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Large Archaeohyracids (Typotheria, Notoungulata) from Central Chile and Patagonia, Including a Revision of *Archaeotypotherium*

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Large Archaeohyracids (Typotheria, Notoungulata) from Central Chile and Patagonia, Including a Revision of *Archaeotypotherium*

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Abstract

The Tinguiririca Fauna of the Andean Main Range of central Chile is remarkable for its abundant and diverse archaeohyracids. This study recognizes four relatively large-bodied species from the Tinguiririca Fauna, two of which are new. Together with two previously described small-bodied forms, the total of six species makes the archaeohyracid assemblage from Tinguiririca the most diverse known, representing the co-occurrence of at least 40% of all archaeohyracid species in a single fauna. The two new archaeohyracids are referred to *Archaeotypotherium* (*A. tinguiriricaense* and *A. pattersoni*), for which a revised diagnosis also is presented. The revision synonymizes the Argentine taxa *Archaeohyrax propheticus, Archaeotypotherium transitum,* and *Archaeohyrax* ("*Bryanpattersonia*") *nesodontoides* under *Archaeotypotherium propheticus* (new combination). Four specimens from central Chile, including three mandibular fragments and one partial upper dental series, are referred to the two existing species of *Pseudhyrax.* The upper dental series is one of the best examples known for the taxon, and is referred to *Pseudhyrax* cf. *P. eutrachytheroides.* Based on a metric study of *Pseudhyrax* specimens from Argentina, one of the Chilean mandibles is referred to *Pseudhyrax eutrachytheroides,* one to *Pseudhyrax strangulatus,* and a third to *Pseudhyrax* sp. indet. Analysis of a large sample of *Archaeohyrax* specimens from Salla, Bolivia, provides the basis for interpreting wear-related metric variation in archaeohyracid tooth dimensions. It demonstrates that most cheek teeth decrease in length and increase in width through increasing wear, although upper and lower third molars are exceptions. Owing to the dramatic metric and morphologic differences between worn and unworn archaeohyracid teeth, care should be taken when interpreting the systematic significance of metric differences among specimens of different wear states. A preliminary phylogenetic analysis suggests that taxa traditionally included in the Archaeohyracidae do not form a monophyletic group exclusive of Hegetotheriidae and that a comprehensive review of the names associated with major clades of typothere notoungulates is needed.

Introduction

Despite the rich Cenozoic record of South American fossil mammals, significant gaps punctuate the sequence of South American Land Mammal "Ages" (SALMAs; Flynn & Swisher, 1995). Until recently, faunas between the well-known Mustersan (late Eocene) and Deseadan (mid- to late Oligocene) SALMAs were not known or recognized as such (Wyss et al., 1990, 1994). In 1988, a small prospecting team from our research group (see Novacek, 2002) discovered the first specimens of a diverse fossil assemblage in central Chile, later known as the Tinguiririca Fauna (Novacek et al., 1989; Wyss et al., 1990, 1994, 1996; Flynn & Wyss, 1990, 1999; Charrier et al., 1990, 1996; Wyss & Flynn, 1991; Flynn et al., 1991, 2003; Wyss, Flynn, et al., 1992; Wyss, Nor-

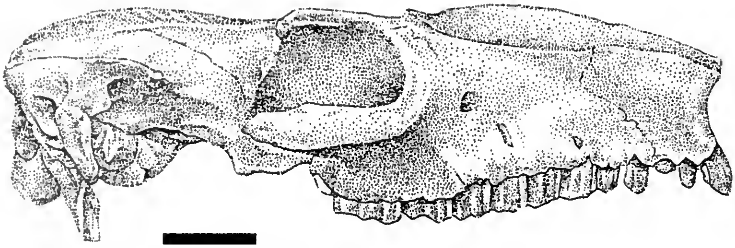

FIG. 1. MACN A52-617, holotype of *Archaeohyrax patagonicus,* left side of skull, viewed as right (adapted from Ameghino, 1897). Scale bar = 1 cm.

ell, et al., 1992; Wyss, Flynn, et al., 1993; Wyss, Norell, et al., 1993). Subsequent studies have revealed that the Tinguiririca Fauna helps fill this long and important late Eocene–early Oligocene gap in the SALMA sequence and provides important evidence regarding the response of South American mammal faunas to the worldwide cooling event and environmental transformation known as the Eocene-Oligocene Transition (Flynn & Wyss, 1998; Flynn et al., in press). Additionally, it has clarified the interpretation of several other faunas from Argentina that were previously regarded as Mustersan in age or mixtures of separate Casamayoran, Mustersan, and Deseadan faunas (Wyss et al., 1994; Bond et al., 1996; Bond, López, et al., 1997; Bond, Reguero, et al., 1997; Reguero, 1998; Hitz et al., 2000; Flynn et al., 2003; Reguero et al., 2003).

We have presented robust evidence elsewhere that the Tinguiririca Fauna from Chile represents a new SALMA (e.g., Wyss et al., 1990, 1994; Wyss, Flynn, et al., 1993). This biochronologic interval was informally referred to as New SALMA ("Tinguirirican") in the SALMA chronology of Flynn and Swisher (1995) and is named and defined formally as a new SALMA, the Tinguirirican, in Flynn et al. (2003). The stratotype sequence for this SALMA assemblage is a composite section representing the basal Abanico (=Coya-Machalí) Formation near Termas del Flaco, in the upper Río Tinguiririca valley, Chile (Charrier et al., 1996; Flynn et al., 2003), with correlative assemblages in Argentina, including those from the "Astraponotéen plus supérieur" ("APS") of the Gran Barranca, Chubut (see Bond et al., 1996; Bond, Reguero, et al., 1997; Reguero, 1998; Kay et al., 1999; Hitz et al., 2000). Levels in the stratotype producing the Tinguiririca Fauna have yielded high-precision ^{40}Ar/^{39}Ar radioisotopic dates, as have underlying nonfossiliferous beds, indicating that the fauna is at least 31.5 Ma in age, spanning a range potentially as large as 31.5–37.5 Ma or more (spanning the Eocene-Oligocene transition). Various lines of evidence suggest that it might be only of very short duration (possibly less than 2 m.y. and entirely earliest Oligocene, ~31–33 Ma; Flynn et al., in press.). Horizons unconformably bracketing the correlative Tinguirirican "APS" faunas in the Gran Barranca of Argentina have yielded radioisotopic dates and paleomagnetic stratigraphies, including a K-Ar date of 28.8 ± 0.9 Ma (Marshall et al., 1986) above and 36–38.5 Ma below (Kay et al., 1999; see also Flynn & Swisher, 1995 and Flynn et al., 2003).

The abundance and diversity of its archaeohyracid assemblage are among the most distinctive features of the Tinguiririca Fauna (Wyss, Norell, et al., 1993; Wyss et al., 1994; Croft, 1998, 2000; Reguero et al., 2003; Flynn et al., 2003). At least six archaeohyracid species occur at Tinguiririca (40% of all currently recognized archaeohyracid species), the greatest diversity of archaeohyracids known from a single fauna. These six taxa include two new species of *Protarchaeohyrax* (Reguero et al., 2003), two new species of *Archaeotypotherium* (present study), and two previously described species of *Pseudhyrax* (Simpson, 1967). Based on the new material from the Tinguiririca Fauna and detailed comparative studies of Argentine specimens, revised diagnoses of both *Archaeotypotherium* and *Pseudhyrax* are presented here.

