks he has discovered a new taxon in these faunas is ethically obliged to consider the[ir] possible applicability. . . ," even though these names may have "no real meaning at present" (Simpson, 1967: 189). Taxonomists revising these faunas therefore face a recurring conundrum: Is it preferable to salvage "classic" names based on inadequate holotypes, effectively "rehabilitating" such names by referring more clearly diagnosable material to them, or are we better served in marginalizing very poorly substantiated names by expressly declining to add to their hypodigms? Even if the second alternative is followed, as Simpson (1967: 189) lamented, "it is vexatious that there is no way to jettison the latter [names that are unlikely ever to acquire any meaning or value] permanently and thus clear up accumulated clutter in this science." For reasons outlined below we favor proposing new names over resurrecting problematic older ones.

Systematic Paleontology

Mammalia Linnaeus, 1758
Notoungulata Roth, 1903
Archaeohyracidae Ameghino, 1897

***Protarchaeohyrax,* gen. nov.**

Archaeohyrax Ameghino, 1897 (partim): 431–432.
Bryanpattersonia Simpson, 1967 (partim): 113.
?*Eohegetotherium* Ameghino, 1901: 370; Simpson 1967; 115–116, figs. 31a, b.

TYPE SPECIES—*P. gracilis* (=*Archaeohyrax gracilis*).

COMMENTS—Patterson (MS) and Simpson (1967) recognized *Archaeohyrax sulcidens* and *A. gracilis* as belonging to a genus distinct from but closely related to *Bryanpattersonia* (and also distinct from *Archaeohyrax*), although neither ever named it formally. Nonetheless, not having seen Roth's material, Simpson (1967) elected to provisionally assign both *A. sulcidens* and *A. gracilis* to a single species of his newly erected genus *Bryanpattersonia* (*B. sulcidens,* which had priority over *gracilis*), along with a second, clearly distinct species, *B. nesodontoides* (the genotypic species). Simpson's (1967) *B. sulcidens* thus has yet to receive distinct generic recognition, an action taken below. It merits note that M. T. Cabrera's sketches of Roth's "*A.*" *gracilis* type material (appearing as figures 29 and 30 in Simpson, 1967) are not entirely accurate, thus bearing on assignment of that material.

Even though both Patterson (MS) and Simpson (1967) argued for the synonymy of *Archaeohyrax sulcidens* and *A. gracilis,* one of us (Reguero, 1998) has recently shown that a name proposed still earlier, *Eohegetotherium priscum,* placed by Ameghino (1901: 24) in the Hegetotheriidae, might represent the same taxon. Thus, if "*sulcidens,*" "*gracilis,*" and "*priscum*" could indeed be shown to be synonyms, *Eohegetotherium* would be the valid generic name. Unfortunately, the types and hypodigms of "*sulcidens*" and "*priscum*" offer such scant basis for comparison (see below) that assignment to various earlier named archaeohyracid species (each inarguably distinct) cannot be excluded. The case for synonymy is thus based less on the unmistakable morphologic similarity of these forms than on there being so little to compare that they can't be shown to be different. Of these three names, therefore, only "*gracilis*" is based on reasonably diagnosable material. Ongoing work (Reguero & Cifelli, 1997; Croft et al., 2003; Patterson et al., in prep.) has shown that Deseadan SALMA archaeohyracids form a distinct clade (from which "*gracilis*" is excluded), members of which preoccupy the name *Archaeohyrax.* For these reasons we propose a new genus, *Protarchaeohyrax,* to receive "*gracilis.*"

DIAGNOSIS—"Significantly smaller than [*Archaeohyrax* = *Bryapattersonia*] *nesodontoides*" (Simpson, 1967: 114). More brachydont than *Archaeohyrax*; labial fossettes of upper molars persist little into wear. Parastyle large, more prominent, and situated further labially relative to paracone than in *Archaeohyrax.* Paracone well developed. Lingual sulcus on upper molars. Prolongation of M3 ectoloph forms a posterior lobe.

DISTRIBUTION—Tinguiririca Fauna, Abanico (= Coya-Machalí) Formation, Chile, of early Oligocene (to possibly late Eocene) age, Tinguirirican SALMA (Flynn et al., 2003); presumably the Sarmiento Formation, Chubut, Argentina (Roth, 1903); Fray Bentos Formation, Uruguay (Reguero et al., 1995). The occurrence of the genus in Uruguay represents a new species that will be described elsewhere.

Protarchaeohyrax gracilis
(Figures 1–3)

Archaeohyrax gracilis Roth, 1903: 22.
?*Archaeohyrax sulcidens* Ameghino, 1902: 10.
?*Bryanpattersonia sulcidens* Ameghino, 1902: 10; Simpson, 1967: 113.
?*Eohegetotherium priscum* Ameghino, 1901: 370; Simpson 1967: 115–116, figs. 31a, b.

HOLOTYPE OF *ARCHAEOHYRAX GRACILIS*—MLP 12-1522, fragment of left maxilla bearing P1–M3 (Fig. 1A), and MLP 12-1518 (Roth's No. 4978), left mandibular fragment with p1–m2 (both specimens probably of the same individual, but with MLP 12-1522 becoming lectotype should this association prove incorrect; Simpson, 1967) (Fig. 1B).

LECTOTYPE OF *A. SULCIDENS*—Based on Ameghino's description, Simpson (1967: 113) selected MACN A-10906a (misprinted as MACN 1096 by Simpson), a left m1 measuring 6.5 by 3.6 mm, as lectotype. The lectotype is from a lot of 24 teeth, 14 of them lowers, two of which match Simpson's