The Archaeohyracidae was named by Ameghino in 1897 and placed in the Hyracoidea, an otherwise Old World group. He based *Archaeohyrax,* and his taxonomic placement of the group, on the type specimen of *Archaeohyrax patagonicus* (MACN A52-617), an excellent skull and mandibles from the Deseadan SALMA of Chubut, Argentina (Fig. 1). Although Ameghino believed the Archaeohyracidae to be allied with hyraxes, most other early workers (e.g., Sinclair, 1909; Loomis, 1914) recognized that archaeohyracids (and other typotheres) were members of the endemic South American group Notoungulata. George Gaylord Simpson's views on the taxonomic position of the Archaeohyracidae changed during the course of his studies. In his landmark classification of mammals (Simpson, 1945), he placed the Archaeohyracidae in the Toxodontia (contra Sinclair, 1909), but later allied them with the hegetotheriids in the Hegetotheria (Simpson, 1967). Although some studies have suggested that hegetotheriids are more closely related to mesotheriids than to archaeohyracids (Wyss, Norell, et al., 1993; Croft, 1998), most recent phylogenetic studies have supported the close relationship between archaeohyracids and hegetotheriids (Cifelli, 1993; Hitz, 1995; Reguero, 1998; Croft, 2000).

For many years MACN A52-617 (the holotype of *Archaeohyrax patagonicus*; Fig. 1) was the only archaeohyracid skull known. Until this study, it remained the only one figured and described.[1] As exemplified by MACN A52-617, taxa currently included within the Archaeohyracidae are characterized by a complete (3/3, 1/1, 4/4, 3/3) and essentially closed dentition (lacking significant diastemata), with enlarged and procumbent first incisors and an evenly graded cheek tooth series. The skull is low and broad across the orbits and occiput but narrow across the snout. Archaeohyracids are small- to medium-sized mammals; the maximum length of the skull of MACN A52-617 is approximately 15 cm, and Tinguiririca archaeohyracids are estimated to have had body masses between 250 g and 4 kg (Croft, 2000; Flynn et al., 2003). No postcranial bones definitely attributable to the family Archaeohyracidae have yet been described, although currently unprepared specimens are present in the Tinguiririca Fauna.

Until recently, archaeohyracids have been the subject of very few studies. This has been due primarily to the scarcity of archaeohyracid material, even in many well-sampled faunas. The discovery of the Tinguiririca Fauna has renewed interest in this group of notoungulates (Wyss, Norell, et al., 1993; Wyss et al., 1994; Reguero, 1993, 1998; Croft, 1998, 2000; Reguero & López, 1999; Reguero et al., 2003), as has continued collecting in the archaeohyracid-rich Deseadan Salla Beds of Bolivia (MacFadden et al., 1985; Shockey, 1997; Reguero & Cifelli, 1997). The present study strives to clarify some of the taxonomy and nomenclature of the Archaeohyracidae as a basis for future comprehensive studies on the phylogeny, biogeography, biochronology, and paleobiology of the group.

Taxonomic Notes

Most recent phylogenetic analyses suggest that the Archaeohyracidae (as that name is currently employed) represents a paraphyletic assemblage of taxa closely related to hegetotheriids (Cifelli, 1993; Hitz, 1995; Croft, 1998, 2000; Reguero, 1999; see also the phylogenetic analysis below). However, the relationships among archaeohyracids and hegetotheriids have yet to be rigorously tested. Because the term Archaeohyracidae is familiar to South American paleomammalogists, and because no one has proposed a phylogenetic definition and/or alternative name for the least inclusive clade encompassing these taxa, we use the terms Archaeohyracidae and archaeohyracids in their traditional sense for the purposes of this publication.

Taxonomic names that are potentially invalid due to synonymy (e.g., "*Archaeohyrax concentricus*") are indicated through the use of quotation marks.

Abbreviations

AMNH, American Museum of Natural History, New York; MLP, Museo de La Plata, Argentina; SGOPV, vertebrate paleontology collections, Museo Nacional de Historia Natural, Santiago; MACN, Museo Argentino de Ciencias Naturales, "Bernardino Rivadavia," Buenos Aires; APS, "Astraponotéen plus supérieur"; CV, coefficient of variation; FA, first occurrence; HI, hypsodonty index (height of unworn tooth/length of tooth); K, potassium; Ar, argon; Ma, megannum; m.y., millions of years; mm, millimeter; cm, centimeter; g, gram; kg, kilogram; SALMA, South American Land Mammal "Age." Upper tooth loci are indicated by uppercase letters (e.g., I1, P2, M1) and lower tooth loci by lowercase letters (e.g., i1, p2, m1); deciduous teeth are indicated by a "d/D" preceding the tooth position.

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[1] Other skulls are known from both the Tinguiririca Fauna (Tinguirirican SALMA) and Salla, Bolivia (Deseadan SALMA).

TABLE 1. Measurements of upper and lower teeth of *Archaeohyrax* sp. nov. (Reguero & Cifelli, 1997) from the Deseadan SALMA deposits at Salla, Bolivia. Measurements are made to the nearest 0.1 mm. Coefficient of variation (CV) = 100 × (standard deviation/mean).

	P3		P4		M1		M2		M3	
Upper dentition	L	W	L	W	L	W	L	W	L	W
All teeth	(n = 13)	(n = 13)	(n = 16)	(n = 16)	(n = 22)	(n = 22)	(n = 23)	(n = 23)	(n = 14)	(n = 14)
Mean ± SD	5.4 ± 0.5	5.5 ± 0.7	5.9 ± 0.7	5.9 ± 0.8	7.3 ± 1.2	6.3 ± 0.8	8.8 ± 0.8	6.3 ± 0.6	10.6 ± 1.4	5.4 ± 0.8
Range	4.5–6.3	4.7–6.6	4.6–7.4	4.7–6.9	5.8–10.7	4.8–7.3	7.3–9.9	5.1–7.2	8.3–13.0	4.4–7.0
Range (% of mean)	83%–117%	85%–120%	78%–125%	80%–117%	79%–147%	76%–116%	83%–113%	81%–114%	78%–123%	81%–130%
CV	9.3	12.7	11.9	13.6	16.4	12.7	9.1	9.5	13.5	14.2
Little wear	(n = 0)	(n = 0)	(n = 0)	(n = 0)	(n = 2)	(n = 2)	(n = 6)	(n = 6)	(n = 2)	(n = 2)
Mean ± SD	—	—	—	—	10.5 ± 0.3	5.0 ± 0.3	8.8 ± 0.7	5.9 ± 0.5	8.8 ± 0.7	4.5 ± 0.1
Range	—	—	—	—	10.3–10.7	4.8–5.2	7.9–9.6	5.1–6.5	8.3–9.3	4.4–4.6
Range (% of mean)	—	—	—	—	98%–102%	96%–104%	90%–109%	86%–110%	94%–106%	98%–102%
CV	—	—	—	—	2.9	6.0	8.0	9.2	8.5	2.2
Moderate wear	(n = 3)	(n = 3)	(n = 6)	(n = 6)	(n = 6)	(n = 6)	(n = 9)	(n = 9)	(n = 4)	(n = 4)
Mean ± SD	5.9 ± 0.4	5.5 ± 0.8	6.6 ± 0.6	5.9 ± 0.9	7.6 ± 0.6	6.3 ± 0.6	9.2 ± 0.6	6.4 ± 0.5	10.0 ± 0.7	5.4 ± 0.7
Range	5.5–6.3	5.1–6.4	5.7–7.4	4.7–6.9	6.8–8.3	5.6–7.0	8.0–9.9	5.4–7.0	9.3–10.8	4.7–6.1
Range (% of mean)	93%–107%	93%–116%	86%–112%	80%–117%	89%–109%	89%–111%	87%–108%	84%–109%	93%–108%	87%–113%
CV	6.8	14.5	9.1	15.3	7.9	9.5	6.5	7.8	7.0	13.0
Heavy wear	(n = 10)	(n = 10)	(n = 10)	(n = 10)	(n = 14)	(n = 14)	(n = 8)	(n = 8)	(n = 8)	(n = 8)
Mean ± SD	5.3 ± 0.5	5.5 ± 0.7	5.4 ± 0.4	5.9 ± 0.7	6.7 ± 0.4	6.4 ± 0.7	8.3 ± 0.8	6.3 ± 0.7	11.3 ± 1.3	5.7 ± 0.8
Range	4.5–6.2	4.7–6.6	4.6–5.9	4.8–6.7	5.8–7.4	5.2–7.3	7.3–9.6	5.4–7.2	9.4–13.0	4.9–7.0
Range (% of mean)	85%–117%	85%–120%	85%–109%	81%–114%	87%–110%	81%–114%	88%–116%	86%–114%	83%–115%	86%–123%
CV	9.4	12.7	7.4	11.9	6.0	10.9	9.6	11.1	11.5	14.0

	p3		p4		m1		m2		m3	
Lower dentition	L	W	L	W	L	W	L	W	L	W
	(n = 21)	(n = 21)	(n = 36)	(n = 36)	(n = 49)	(n = 49)	(n = 45)	(n = 45)	(n = 31)	(n = 31)
Mean ± SD	5.4 ± 0.8	4.1 ± 0.3	5.9 ± 0.8	4.5 ± 0.5	6.8 ± 0.7	4.7 ± 0.5	7.8 ± 0.7	4.4 ± 0.5	11.3 ± 1.4	4.0 ± 0.3
Range	4.4–7.1	3.6–4.6	4.7–8.4	3.5–5.6	5.6–8.1	3.8–5.9	5.9–9.4	3.6–5.2	8.6–14.7	3.4–4.5
Range (% of mean)	81%–131%	88%–112%	80%–142%	78%–124%	82%–119%	81%–126%	76%–121%	82%–118%	76%–130%	85%–113%
CV	14.8	7.3	13.6	11.1	10.3	10.4	9.0	11.4	12.4	7.5
Little wear	(n = 2)	(n = 2)	(n = 7)	(n = 7)	(n = 11)	(n = 11)	(n = 24)	(n = 24)	(n = 10)	(n = 10)
Mean ± SD	7.0 ± 0.1	4.0 ± 0.1	6.8 ± 0.9	3.9 ± 0.3	7.7 ± 0.4	4.2 ± 0.2	7.9 ± 0.5	4.2 ± 0.4	10.4 ± 1.2	3.8 ± 0.3
Range	6.9–7.1	3.9–4.1	5.8–8.4	3.5–4.4	7.0–8.1	3.8–4.5	7.0–9.4	3.6–5.0	8.6–12.0	3.5–4.3
Range (% of mean)	99%–101%	98%–102%	85%–124%	90%–113%	91%–105%	90%–107%	89%–119%	86%–119%	83%–115%	92%–113%
CV	1.4	2.5	13.2	7.7	5.2	4.8	6.3	9.5	11.5	7.9

TABLE 1. *Continued.*

Lower dentition	p3		p4		m1		m2		m3	
	L	W	L	W	L	W	L	W	L	W
Moderate wear	(n = 5)	(n = 5)	(n = 9)	(n = 9)	(n = 15)	(n = 15)	(n = 7)	(n = 7)	(n = 8)	(n = 8)
Mean ± SD	5.5 ± 0.2	4.0 ± 0.4	6.1 ± 0.6	4.2 ± 0.5	7.0 ± 0.5	4.6 ± 0.3	7.9 ± 0.7	4.7 ± 0.5	12.1 ± 1.5	4.2 ± 0.4
Range	5.4–5.9	3.7–4.6	5.2–7.2	3.6–4.9	6.4–7.9	4.1–5.1	7.0–9.0	3.8–5.2	9.8–14.7	3.4–4.5
Range (% of mean)	98%–107%	93%–115%	85%–118%	86%–117%	91%–113%	89%–111%	89%–114%	81%–111%	81%–121%	81%–107%
CV	3.6	10	9.8	11.9	7.1	6.5	8.9	10.6	12.4	9.5
Heavy wear	(n = 14)	(n = 14)	(n = 20)	(n = 20)	(n = 23)	(n = 23)	(n = 14)	(n = 14)	(n = 13)	(n = 13)
Mean ± SD	5.1 ± 0.7	4.1 ± 0.3	5.4 ± 0.5	4.8 ± 0.4	6.2 ± 0.5	5.1 ± 0.5	7.7 ± 0.8	4.5 ± 0.4	11.5 ± 1.3	4.0 ± 0.3
Range	4.4–7.1	3.6–4.5	4.7–6.8	4.0–5.6	5.6–7.2	3.9–5.9	5.9–9.0	4.0–5.1	9.4–13.5	3.6–4.4
Range (% of mean)	86%–139%	88%–110%	87%–126%	83%–117%	90%–116%	76%–116%	77%–117%	89%–113%	82%–117%	90%–110%
CV	13.7	7.3	9.3	8.3	8.1	9.8	10.4	8.9	11.3	7.5

Tooth Wear and Dental Measurements

The early attainment of hypsodonty (the presence of high-crowned teeth) is one of the most distinctive features of the Archaeohyracidae. Indeed, archaeohyracids are among the—if not *the*—earliest notoungulates to exhibit this feature, although the Casamayoran *Eohyrax* is certainly much less hypsodont than later archaeohyracids. Associated with increased hypsodonty is an increasingly dramatic difference in size and shape of the occlusal surface between unworn and heavily worn teeth within a given species; relatively low-crowned archaeohyracids (e.g., *Eohyrax*) demonstrate this phenomenon only to a minor extent, but extremely hypsodont taxa (e.g., *Archaeohyrax*) display significant differences between newly erupted and heavily worn teeth. Such wear-related changes make it difficult to accurately describe and diagnose archaeohyracid taxa in the absence of a large sample that includes specimens in varying stages of wear. Unfortunately, archaeohyracids are rare in most faunas, making such extensive collections uncommon. A conspicuous exception is the Deseadan-aged fauna from Salla, Bolivia. In contrast to Deseadan faunas from Patagonia, archaeohyracids are among the most common taxa at Salla (MacFadden et al., 1985; Reguero & Cifelli, 1985), thus permitting studies requiring large sample sizes. Although archaeohyracid specimens are numerous in the Tinguiririca Fauna, the extremely hard matrix has greatly limited the number of specimens that have been prepared and thus are presently available for study. Each of the Tinguiririca taxa described below is represented by only a small number of specimens, and consequently it has not been possible to document wear-related metric and morphologic variation directly. Instead, we apply an estimate of the expected range of variation with wear for individuals within a single species, based on an analysis of the extensive material from Bolivia.