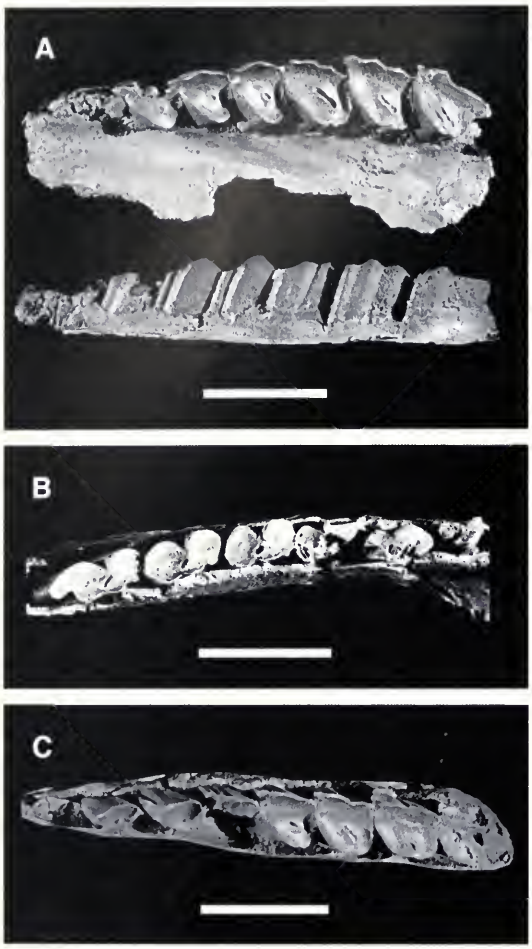

FIG. 1. Epoxy casts of specimens collected by Carlos Ameghino and Santiago Roth referred here to *Protarchaeohyrax gracilis* (gen. nov.). Holotypes of "*A.*" *gracilis,* including (**A**) fragment of left maxilla with P1–M3 (MLP 12-1522) in occlusal (top) and labial (bottom) views and (**B**) occlusal view of left mandibular fragment with p1–m2 (MLP 12-1518). (**C**) Right maxillary fragment with C, P1–2, P3 (broken), P4–M3 (MLP 12-1478) (alveoli for I1–3 not visible on cast). Scale bar = 10 mm.

description. Of these two teeth (m1 or possibly m2), we designate the one less encrusted in manganese and clearly showing the central fossette between the trigonid and talonid as the lectotype. Among the various labels accompanying these teeth, one, apparently an annotation by B. Patterson, reads, "*Archaeohyrax sulcidens* Ameghino . . . (2 niveles)." Another reads "*Eohegetotherium priscum* Tipo," and "*Astraponotus.*"

PARALECTOTYPES OF *A. SULCIDENS*—MACN A-10906b, left m1; MACN A-10906c, left m1 or m2; MACN A-10906d, right m1 or m2; MACN A-10906e, right m1 or m2; MACN A-10906f, left m3; MACN A-10909, left m3.

LECTOTYPE OF *EOHEGETOTHERIUM PRISCUM*—MACN A-10988a, right M1 or 2.

PARALECTOTYPE OF *EOHEGETOTHERIUM PRISCUM*—MACN A-10988b, left M1 or 2, MACN A-10988c, right M1 or 2.

HYPODIGM—The holotype of *Archaeohyrax gracilis* and the following specimens: MLP 12-1478, cranial fragment with alveoli for right I1–3, right C, P1–2, P3 (broken), and P4–M3 (Fig. 1C); MLP 12-1513a, left mandibular fragment with p4–m3; MLP 12-1513b (Roth's No. 4893), right mandibular fragment with p2–m3; MLP 12-1539, left mandibular fragment with m1–3; MLP 52-XI-4-168 (Roth's No. 4894), left maxillary fragment with dP2–4, M1–2 (consisting of two pieces with a very good contact); SGOPV 2954, right mandibular fragment with p1–m3 and portion of left mandibular ramus bearing lingual slivers of posterior teeth (Fig. 2); and SGOPV 2982, rostrum with left and right dC, P1, dP2–4, M1–2; the left successional canine can be seen emerging above its deciduous precursor, while on the right side of the specimen P2–4 are visible in their crypts, nestled above their precursors (Fig. 3). (The first postcanine teeth in notoungulates are generally unreplaced, leading to ambiguity over their proper designation. Are these retained deciduous teeth [dP1/dp1] or successional teeth that erupt unusually early [P1/p1]? Inasmuch as complete ontogenetic series are needed to decide this question in modern forms, it will likely never be conclusively resolved for notoungulates. Consistent with the traditional designation, we identify these teeth as P1/p1.)

LOCALITIES—The provenience of the lectotype of *B. sulcidens* is uncertain, Simpson (1967: 114) simply indicating it to be from the Mustersan (SALMA) of Patagonia (see above, and Temporal Correlation section below). Similarly, the locality from which the lectotype of *E. priscum* (MACN A-10988) derives is not known but is thought to be in central Chubut Province. (MACN A-10988 was found among the syntypes of *A. sulcidens;* it was separated from this lot of specimens and given its present number during intervening work on the collections.)

Specimens bearing Museo de La Plata numbers are part of Roth's collection from Cañadón Blanco, the precise location of which is now lost (see above). Roth labeled these specimens "T.i.C.B."

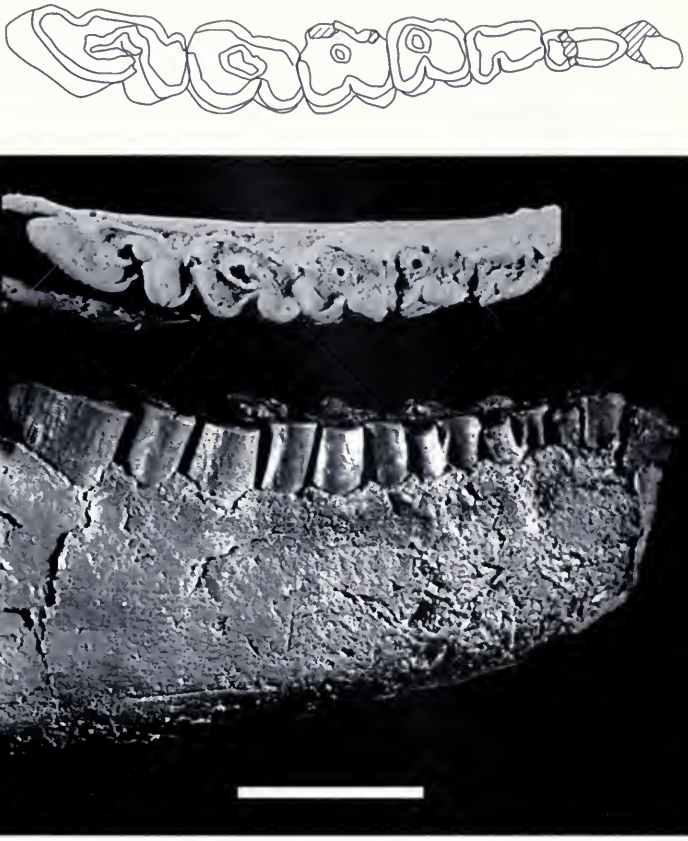

FIG. 2. Epoxy cast of specimen from the Tinguiririca Fauna of Chile referred to *Protarchaeohyrax gracilis* (gen. nov.). Mandibular fragment (SGOPV 2954) with right p1–m3 and slivers of left posterior teeth. Occlusal (line drawing and top photograph) and right lateral (bottom photograph) views. Only the right side of the specimen is shown, and p1–2 are not visible in the occlusal photograph. Scale bar = 10 mm.