To estimate the amount of dental variation expected within a single Tinguiririca archaeohyracid species, metric changes were investigated using a large sample (71 mandibular and 34 maxillary fragments) of *Archaeohyrax* sp. nov. (Reguero & Cifelli, 1997) from Salla, Bolivia. Each tooth was measured to the nearest 0.1 mm using digital calipers and was assigned to one of three wear stages: little wear (central fossa not yet isolated), moderate wear (central fossa completely isolated), or heavy wear (central fossa absent; featureless occlusal surface). Although division of tooth wear into a greater number of stages would have been desirable, the morphology of the teeth was such that this could not have been done in an objective way without a more detailed study of the dentition of this undescribed species (currently underway by one of us [M.R.] and R. Cifelli). Moreover, these three categories can be generalized to other archaeohyracids without having to worry about differences in hypsodonty and relative depth of accessory fossettes/fossettids (which could potentially be used to further subdivide wear stages). In addition to individual tooth lengths, molar row lengths were recorded for the Salla *Archaeohyrax* specimens, as well as for a complementary but smaller sample of *Pseudhyrax* specimens from Chubut, Argentina.[2] Upper tooth lengths were measured parallel to, and widths perpendicular to, the ectoloph. Lower tooth lengths were measured parallel to, and widths perpendicular to, the long axis of the tooth. It should be noted that since each tooth is scored for wear individually, some mandibular fragments include teeth of all three wear states. Graphical and statistical procedures were performed using Microsoft Excel 4.0 or StatView 4.1 for the Macintosh computer.

Table 1 lists univariate statistics for all the molars and the last two premolars. The coefficient of variation (CV) was calculated as CV = 100 × (standard deviation/mean), following Gingerich (1974). Values for the entire sample, along with wear stage, are given by tooth position.

Several generalizations can be drawn from the data. Disregarding wear, the coefficients of variation for each tooth position are very high for a single population from a single locality. In most cases, CVs decrease when each wear category is considered separately. Therefore, when comparing metric values from different specimens to determine their taxonomic affinity, it is important to compare specimens displaying similar wear. Even when comparing similarly worn teeth, however, significant variation persists. A tooth 20% larger or smaller than the mean is not unusual, and two teeth may vary by as much as 40% in their dimensions (although the large variation in *Archaeohyrax* sp. nov. may result in part from pooling specimens from different stratigraphic levels within the Salla beds[3]). This has important implications for the use of these sorts of metric values alone to distinguish archaeohyracid species (see recommendations below).

The data also demonstrate that as teeth undergo wear, they generally become shorter (mesiodistally) and wider (buccolingually). The relationship between tooth wear and tooth shape is most easily seen in bivariate plots of tooth length and width for upper and lower first molars (Fig. 2). The M1–2 and m1–2 become shorter and broader with increasing wear. Accordingly, in comparing specimens of unequal wear, if the longer one is more worn, it is more likely that these differences reflect taxonomic rather than individual (species or ontogenetic) variation; the reverse is true when the longer tooth is less worn, since it can be inferred that it would shorten with additional wear. Upper and lower third molars do not follow this trend (Fig. 3); upper third molars increase in length with wear, and whereas the plot for lower third molars suggests a similar trend may exist, the large amount of overlap among wear categories precludes useful differentiation.

Finally, molar row lengths (M/m1–3) tend to be less variable than individual tooth lengths (Table 2). *Archaeohyrax* specimens from Salla and specimens of *Pseudhyrax* from Chubut both have small molar row length CVs (<10), with nearly all specimens (28 out of 30 *Archaeohyrax* specimens, all *Pseudhyrax* specimens) varying within 10% of the mean. Two factors might contribute to this lower variability. One possibility is that measuring tooth-row lengths tends to "average out" wear-related size differences between teeth. Specimens with the molars in different wear stages (due to different eruption times) are common, while specimens having either all unworn or entirely heavily worn molars are rare. Thus, comparisons between the extremes of the wear spectrum are much less common for molar rows than for individual teeth. Also, as noted previously, because third molars tend to lengthen with wear, this may offset some of the shortening associated with wear in the more anterior molars. Regardless of the precise cause, this study documents that molar row lengths are less variable than individual tooth lengths and should be used whenever possible in taxonomic studies. This is especially true for more hypsodont archaeohyracids, as suggested by the

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[2] Individual tooth lengths were also recorded for the *Pseudhyrax* specimens but are not included in the present study due to the small sample size.

[3] Testing for the effects of stratigraphic level on size was precluded by the lack of stratigraphic data for the majority of specimens measured.

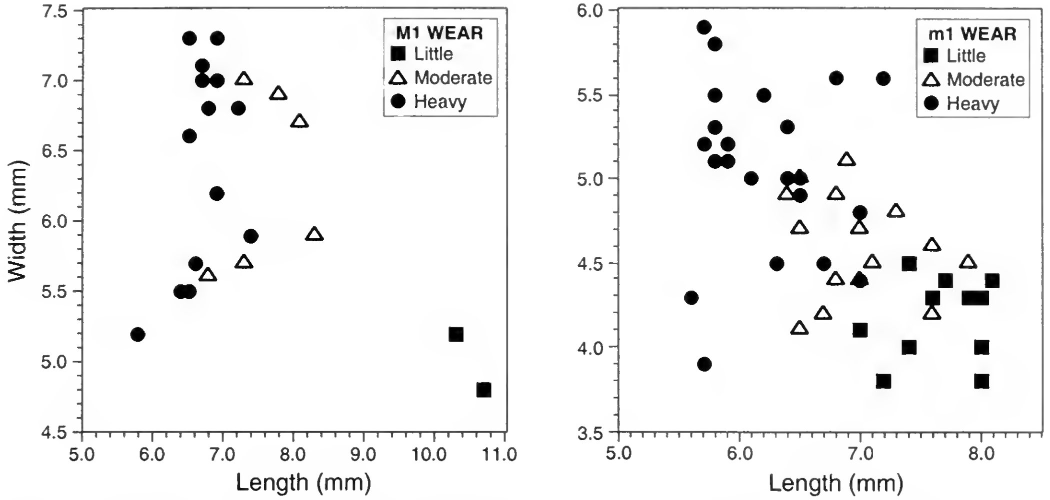

FIG. 2. Bivariate plots of upper and lower first molars, sorted by wear, from specimens of *Archaeohyrax* sp. nov. (Reguero & Cifelli, 1997) from the Deseadan SALMA deposits at Salla, Bolivia.

smaller CV for *Pseudhyrax* molar rows as compared to *Archaeohyrax* lower molar rows. *Pseudhyrax,* with lower CVs, is moderately high-crowned, whereas *Archaeohyrax* sp. nov., with its much higher CVs, represents maximum hypsodonty for the Archaeohyracidae (and therefore probably exhibits maximum variation in metric values with wear).

Based on the above observations, we recommend that (in the absence of other corroborating morphologic distinctions), whenever possible, only tooth rows of similar wear be compared when attempting to distinguish between morphologically similar archaeohyracids (or other notoungulates with hypsodont, but rooted, cheek teeth) using size alone. Where such comparisons of linear tooth-row measures are possible, the larger taxon should exceed the smaller by at least 10%. If only individual molars are available for comparison, then the larger should exceed the smaller by at least 30%. If only isolated first or second molars of different wear states are available for comparison, then the larger should exceed the smaller by 50% if it is the less worn, and by

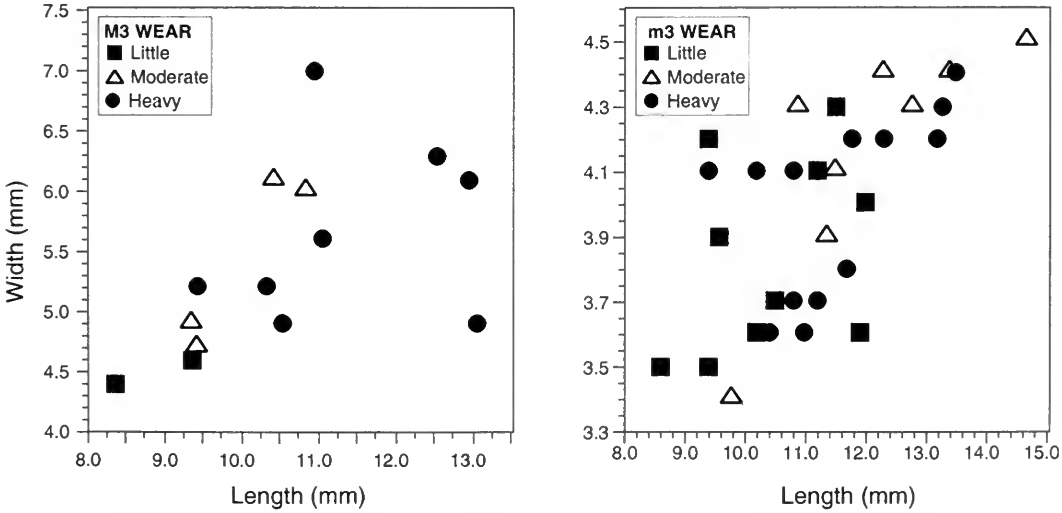

FIG. 3. Bivariate plots of upper and lower third molars, sorted by wear, from specimens of *Archaeohyrax* sp. nov. (Reguero & Cifelli, 1997) from the Deseadan SALMA deposits at Salla, Bolivia.

TABLE 2. Measurements of molar row lengths for specimens of *Archaeohyrax* sp. nov. (Salla, Bolivia; Deseadan SALMA) and *Pseudhyrax* species (Chubut, Argentina; Mustersan SALMA). Measurements are made to the nearest 0.1 mm. Coefficient of variation (CV) = 100 × (standard deviation/mean).

	Salla *Archaeohyrax*		**Chubut *Pseudhyrax***
	M1–3 (n = 11)	**m1–3 (n = 19)**	**m1–3 (n = 5)**
Mean ± SD	25.0 ± 1.3	26.0 ± 1.8	30.8 ± 0.8
Range	22.3–26.8	23.2–29.7	30.0–31.8
Range (% of mean)	89%–108%	89%–114%	97%–103%
CV	5.1	6.9	2.6

15% if it is the more worn; this should be reversed for isolated M3s (i.e., the difference should be greater if the larger specimen is the more worn, less if it is the less worn). Individual lower third molars of different wear states should differ by at least 30%.

Systematic Paleontology

Mammalia Linnaeus, 1758
Notoungulata Roth, 1903
Typotheria Zittel, 1892
Hegetotheria Simpson, 1945
Archaeohyracidae Ameghino, 1897

Archaeotypotherium Roth, 1903

Archaeohyrax Ameghino, 1897 (partim): 435.
Archaeohyrax Ameghino, 1901 (partim): 361–362.
Eomorphippus Ameghino, 1901 (partim): 373.
Bryanpattersonia Simpson, 1967 (partim): 115.

TYPE SPECIES—*Archaeotypotherium transitum* Roth, 1903, here regarded as a junior synonym of *Archaeotypotherium propheticus* (Ameghino, 1897).

COMMENTS—*Archaeotypotherium transitum* was recognized by Roth (1903) on the basis of a maxillary fragment from Cañadón Blanco, in Chubut, Argentina. (For a discussion of this enigmatic locality, see Wyss et al., 1994; Flynn et al., 2003.) Although this taxon was ignored by most subsequent authors, we recognize it here as distinct from all other described archaeohyracids, consistent with Roth's view. Moreover, we consider the various specimens/species previously allocated to *Archaeohyrax, Eomorphippus,*[4] and *Bryanpattersonia* as more properly included in *Archaeotypotherium.* These specimens/species all appear to be conspecific, and the name *Archaeotypotherium propheticus* has chronologic priority. Given the temporal congruence of the specimens referred to *Archaeotypotherium* (Wyss et al., 1994; Flynn et al., 2003; see also Reguero, 1993, 1998; Bond et al., 1996; Kay et al., 1999; Hitz et al., 2000), this synonymy is not surprising.

INCLUDED SPECIES—The type, *Archaeotypotherium tinguiriricaense* (new species, below), and *Archaeotypotherium pattersoni* (new species, below).

DIAGNOSIS—A member of the Hegetotheria that differs from Hegetotheriidae in the absence of hypselodont (ever-growing) cheek teeth, absence of hypselodont I1, absence of straight lingual face on lower molars, presence of fossettes/fossettids at some stages of wear in upper and lower molars, and presence of significant change in cheek tooth occlusal shape with wear. Differs from *Archaeohyrax* in its lower-crowned cheek teeth (newly erupted teeth are rooted in *Archaeotypotherium,* unrooted in *Archaeohyrax*; HI = 1.75–2.25 in *Archaeotypotherium,* HI > 2.5 in *Archaeohyrax*), relatively larger I1, less triangular upper molars, more elongate central fossae on upper and lower molars, larger lower premolars, more persistent accessory fossettes/fossettids on upper and lower molars, M3 without posterior lobe formed by metastyle, m3 proportionately shorter, and labial sulcus on m3 talonid less pronounced. Differs from *Protarchaeohyrax* by more persistent accessory fossettes/fossettids on upper and lower molars, absence of lingual sulcus on uppers molars, M3 without posterior lobe formed by metastyle, and

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[4] Roth misidentified several specimens of *Archaeotypotherium* as *Eurystomus stehlini,* a junior synonym of *Eomorphippus obscurus* (Simpson, 1967).

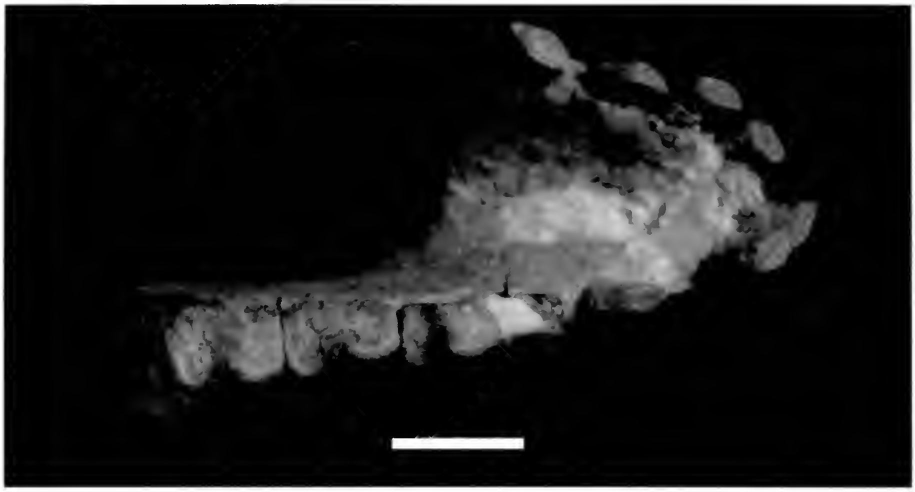


FIG. 4. MACN A52-618, holotype of *Archaeotypotherium propheticus*, mandibular symphysis and portion of right horizontal ramus with right i1–2, c, p2–4 and left i2–3, c, p1, occlusal view (from Ameghino, 1897). Scale bar = 1 cm.