([Formación] Terciario inferior de Cañadón Blanco [Territorio del Chubut]).

The Chilean specimens SGOPV 2954 and 2982 were recovered near Termas del Flaco. Specimen SGOPV 2954 is from locality C-89-39 (see Flynn & Wyss, 1999; Locality Set 3 of Flynn et al., 2003), 34°59′S, 70°26′W, approximately 2 km northwest of town (i.e., north of the Río Tinguiririca; see map in Wyss et al., 1994). It was collected (like the majority of fossils from this site) in situ on a veneer of volcaniclastic sediment adhering to a high-angle face created by a resistant dike. SGOPV 2982 derives from the primary set of localities producing the Tinguiririca Fauna (Locality Set 1 ["East Ridge"] of Flynn et al., 2003), those straddling the Portezuelo El Fierro (identified by its elevation, 2738 m, on the current topographic map; Anonymous, 1985) approximately 3 km due south of Termas del Flaco and the Río Tinguiririca.

AGE—Early Oligocene (to possibly late Eocene), Tinguirirican SALMA. Radioisotopic age estimates are available only for specimens from Chile. Due to alteration, only the fossil-bearing horizons and conformably underlying strata south of the Río Tinguiririca (including the locality for SGOPV 2982) have been dated directly at ~31.5 Ma. This species represents a key biostratigraphic tie between the laterally discontinuous sections of the Abanico Formation exposed north and south of the Río Tinguiririca.

DIAGNOSIS—As for genus. The species is substantially larger than *P. minor* (named below), and the mandibular corpus is deeper than in *P. intermedium* (also named below).

COMMENTS—Material previously referred (not

FIG. 3. Epoxy cast and line drawing of specimen from the Tinguiririca Fauna of Chile referred to *Protarchaeohyrax gracilis* (gen. nov.). Rostrum (SGOPV 2982) with left and right dC, P1, dP2–4, M1–2 shown in occlusal view (line drawing—left dentition only, and upper photograph). The slightly oblique right lateral view (lower photograph) shows P2–4 exposed within their crypts. Anterior is to the left in all views. Scale bar = 10 mm.

all of it correctly) to *E. priscum* included three mandibular fragments and 21 isolated cheek teeth; this was accompanied by a small note in Ameghino's handwriting identifying it as the type of this species (Simpson, 1967). Out of this lot, Simpson selected as lectotype (and provided a rough illustration, his figure 31) an upper molar (presumed to be M1) most closely matching Ameghino's description. Simpson considered the taxon a questionable member of the Hegetotheria.

Archaeohyrax gracilis was described as follows (translated from Roth, 1903: 22): "The form of the teeth is similar to *Archaeohyrax patagonicus.* The labial face is slightly convex, with poorly marked crests. The second molar has a sulcus on its lingual face. On the lower molars the internal

sulci are not deep; on the first molar a sulcus can barely be distinguished on the internal part of the anterior lobe. This species is smaller than *Archaeohyrax sulcidens.*" Later he added: "intermediate between the families Notopithecidae and Hegetotheriidae." Roth did not figure the type material.

In sum, the lectotypes of "*B.*" *sulcidens* and "*E.*" *priscum* each consist of a single isolated upper cheek tooth of uncertain tooth position, the geographic/stratigraphic sources of which are uncertain (although both are from Gran Barranca, see below). Needless to say, securely associated faunal elements are lacking. By contrast, the type of "*A.*" *gracilis* is more than adequate for diagnosis; although its locality cannot now be found, its biostratigraphic context is currently understood. Because of their high degree of hypsodonty, most post-Mustersan SALMA archaeohyracid cheek teeth vary significantly in size and shape during wear, hampering identification of isolated teeth. Although the lectotypes of "*B.*" *sulcidens* and "*E.*" *priscum* and the holotype of "*A.*" *gracilis* could all pertain to the same species, the first two names are based on such meager material that referral to other archaeohyracid species cannot be ruled out. Thus we regard the synonymy of "*B.*" *sulcidens,* "*E.*" *priscum,* and "*A.*" *gracilis* as likely but indemonstrable (identifying it above with a query). We therefore feel justified in bypassing "*sulcidens*" and "*priscum*" as possible senior synonyms, basing the new genus recognized here on the more definitively diagnosable type material "*gracilis.*" We favor a situation wherein well-preserved and diagnostic material is given a new name (and earlier, poorly founded names are essentially ignored) over one in which the valid name of otherwise easily identified specimens must always remain in doubt. It creates less confusion to admit that "*E.*" *priscum* is conceivably the senior synonym of *Protarchaeohyrax gracilis* than to have to always qualify, with a query, referrals of much better material to the earlier proposed name. Thus, excellent material currently allows recognition of three small species of archaeohyracids from a restricted temporal interval. Insofar as we cannot establish to which of these three species, if any, the poor types of *priscum* and *sulcidens* properly refer, proposing new names for some of these three seems justified. Among other benefits, a desirable side effect of designating "*gracilis*" as the type of a new genus is that this name now becomes biostratigraphically useful—"*gracilis*" not being known from well-sampled (but as yet incompletely described) Mustersan SALMA faunas from Patagonia or from the Deseadan SALMA.

DESCRIPTION—Of the skull, little more than a poorly preserved anterior fragment of MLP 12-1478 is currently available for study (although SGOPV 2982 consists of a well-preserved rostrum—and possibly more of the skull—only the dentition, anterior root of the zygomatic arch, and portions of the palate have been prepared, the remainder of the specimen being encased in extremely hard volcaniclastic matrix). The rostrum is apparently long and dorsoventrally compressed; the premaxilla is small and triangular in lateral view. The anterior root of the zygoma lies opposite M2–3 (M1–2 in SGOPV 2982, a juvenile) and otherwise is of primitive notoungulate form, not being marked by a descending process or zygomatic plate. This feature may have changed ontogenetically (as in mesotheres and certain other notoungulates), but evidence for this is lacking in the available material.

Upper Dentition—Aside from the alveoli for I1–3 on MLP 12-1478, little is known of the anterior dentition. The alveolus for I1 suggests that this tooth was substantially larger than the other incisors. The lot of teeth containing the lectotype of *Eohegetotherium priscum* includes an isolated right upper incisor (I1, MACN A-10988d). This large tooth is smooth both labially and lingually. The enamel, which is restricted to the crown, is thin labially. A shallow groove runs along the internal face of the long, curved root. The long axis of the alveolus for I2 is oriented anteroposteriorly, suggesting that this tooth was little specialized. The I3 alveolus is very small; it preserves part of the root, which is circular in cross-section.