much larger size. Differs from *Pseudhyrax* by higher-crowned cheek teeth (HI = 1.3–1.6 in *Pseudhyrax*), relatively larger I1, less pronounced paracone and parastyle ridges on upper molars, larger lower premolars, and proportionately longer talonids on lower molars. Differs from the new archaeohyracid taxon from Antofagasta de La Sierra (López, 1997; Reguero & López, 1999) by its much larger size, higher-crowned cheek teeth (HI of Antofagasta form similar to that of *Pseudhyrax*), longer molar talonids, and more persistent talonid fossettids. Differs from *Eohyrax* by much higher-crowned cheek teeth (HI < 1.25 in *Eohyrax*) and much larger size.

AGE AND DISTRIBUTION—Earliest Oligocene Tinguirirican SALMA (Flynn et al., 2003) of Patagonia and east-central Chile: Abanico (=Coya-Machalí) Formation, Chile; Cañadón Blanco, presumably the Sarmiento Formation, Chubut, Argentina (Roth, 1903); "Astraponotéen plus supérieur" (APS) horizon of the Sarmiento Formation at the Gran Barranca south of Lake Colhué Huapi, Chubut, Argentina. Horizons bearing the Chilean Tinguiririca Fauna have yielded two high-precision $^{40}Ar/^{39}Ar$ dates near 31.5 Ma (the range of the means and associated errors spanning ~31–32 Ma), and they are underlain by a basalt unit whose upper part also was dated at about 31.5 ± 1.0 Ma. Available radioisotopic dates from horizons bracketing Tinguirirican "APS" levels in the Gran Barranca of Argentina (Kay et al., 1999) are generally congruent with the geochronologic information from Chile.

Archaeotypotherium propheticus **(Ameghino, 1897), new combination**

(Figures 4–6)

Archaeohyrax propheticus Ameghino, 1897: 435.
Archaeohyrax nesodontoides Ameghino, 1901: 361; Simpson, 1967: 113.
Archaeohyrax concentricus Ameghino, 1901: 361–362.
Eomorphippus rutilatus Ameghino, 1901: 373.
Archaeotypotherium transitum Roth, 1903: 22–23.
Bryanpattersonia sp. Simpson, 1967: 115.

HOLOTYPE OF *ARCHAEOHYRAX PROPHETICUS*—MACN A52-618, mandibular symphysis and portion of right horizontal ramus with right i1–2, c, p2–4 and left i2–3, c, p1 (Fig. 4).

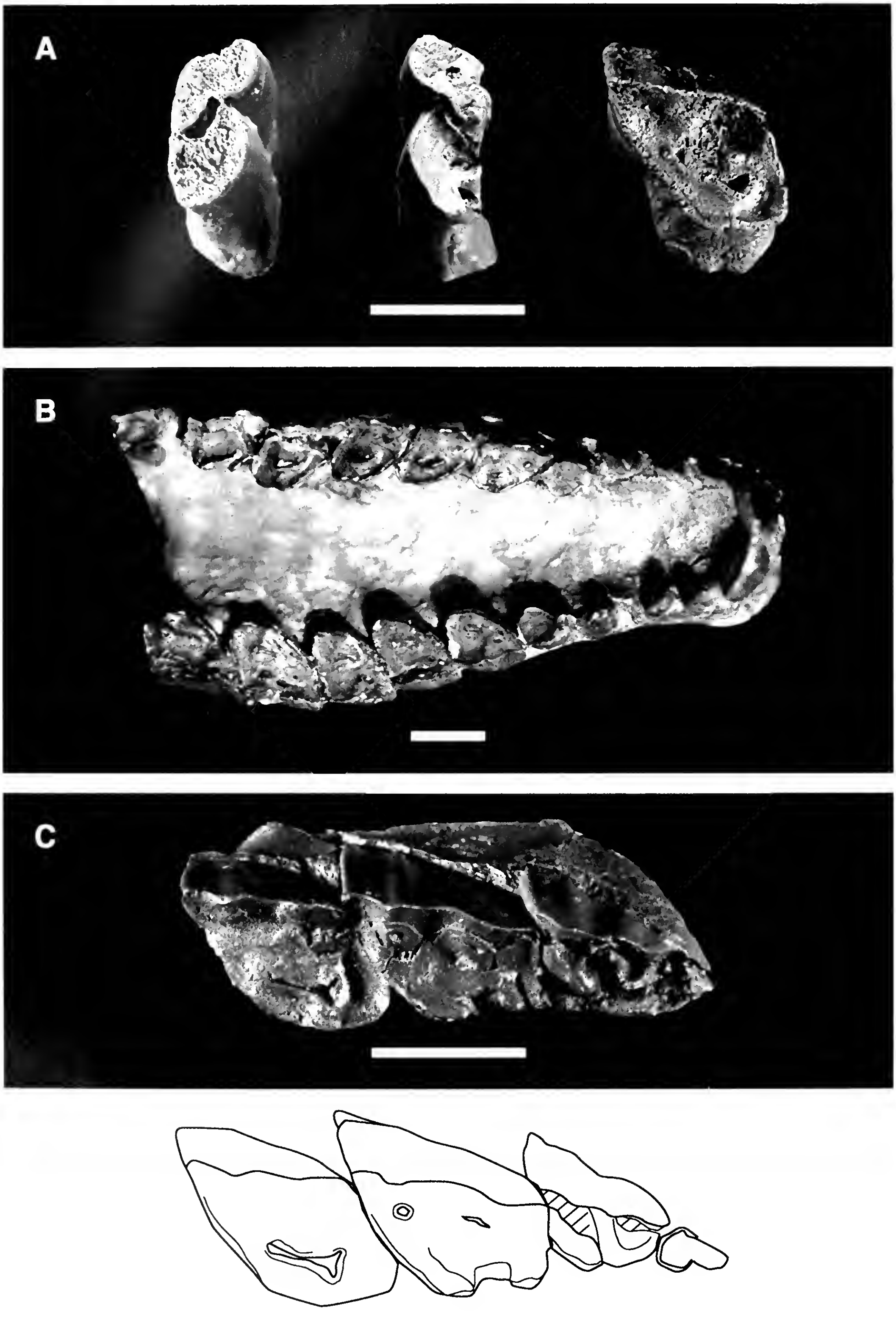
LECTOTYPE OF *ARCHAEOHYRAX NESODONTOIDES*—MACN 10905a, a right m1 measuring 12.2 by 6.3 mm (Fig. 5A).

PARALECTOTYPES OF *ARCHAEOHYRAX NESODONTOIDES*—MACN 10905 (9 isolated lower cheek teeth [catalogued b to j] and 7 isolated upper cheek teeth [catalogued k to q]; selected specimens illustrated in Fig. 5A).