A short diastema separates the canine from I3. The canine is simple in form and not markedly reduced. The tooth is distinctly caniniform and apparently bore two roots. The premolariform teeth preserved in this position on SGOPV 2982 are clearly deciduous; the left permanent canine is seen in the process of replacement.

The first premolar (which evidently is not replaced and begins to wear before dP2–4 are shed) is longer and wider than the canine; it bears a weak parastyle and is double-rooted.

The second premolar is much larger than P1; a well-developed parastyle projects anteriorly. A faint sulcus marks the lingual surface of the tooth anteriorly.

The third and fourth premolars are closely similar, except for the larger size of P4. Parastyles are

well developed and the vertical grooves separating them from the paracone column of the external face are more clearly marked than on the preceding teeth. Both teeth possess small central fossettes and a single elevated cusp on the ectoloph (paracone). There are no traces of lingual sulci. Although P3 and P4 are submolariform, both are distinctly more triangular in occlusal outline than are the molars.

The first two molars are trapezoidal in outline and very similar in form. The parastyle is weakly developed, a shallow vertical groove demarcating it posteriorly. The ectoloph is distinctly sinuous, owing to strong expression of the paracone and metacone columns on the external face, the former of which is more prominent. The internal fossette is oriented obliquely, paralleling the anterior edges of these teeth. The lingual sulcus persists as a faint vertical depression, even through moderate wear. During early wear stages (as shown by SGOPV 2982) this sulcus forms an open cleft that is continuous with the central fossa. Other aspects of the buccal morphology of M1 are also well displayed in SGOPV 2982. The crochet is well developed and extends nearly to the ectoloph, accounting for the small size of the central fossa. A single, small, median external fossette is present between the crochet and the ectoloph, but this would likely have vanished with little additional wear. An unworn posterior cingulum is present at a height just dorsal to the slightly worn metaloph. A small depression occurs between these two structures, but it is unclear whether this would have formed a fossette during wear or whether the cingulum and metaloph would simply have coalesced. A moderately worn M1 and a very lightly worn M2 are preserved on MLP 52-XI-4-168. On both, the paracone is more prominent than the metacone. On M1 (as in SGOPV 2982), an internal bifid sulcus persists through early wear. The M2 is longer than wide. The lingual vertical sulcus is wide and deep, delimiting a median lobe. The posterior cingulum forms a distinct shelf, less elevated than the metaloph, and merging with the remainder of the crown early in wear. This shelf is separated from the hypocone lingually by a very shallow groove. The hypocone is distinct and high. The left M1–2 of MLP 12-1517 bear three short roots, the two labial ones being smaller than the lingual.

The occlusal surface of the mildly worn M3 of MLP 12-1478 is slightly more triangular than those of the preceding molars, the lingual margin of the tooth being broadly rounded. A moderately worn, isolated, right M3 (MACN A-10988e) lacks roots, the base of the tooth being completely open. As in other archaeohyracids, a posterior prolongation of the ectoloph is not developed during early wear stages. The lingual sulcus is weak, becoming barely discernible in late wear.

The deciduous premolars are well preserved on SGOPV 2982 (Fig. 3). The anterior replacing cheek tooth, dP2, is longer than wide and bears a prominent parastyle. Although molariform, dP3 is more triangular than the permanent molars. A short sulcus occurs between the parastyle and paracone. A slight paracone ridge is developed. An obliquely oriented fossette occurs centrally toward the labial side of the tooth. The internal face is flat and rounded. Although low-crowned, dP4 is otherwise quite molariform, bearing a paracone ridge that is even more prominent than those on the permanent molars. A short, shallow groove occurs on the tooth's lingual face. As shown by MLP 52-XI-168 and SGOPV 2982, dP4 bears three roots.

Lower Dentition—The mandibular corpus is deep and robust. The symphysis is not expanded posteriorly, extending only to approximately the middle of p2. The dentition anterior to p1 is unknown.

Little can be said about the first lower premolar, as no undamaged examples are known; the tooth is simple in form (apparently unicuspate) and laterally compressed.

The second lower premolar is considerably larger than p1 and is apparently double-rooted. The tooth is dominated by a large, crescentic trigonid, as in certain interatheres (e.g., *Notopithecus* and *Cochilius*). The talonid is about one-half the length of the trigonid and is roughly circular in cross-section. A vertical groove marks the trigonid-talonid junction throughout the height of the crown labially; lingually only a short, shallow groove (obliterated by slight wear) occurs.

The trigonids of p3–4 are less anteroposteriorly expanded than on p2, with the steeply sloping basins between the paraconids and metaconids closing lingually after moderate wear. In SGOPV 2954 the roots of the premolars are visible just above the edges of the alveoli, while in the Argentine specimens (e.g., MLP 12-1518) none of the roots are visible, a difference probably attributable to heavier wear on the Chilean specimen.

The early wear stage morphology of m1–3 is well displayed by MLP 12-1513b and MLP 12-1539. The m1 and m2 are approximately equidi-

mensional and are otherwise very similar in morphology.

The trigonid of m3 is square, with a small postmetastylid projecting posteriorly. The m3 talonid differs from those of m1–2 in its more posteriorly projecting hypoconulid, which forms a continuous bladelike lophid. A broad posterolingual groove separates the entoconid and hypoconulid. On SGOPV 2954 the m3 is moderately worn; here the postmetastylid connects with the anterior face of the entoconid, producing a narrow isthmus lingually that persists through the remainder of wear. In this specimen a projection of the central fossettid into the talonid is present, the fossettid not having yet become completely isolated; in addition, the lingual groove separating the entoconid and hypoconulid is quite shallow.

Despite the seemingly more advanced state of wear in of SGOPV 2954, a projection of the central fossettid into the talonid persists, while in the less worn MLP 12-1518 this extension forms a small, faint, but completely isolated fossettid. This, along with other features, including metric differences in the dentition and mandible (Table 1), hints that SGOPV 2954 (and possibly SGOPV 2982) may warrant recognition of a separate species (Croft, 2000). Given, however, the small sample size currently available—including the lack of an adult upper dentition from Chile—we take the conservative approach, tentatively referring these specimens to *P. gracilis*. This new taxon is listed as "Archaeohyracidae, New taxon A1" in Flynn et al. (2003, tables 1 and 2).

***Protarchaeohyrax minor* sp. nov.**
(Figure 4)

HOLOTYPE—MLP 52-XI-4-168a, maxillary fragment with right P4–M2 (possibly P3–M1).

HYPODIGM—The type only.

LOCALITY—Santiago Roth collected the type and only known specimen from Cañadón Blanco, Chubut, Argentina (see above).

AGE—Early Oligocene (to possibly late Eocene; as for *P. gracilis*), based on correlation of its associated fauna with elements of the radioisotopically dated Tinguiririca Fauna.

DIAGNOSIS—*Protarchaeohyrax minor,* the smallest archaeohyracid known, is clearly smaller than *P. gracilis* and all other described archaeohyracids, including another new taxon (see below). In addition, the posterior cheek teeth do not display the graded increase in size from P2 through M2 typical of other archaeohyracids.

ETYMOLOGY—In reference to its small size.

DESCRIPTION—Only a small right maxillary fragment bearing three teeth is currently known. There is some question about the tooth positions represented by the teeth, P4–M2 (or possibly P3–M1). We initially regarded MLP 52-XI-4-168a as perhaps referable to the small taxon named below (*P. intermedium*), an assignment plausible—on the basis of size—only if a P3–M1 identification is accepted. For reasons discussed below, however, MLP 52-XI-4-168a most likely includes two molars and thus represents a distinct, very small taxon. This species is listed as "Archaeohyracidae, New taxon A3" in Flynn et al. (2003, table 2).

Upper Dentition—Although MLP 52-XI-4-168a compares fairly closely with a small palate from the Tinguiririca Fauna (SGOPV 2998, assigned to another new taxon below), this maxilla is unusual in that the three teeth do not grade evenly from one to another in size. Instead, the two posterior teeth are about equal in size—the middle one perhaps being slightly larger—and the anterior one is only slightly smaller than the others. This contrasts with the condition in *P. gracilis* and the taxon named below, wherein successive teeth increase in size from P2 through at least M2. The size and general shape of the three teeth in MLP 52-XI-4-168a agree fairly closely with the P3–M1 of the new taxon represented by SGOPV 2998. However, a pronounced groove separating the paracone and parastyle on the anterior tooth of MLP 52-XI-4-168a suggests, in combination with the feeble expression of this structure on the two succeeding teeth, that the anterior tooth represents P4 (and hence the others represent M1–2). Therefore, since P4–M2 are the most plausible tooth loci represented in MLP 52-XI-4-168a, it follows that this specimen pertains to a taxon considerably smaller than that represented by SGOPV 2998 (M2 in the latter specimen measures 5.4 mm long by 4.2 mm wide, versus 4.2 × 3.2 mm in MLP 52-XI-4-168a).

P4 is triangular in occlusal outline. A central basin and its single median fossette are rimmed labially by an elevated paracone and parastylar spur. The molars are more anteroposteriorly elongate than is the premolar, being more trapezoidal in outline. In addition, as mentioned above, the buccal surfaces of the molars are topographically simpler than that of the premolar; the paracone and metacone folds, as well as the parastylar

TABLE 1. Measurements of teeth of *Protarchaeohyrax gracilis, P. intermedium,* and *P. minor* (mm).

Protarchaeohyrax gracilis

	P1		P2		P3		P4		M1		M2		M3	
Upper dentition	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**
MACN A52-623a									7.2	5.3				
MACN A-10911o									7.1	5.8				
MACN A-10911p							5.8	6.9						
MACN A-10988a									6.5	5.3				
MACN A-10988b									6.4	5.5				
MACN A-10988c									6.4	5.5				
MLP 12-1522			5.2	3.5	4.6	4.5	4.3	5.1	6.7	5.0	7.5	5.0	7.4	4.2
MLP 12-1478	3.9	2.3	4.7	2.9										
MLP 52-XI-4-168	4.3	2.5	4.8	3.4	5.2	3.7	5.7	3.8	6.4	3.4				
SGOPV 2982			4.9*	3.6*	4.6*	4.8*	5.8*	4.8*	6.9	4.3	—	—	—	—

* These values are for deciduous teeth.

	p1		p2		p3		p4		m1		m2		m3	
Lower dentition	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**
MACN A52-623b									8.0	3.5				
MACN A-10906a											6.5	3.5		
MACN A-10906b							6.7	3.6						
MACN A-10906c											7.1	3.3		
MACN A-10906d											7.5	3.5		
MACN A-10906e									7.1	3.4				
MACN A-10906f													7.5	3.5
MACN A-10906g							6.0	3.4						
MACN A-10906h											6.9	3.4		
MACN A-10906i									6.4	3.3				
MACN A-10906j									6.7	3.6				
MLP 12-1518	3.4	2.0	4.6	2.2	4.7	3.0	5.1	2.6	4.7	3.3	5.2	3.5	7.1	3.1
MLP 12-1513a							6.1	3.3	6.0	3.9	6.7	3.8	7.0	3.1
MLP 12-1513b			5.1	2.1	5.5	2.6	5.6	2.6	6.2	3.4	7.4	3.5	7.1	3.5
MLP 12-1539									5.1	3.2	5.8	3.3	6.0	2.5
MLP 61-VIII-3-398			4.7	2.7	4.7	3.3	5.1	3.8	6.9	3.8				
MLP 59-II-26-85							6.0	3.4						
MLP 61-IV-14-3									6.1	3.4				
MLP 52-XI-4-196					4.5	3.3	5.0	3.4	6.1	3.5			8.2	3.3
SGOPV 2954			3.7	1.9	3.5	2.8	3.8	3.6	4.2	4.0	5.2	4.3	7.4	3.5

Mandible	**Midline distance between posteriormost extent of mandibular symphysis and posterior edge of m3**	**Depth of ramus just posterior to m3**
MLP 12-1518	approx. 32.5 mm	3.6
SGOPV 2954	approx. 24 mm	4.6

Protarchaeohyrax intermedium

	P1		P2		P3		P4		M1		M2		M3	
Upper dentition	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**
SGOPV 2998			2.9	3.2	3.2	4.1	3.9	4.7	4.0	5.1	5.4	4.6	5.8	3.9

	p1		p2		p3		p4		m1		m2		m3	
Lower dentition	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**
SGOPV 3065			—	—	4.6	1.8	4.6	2.0	4.7	2.5	5.7	2.6	—	—
SGOPV 5007			—	—	3.9	2.3	4.1	2.4	4.4	2.7	5.1	3.0	(6.3)	2.6

TABLE 1. *Continued.*

Protarchaeohyrax minor	P3		P4		M1		M2	
	L	W	L	W	L	W	L	W
MLP 52-XI-4-168a			3.7	4.3	5.0	4.0	5.0	3.6

groove, form little more than low-amplitude ripples. A vertical groove separates the protocone and hypocone along the internal face of M1; on P4 and M2 this structure is far less distinct.