LECTOTYPE OF *ARCHAEOHYRAX CONCENTRICUS*—MACN A52-625, incomplete facial region of skull with left I1–M2 and right I1–M3 (Fig. 5B).

PARALECTOTYPE OF *ARCHAEOHYRAX CONCENTRICUS*—MACN A52-629, left p4.

LECTOTYPE OF *EOMORPHIPPUS RUTILATUS*—MACN 10915, right upper molar.


A
B
C

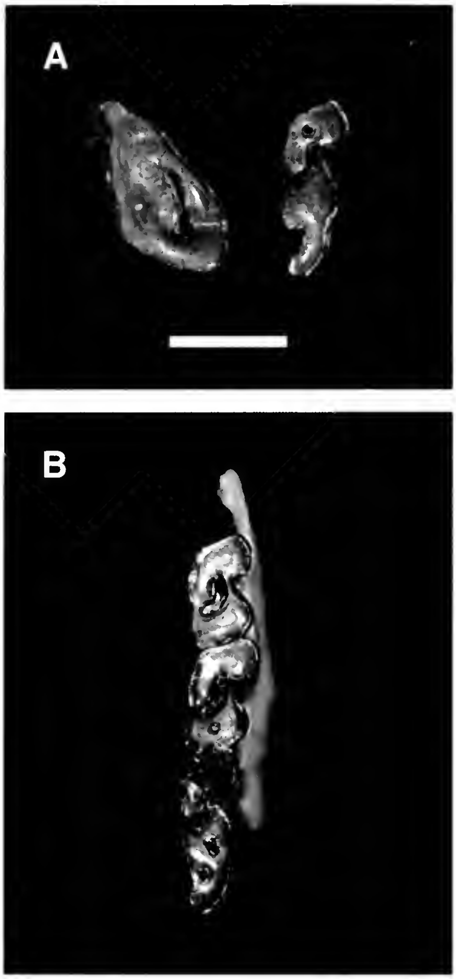


FIG. 6. Specimens included in hypodigm of *Archaeotypotherium propheticus.* **A.** MACN A52-630, right M2 and right m3. **B.** MACN A52-628, partial right mandible with m1–3. Scale bar = 1 cm.

HOLOTYPE OF *ARCHAEOTYPOTHERIUM TRANSITUM*—MLP 12-1524a, left maxilla bearing M1–3 (M3 partially erupted; Fig. 5C).

HYPODIGM—Holotype of *A. propheticus*; all specimens included in junior synonyms above; MACN A52-630, right M2 and right m3 (Fig. 7); MACN A52-628, partial right mandible with m1 (Fig. 6B); AMNH 28943, nearly unworn isolated left M3; AMNH 28955, damaged left P2–M3; MLP 89-XII-21-1 (Roth's Nos. 1414), left M1, left m1, and right m1; MLP 69-III-31-2, right upper molar; MLP 12-1516, left mandible with m1–3.

LOCALITIES—Only one of the type specimens of "*Archaeohyrax concentricus*" (MACN A52-625) is accompanied by a locality label. This label reads "Coluapi *Pyrotherium,*" indicating a ?Deseadan SALMA locality—precisely which one is uncertain—near or at the south end of Gran Barranca, Chubut. Similarly, only a single specimen assigned to "*Archaeohyrax nesodontoides*" (MACN A-10911, perhaps part of the hypodigm for that taxon) has geographic provenience data. The accompanying label reads: "Colhuapi *Notostylops* (parte sup.)," the "parte sup." indicating a level in the Gran Barranca distinct from that where Casamayoran SALMA fossil vertebrates were collected. It appears to correspond to the portion of profile M of Simpson that Bond et al. (1996) correlated with the "Astraponotéen le plus supérieur" of Ameghino (1901). It is not improbable, then, that all of the specimens referred to "*Archaeohyrax nesodontoides*" come from the Gran Barranca. Ameghino's placement of "*A. nesodontoides*" (*Archaeotypotherium propheticus* of this study) and "*A. sulcidens*" (*Protarchaeohyrax gracilis* of Reguero et al., in press) in the "Capas con *Astraponotus*" (Mustersan SALMA; Ameghino 1901, 1902) appears to be incorrect, taking into account the recent stratigraphic data collected from the Gran Barranca by M. Bond and one of the authors (M.R.) and, more recently, by joint Argentine–U.S. teams led by R. Kay. Moreover, at typical Mustersan localities (La Gran Hondonada, Cerro del Humo, and Laguna del Mate), *Pseudhyrax* is the only archaeohyracid present.

The type of *Archaeotypotherium* "*transitum*" (MLP 12-1524a) and MLP 12-1516 come from Cañadón Blanco, Chubut. The former has a label that reads "T.i.C.B.", indicating "Terciario inferior de Cañadón Blanco" ("Formación terciaria inferior, Cañadón Blanco [Territorio del Chu-

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FIG. 5. Epoxy casts of species synonymized under *Archaeotypotherium propheticus.* **A.** MACN 10905, selected syntypes of *Archaeohyrax nesodontoides* including (from left to right) right m1 (lectotype, MACN 10905a); left m1 or m2 with little wear (paralectotype, MACN 10905g or 10905h); right P4 (paralectotype, MACN 10905p). **B.** MACN A52-625, lectotype of *Archaeohyrax concentricus,* incomplete facial region of skull with left I1–M2 and right I1–M3. **C.** MLP 12-1524a, holotype of *Archaeotypotherium transitum,* left maxilla with M1–3 (M3 partially erupted). Scale bar = 1 cm.

TABLE 3. Measurements to the nearest 0.1 mm for specimens of *Archaeotypotherium propheticus*. Specimens are arranged in order of increasing wear as determined by various morphologic indicators (e.g., presence or absence of fossettes, height of cheek teeth). Measurements in parentheses are estimated.

Upper dentition

		P1		P2		P3		P4		M1		M2		M3	
Specimen	**Wear**	L	W	L	W	L	W	L	W	L	W	L	W	L	W
AMNH 28955	Light			10.5	(9)	10.0	—	10.4	(10.5)	10.9	(11)	13.0	(10)	12.8	(8)
MLP 12-1524a	Light									13.6	10.5	13.7	9.1	5.8	4.7
MLP 12-1549a	Light									10.1	9.5	11.5	9.8		
MLP 12-3162	Light									14.2	8.0				
MLP 89-XII-29-1	Light									10.9	10.4				
MACN A52-625*	Moderate	7.5	5.9	9.9	7.9	8.4	9.8	8.7	9.5	9.7	10.1	11.0	9.2		
MACN A10905n	Moderate					8.2	12.8								
MACN A10905o	Moderate							9.6	11.4						
MACN A10905m	Moderate							11.4	9.8						
AMNH 28944	Moderate							10.6	6.2			10.0	6.3		
MACN A10905p	Moderate							9.6	11.2						
MACN 10915†	Moderate									10.8	10.4				
MACN A52-630*	Moderate											10.7	14.0		
MLP 69-III-31-2	Moderate											12.2	7.1		
MACN A10905l	Moderate											12.0	10.5		
MACN A0905k	Heavy									12.4	10.1				
MACN A10905q	Heavy									15.6	11.5				