***Protarchaeohyrax intermedium* sp. nov.**
(Figures 5–7)

HOLOTYPE—SGOPV 3065 paired dentaries with left p2 (damaged), p3–m3, and right p3–4, slices of m1 trigonid and m2 talonid, and m3 (Fig. 5).

HYPODIGM—The type, and SGOPV 5007, paired dentaries bearing right p2 (damaged), p3–m3, plus fragmentary portions and lingual impressions of several left cheek teeth, including largely intact m2–3 (Fig. 6); and SGOPV 2998, partial palate bearing left and right P2–M3 (Fig. 7).

LOCALITY—From near Termas del Flaco, Chile, all from localities south of the Río Tinguiririca (see localities for *P. gracilis*).

FIG. 4. Epoxy cast of right maxillary fragment (MLP 52-XI-4-168a) collected by Santiago Roth from Cañadón Blanco and here referred to *Protarchaeohyrax minor* (gen. et sp. nov.). Top, occlusal view; bottom, lateral view (anterior to the left in both). Scale bar = 10 mm.

AGE—Early Oligocene (to possibly late Eocene; as for *P. gracilis*).

DIAGNOSIS—*P. intermedium* is intermediate in size between *P. gracilis* and *P. minor*. In addition, the very shallow ramus displayed in SGOPV 3065 clearly differentiates *P. intermedium* from at least *P. gracilis* (the lower dentition of *P. minor* being unknown).

ETYMOLOGY—In reference to its size.

DESCRIPTION—Although much of a palate is preserved (SGOPV 2998), little can be said about this taxon's cranial morphology in the specimen's current state of preparation. The anterior zygomatic root, as shown on the left side of the specimen, lies opposite M3, without obvious evidence of a ventral expansion.

Much of the mandible, including the anterior portion of the ascending ramus, is preserved on the left side of the holotype. The symphysis, if it was fused, was not expanded posteriorly. The only remarkable feature of the ramus is its striking shallowness. The vertical depth of the mandible below p3 in SGOPV 3065 is 5.7 mm, compared to >8.5 mm in specimens referred to *P. gracilis* above. This slender form of the ramus is all the more remarkable given the strong hypsodonty of the cheek teeth. Patches where the external surface of the left mandibular ramus of SGOPV 3065 is not preserved provide partial windows onto the ventral reaches of m1 and m2. Both teeth extend (clearly visible on m2, obscured on m1) as undivided, enamel-covered (i.e., unrooted) columns that reach the base of the ramus (m2 is approximately 19 mm high, of which only about 3.5 mm protrudes above the alveolus).

Lower Dentition—The morphology of the lower dentition is best illustrated by SGOPV 5007 (Fig. 6), a pair of dentaries. The right cheek teeth are well preserved, excepting a damaged and laterally displaced p2 and a missing posterior sliver on the talonid of m3. Significant portions of the left m1–3 are preserved, although there is breakage labially, particularly on m1. The roots and lingual impressions of p3–4 occur on the left side

FIG. 5. Epoxy cast and line drawing of specimen from the Tinguiririca Fauna of Chile referred to *Protarchaeohyrax intermedium* (gen. et sp. nov.). Paired dentaries (holotype, SGOPV 3065) with left p2 (damaged), p3–m3, and right p3–4, slices of m1 trigonid and m2 talonid, and m3, in occlusal (line drawing—left side only, and upper photograph) and left lateral (lower photograph) views. Anterior is to the left in all views. Scale bar = 10 mm.

as well. The molars and posterior premolars of *P. intermedium* tend to have a narrower entoconid region, resulting in flatter lingual faces of these teeth than is the case in *P. gracilis*. Overall, these teeth are considerably thinner than in *P. gracilis*. A fossettid occurs immediately posterior to the trigonid on p3–m3. A sharp vertical groove separates the p2–m3 trigonids and talonids labially throughout most (if not all) of the considerable vertical height of these teeth. A deep notch separates the entoconid and hypoconulid on m3, lending the posterior talonid region a strongly hooked appearance.

Upper Dentition—The second premolar through M2 form a closed and evenly graded series, increasing in size posteriorly. These teeth are

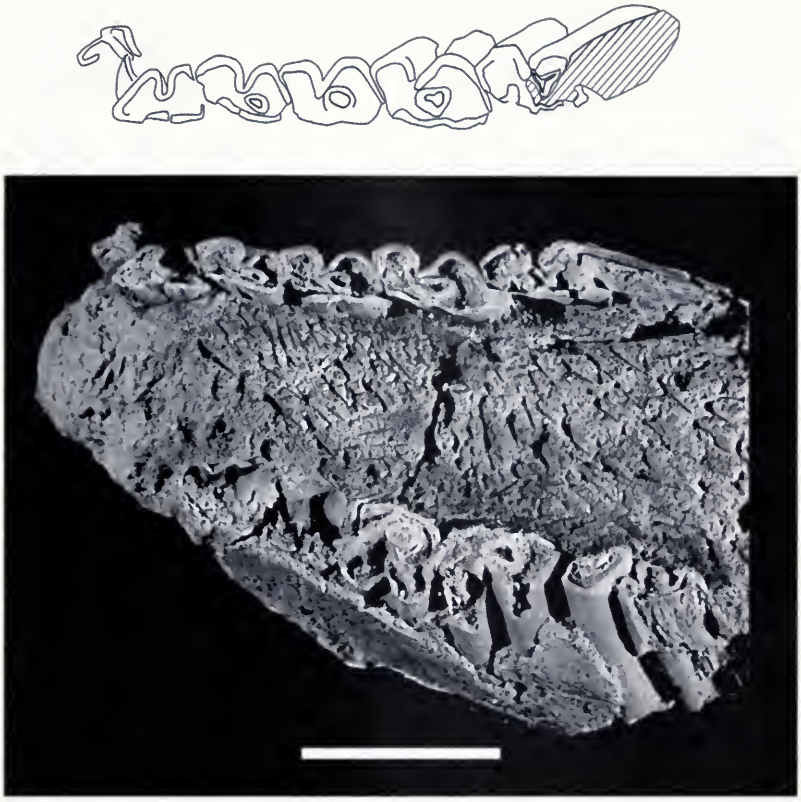

FIG. 6. Epoxy cast and line drawing of specimen from the Tinguiririca Fauna of Chile referred to *Protarchaeohyrax intermedium* (gen. et sp. nov.). Paired dentary fragments (SGOPV 5007) with right p2 (damaged), p3–m3, plus fragments of left cheek teeth, including largely intact m2–3, occlusal view (line drawing of right side only). Anterior is to the left. Scale bar = 10 mm.

all fairly obliquely placed, the internal portions being shifted posteriorly. The upper molars of SGOPV 2998 (Fig. 7) are similar in size to *P. gracilis,* but the premolars are considerably smaller, both in length and in width, the combined length of P2–M3 in SGOPV 2998 approximating that of P3–M3 in MLP 12-1522. The buccal faces of these teeth are smoother and flatter than in *P. gracilis,* the parastyle and paracone folds being more subdued. The central fossa in each tooth does not parallel the front edge of the tooth (as in MLP 12-1522); rather, it is directed more posteriorly, toward the posterolingual corner of the tooth, mimicking the condition seen in the deciduous premolars of SGOPV 2982.

The second premolar is simple and roughly triangular, with a single elevated external cusp and a very weak parastyle. Its degree of hypsodonty is only modest, with the beginnings of the division into roots being visible at the bases of this tooth on both sides of the specimen. Considerably more trapezoidal (and hence molariform) in outline than P2, P3 is still a rather small tooth. A very faint indication of the metacone is present, and the parastyle is enlarged over the condition on P2. The fourth upper premolar is basically an enlarged, transversely expanded version of P3. As on the preceding premolars, the parastylar fold and paracone column are not strongly expressed on the tooth's buccal face. Tapering at the tooth's base indicates a fairly low degree of hypsodonty, as is also the case on P2–3 and M1. A pronounced groove separates the protocone and hypocone along the internal face of M1 and M2; only a faint indication of this structure occurs on M3. The third molar is also distinctive in bearing a narrow parastylar column which projects off its anterolabial corner.

DISCUSSION—Although SGOPV 3065 has fewer preserved teeth than SGOPV 2998 and displays occlusal morphology less clearly than SGOPV 5007, it is selected as the holotype because it ex-

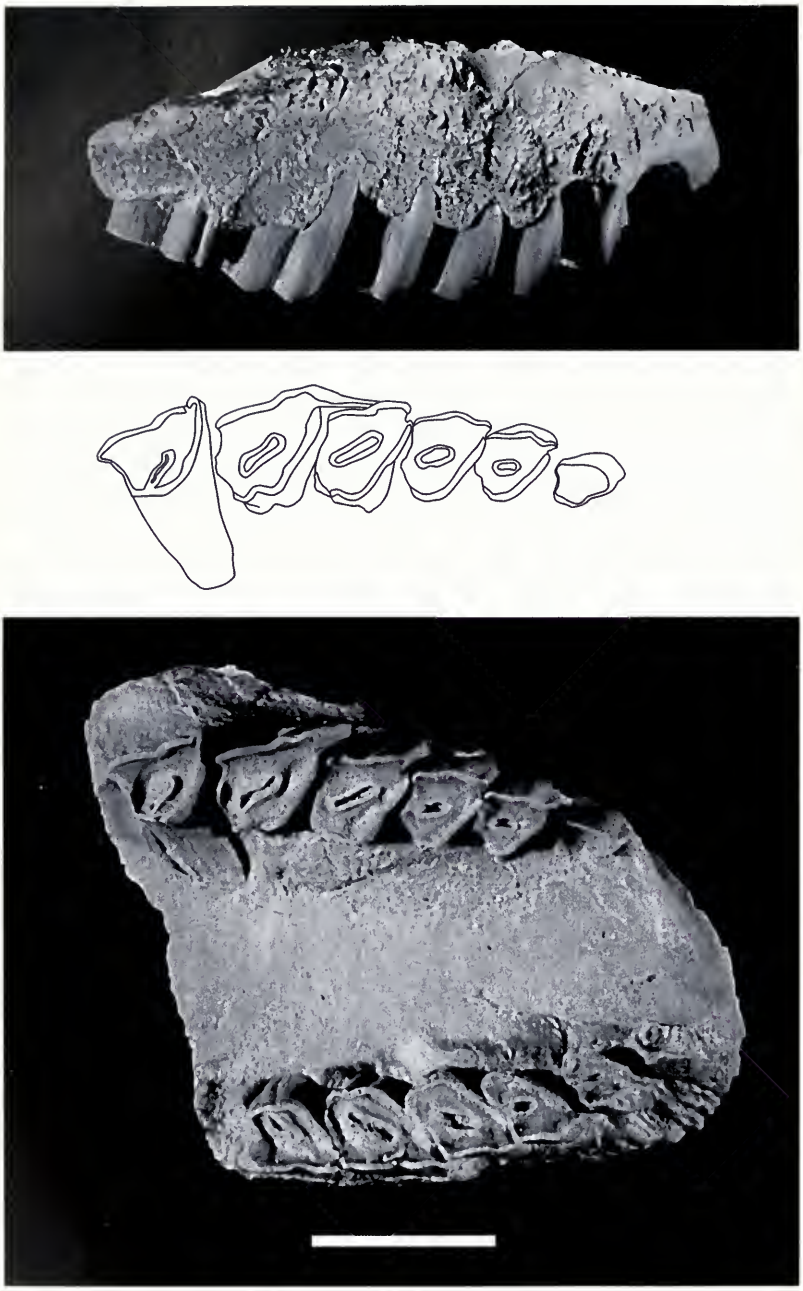

FIG. 7. Epoxy cast and line drawing of specimen from the Tinguiririca Fauna of Chile referred to *Protarchaeohyrax intermedium* (gen. et sp. nov.). Partial palate (SGOPV 2998), with left and right P2–M3, right lateral (upper photograph) and occlusal (line drawing—right side only, and lower photograph) views. Anterior is to the right in all views. Scale bar = 10 mm.

hibits the distinctive mandibular morphology readily distinguishing this taxon from *P. gracilis*. The small size of this taxon relative to *P. gracilis* is most immediately apparent from SGOPV 5007: although its tooth row length is similar to SGOPV 2954 (*P. gracilis*), its teeth are only about 75% as wide. Lower cheek tooth width in *P. intermedium* approaches that of smaller specimens assigned

above to *P. gracilis* (e.g., MLP 12-1518), but the tooth row of the former is shorter (combined p3–m2 length is approximately 17.5 mm in SGOPV 3089h, versus 20.4 mm in MLP 12-1522). This species is listed as "Archaeohyracidae, New taxon A2" in Flynn et al. (2003, tables 1 and 2).

Temporal Correlation and Conclusions

Dating of mammal-bearing sediments at Salla, Bolivia (MacFadden et al., 1985) highlighted a substantial hiatus between the Deseadan and Mustersan SALMAs. In hindsight, we now know that Roth and the Ameghinos uncovered the earliest evidence, long overlooked, of a post-Mustersan, pre-Deseadan faunal interval, but the significance of these early finds did not come into focus until discovery of the Tinguiririca Fauna in central Chile. Thus the Tinguirirican SALMA appears to be recorded at two other locations in southern South America, Cañadón Blanco (Chubut, Argentina), and a horizon ("Astraponotéen plus supérieure") at the Gran Barranca (Chubut, Argentina), the latter of which merits additional comment here. Several specimens referred to *P. gracilis* above, collected by Carlos Ameghino between 1896 and 1899 and published by his brother (Ameghino, 1901, 1902), likely pertain to this interval. Although exact horizons cannot be determined with current data, there are strong indications that these specimens were collected from levels distinctly above those containing typical Casamayoran or Mustersan fossils at Gran Barranca. First, C. Ameghino's handwritten labels for some archaeohyracid specimens described in this paper variously read "Colhuapi Astraponotense más superior" [Astraponotéen plus supérieur—APS—in F. Ameghino's French] or "Colhuapi *Notostylops* (parte sup.)." Colhuapi alludes to the Gran Barranca, and ("más superior/parte sup.") indicates that they were derived from *above* the typical *Notostylops* (Casamayoran) or *Astraponotus* (Mustersan) beds. Although C. Ameghino did not provide precise stratigraphic information, it would appear that he applied different names to the same horizon to reflect which fossils he collected immediately below the ones in question. Thus, several fossils labeled by him as "*Notostylops* (part. sup.)" may actually derive from the same level as those recorded from the "Astraponotense más superior." Perhaps the clearest indication of this is that many of the fossils labeled in these two different ways are indistinguishable (including "*Eohegetotherium priscum*" and "*Archaeohyrax sulcidens*"). At the same time, these fossils are unmistakably distinct from those of the Casamayoran and Mustersan SALMAs. Nevertheless, F. Ameghino never fully elaborated or formally recognized this faunal interval.

One of Simpson's measured stratigraphic sections at Gran Barranca, his profile M (Cifelli, 1985), may coincide with where Carlos Ameghino recovered the specimens just mentioned. Simpson collected three notohippid specimens from this interval, *Eomorphippus obscurus* (AMNH 29462, Field No. 146, "Pink beds just under Upper Channel at 'M'") and ?*Eomorphippus pascuali* (AMNH 29405, Field No. 147, "Under Upper Channel beds at 'M'," and AMNH 29474, Field No. 148, "Upper Channel beds at 'M'"), all of considerable biostratigraphic significance. Cifelli (1985: 9) noted that the notohippids collected by Simpson at Profile M (Fig. 5, points 16 and 17, Section V, p. 11 of Cifelli, 1985) come from levels "nearly 20 m higher than site 4," the latter of which contains typical Mustersan fossils. A taxon very similar to *E. obscurus* occurs in the Tinguiririca Fauna (Wyss et al., 1994), and *E. obscurus* itself is apparently restricted to the "Astraponotéen plus supérieure" (Bond et al., 1996; Reguero, 1998). The *E. obscurus* holotype, (MACN A-10917), and MACN A-10914 (also *E. obscurus*) are almost certainly from the Gran Barranca. Kay et al. (1999, fig. 1) correlated Simpson's "Upper Channel Series" with horizons (MZ-16.1 to MZ-17) of their profile, just above a basalt $^{40}K/^{40}Ar$ dated at 28.8 ± 0.9 Ma (Marshall et al., 1986). The APS level seems to occur below these horizons (the basalt and the Upper Channel Series) within the Puesto Almendra Member of the Sarmiento Formation (Spalletti & Mazzoni, 1979: 273, fig. 2 therein). Kay et al. (1999) report a pre-Deseadan/post-Mustersan fauna from 3 to 5 m below this basalt.

Additional evidence for the existence of a distinct APS horizon at the Gran Barranca comes from the Italian geologist Egidio Feruglio. Feruglio (1938) collected a few specimens between 81 and 95 m (his locality F31, "Hard, concretionary, cornice-forming tuff, so-called 'tosquillas'") above the "argiles fissilaires" beds or "Tobas de Koluel Kaike." One of these, a notohippid, was referred (Simpson, 1967) to *Pseudostylops subquadratus,* a junior synonym of *Eomorphippus obscurus* (Patterson in Simpson, 1967: 184).

The discovery of fossil mammals in the central Andean Main Range of Chile has vastly improved temporal correlations between post-Neocomian lithostratigraphic units located west of the modern Andean divide with their back arc equivalents in Argentina (well east of the current Andean divide). Chronologic information yielded by these fossils establishes the rough temporal equivalence between the largely volcanic and volcaniclastic series of the Abanico (=Coya-Machalí) Formation with portions of the Sarmiento Formation and related units of Argentina (rather than with the Neuquén Group, as has been assumed traditionally). The archaeohyracids discussed herein constitute an important component of this biochronologically based linkage. Similarly, these archaeohyracid taxa form part of the basis for recognizing a South American Land Mammal "Age" interposed between the Deseadan and Mustersan; this biochronologic interval (the Tinguirirican SALMA) has recently been formalized (Flynn et al., 2003).

Acknowledgments

We thank the Museo Nacional de Historia Natural (Santiago), particularly Daniel Frassinetti, for their long-term support of our Andean work. Reynaldo Charrier generously shared his geological expertise of the area. He, along with Gabriel Carrasco and numerous others, provided invaluable assistance in the field. Mariano Bond contributed greatly through his unparalleled knowledge of notoungulate systematics and nomenclature. Barry Albright, José Bonaparte, Bruce MacFadden, and Rosendo Pascual allowed access to specimens under their care. John Weinstein and Mark Widhalm (FMNH) photographed the specimens, and Karen Nordquist scanned the negatives. Line drawings were executed by Marlene Donnelly. This work would not have been possible without the skill and dedication of Andrew Lehman, Robert Masek, William Simpson, and the late Steve McCarroll, who prepared the exceptionally challenging fossil material. We are grateful to Richard Cifelli for an especially helpful review. Richard Madden and Richard Kay provided valuable discussion, and the former gave a detailed critique. Support for this project was provided by NSF grants DEB-9317943 and DEB 9020213 to J.J.F. and A.R.W., as well as the Hinds Fund and NSF Biodiversity Training Grant (GRT-9355032) from the University of Chicago, and the Paleobiological Fund (D.A.C.). A John Simon Guggenheim Foundation fellowship (J.J.F.) facilitated completion of this paper.

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Speculative reconstruction of an indeterminate archaeohyracid. No postcranial elements have been described.

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