Lower dentition

		p1		p2		p3		p4		m1		m2		m3	
Specimen	**Wear**	L	W	L	W	L	W	L	W	L	W	L	W	L	W
MLP 89-XII-29-1	Light									9.8	5.6				
MACN A52-618*	Moderate	5.6	3.2	7.4	4.9	8.4	6.0	8.8	6.5						
MLP 12-1516	Moderate									9.0	7.0	10.3	6.3	16.1	5.4
MACN 10905b	Moderate									10.6	6.5				
MACN 10905e	Moderate									11.8	6.6				
MACN 10905g	Moderate									10.2	5.5				
MACN 10915†	Moderate									11.3	5.8				
MACN 10905d	Moderate											11.4	6.1		
MACN 10905h	Moderate											11.4	5.5		
MACN 10905i	Moderate											11.5	(5.4)		
MLP 93-XI-25-6	Moderate											9.9	5.8		
MACN A52-630*	Moderate													14.7	5.6
MACN A52-629*	Heavy							11.9	5.4						

TABLE 3. *Continued.*

Lower dentition

Specimen	Wear	p1 L	p1 W	p2 L	p2 W	p3 L	p3 W	p4 L	p4 W	m1 L	m1 W	m2 L	m2 W	m3 L	m3 W
MACN A52-628	Heavy											9.9	6.1		
MACN 10905c†	Heavy														
MACN 10905f†	Heavy									10.1	6.2				
MACN 10905a	Heavy									10.7	6.4	11.8	5.9		
MACN 10905j	Heavy									10.3	6.2	13.0	5.8	(14.8)	(5.0)

* Measurements from Patterson (MS).
† Precise tooth position unknown.

but]"). MLP 69-III-31-2 comes from "Campo de Velázquez, Paso de Indios, Chubut." MLP 89-XII-29-1 was collected by Santiago Roth in 1898 and comes from Laguna Sega or Seca, found by Roth situated close to the road between Paso de Indios and Choiquenilahue, near Laguna Palacios, Chubut. AMNH 28955 was collected by Justino Hernández in 1934 from Locality IV of Rinconada de los López, just northeast of Tapera de López, Chubut (Simpson, field notes on file at AMNH; Marshall et al., 1986). MACN 14541 comes from "Chubut km 163," Gran Barranca, Chubut.

AGE AND DISTRIBUTION—Earliest Oligocene Tinguiririca SALMA (Flynn et al., 2003) of Patagonia (see above).

DIAGNOSIS—As for *Archaeotypotherium.* Differs from *A. tinguiriricaense* (new taxon, below) in larger size, more persistent fossettes on upper molars, and presence of trigonid and talonid fossettids on lower molars. Differs from *A. pattersoni* (new taxon, below) in more persistent fossettes on upper molars, presence of trigonid and talonid fossettids, and larger and less quadrangular premolars.

DESCRIPTION—Ameghino (1897) distinguished *Archaeohyrax propheticus* from *Archaeohyrax patagonicus* by the presence of p1 and the relatively larger premolars in *A. propheticus.* The former character was based on a mistaken observation by Ameghino (p1 is present in both *A. propheticus* and *A. patagonicus*), but the latter character, and a variety of others outlined in this study, clearly illustrate the distinctiveness of *A. propheticus* and *A. patagonicus,* consistent with Ameghino's recognition of the two taxa as distinct. Measurements for the upper and lower dentitions of this taxon are presented in Table 3.

Upper Dentition—The upper incisors and canine of *Archaeotypotherium propheticus* resemble those of *Archaeohyrax,* but all are lower-crowned (Fig. 5B). The combination of the relatively low-crowned I1, clearly the major cropping tooth, with the relatively much higher-crowned posterior premolars and molars is a curious feature of this taxon; it is implanted obliquely as in *Archaeohyrax,* hegetotheriids, and mesotheriids. I2 is slightly longer in *A. propheticus* than in *Archaeohyrax,* its anterior portion projecting forward well beyond the root and curving inward a little. I1, I2, I3, and C are offset from each other by short diastemata.

The first premolar differs from that of *Archaeohyrax* in its more convex external face and by the presence of a shallow anterolingual notch. The essential characters of the remaining upper cheek teeth have been given in the diagnosis of *Archaeotypotherium.* Detachment of the facial portion of the right maxilla of MACN A52-625 reveals a progressive, steplike increase in the heights of the premolar crowns, and very clearly shows that *Archaeotypotherium* is less hypsodont than *Archaeohyrax.* The cheek teeth are at an earlier stage of wear than in the type of *A. patagonicus,* yet they are notably lower-crowned. On P2–4 the anteroexternal fossette is more persistent than the posteroexternal fossette, whereas on the molars the reverse is the case. The internal fossette is elongate, and is bifid anteriorly, in P3–M2.

The incomplete M3 of MACN A52-625, the least worn of the available teeth, reveals a few details of crown pattern (Fig. 5B). A shallow notch still persists between the protocone and the slender lingual extremity of the hypocone. The metaloph appears to have been directly transverse in orientation. There is a very small posterior cingulum, interrupted labially and joined lingually to the tip of the hypocone. The posteroexternal fossette is a long slit that curves posteriorly toward the midline, the lingual portion being very shallow. The internal fossette is a mere slit labial to the protocone. Between this fossette and the posteroexternal one is a wide, abraded area. To judge from an unworn M1 of the Mustersan-aged *Pseudhyrax eutrachytheroides,* this area, when newly erupted, consisted of a posterior crista joined to a bulbous cusp or crochet attached to the metaloph.

Lower Dentition—The lower incisors, canines, and p1–3 are known only from the type of *A. propheticus,* a very mature individual in which the dentition is deeply worn (Fig. 4). The teeth at this stage show no appreciable differences in structure from those of *Archaeohyrax.* A comparison of a p4 of *Archaeotypotherium* (MACN A52-629) and a mandible of *Archaeohyrax patagonicus* (MACN A52-624) at similar stages of wear demonstrates that the talonid fossettid and the lingual groove in the trigonid are more persistent in *Archaeotypotherium* than in *Archaeohyrax,* and that the lingual groove posterior to the entoconid is less persistent. They also demonstrate that the lingual groove between the trigonid and talonid is less persistent than the one posterior to the entoconid in *Archaeotypotherium,* whereas in *Archaeohyrax* the reverse is the case. The greater persistence of the trigonid and talonid fossettids in the lower molars of *Archaeotypotherium* is convincingly shown by MACN A52-628 and A52-630 (Fig. 6), both old individuals in which the roots are either formed (m1–2) or forming (m3). A talonid fossettid persists on m2 in both specimens, a trigonid fossettid on m3 of A52-630, and both fossettids on m3 of A52-628.

The facial region and the mandible show no important differences from *Archaeohyrax,* although the muzzle of *A. propheticus* is slightly broader than in *A. patagonicus.*

Archaeotypotherium tinguiriricaense **sp. nov.**
(Figures 7–11)

Holotype—SGOPV 2823, rostrum with left and right C1–M2 (canines barely erupted; Fig. 7).

Hypodigm—Holotype of *A. tinguiriricaense*; SGOPV 2851, palate with highly worn left I1–3, left and right P2–M3 (Fig. 8); SGOPV 2853, right maxilla with transversely crushed C1–M2 (P3 with damaged ectoloph); SGOPV 2900, slightly distorted skull with crushed dentition (left and right I1, right P2–M3, left P2–3, M1–2; Fig. 11A); SGOPV 2909, left maxillary fragment with ?M1–2; SGOPV 3043, partial left and right mandibles (fused) with left i1–3, p1–m3 and right i1–p3 (Fig. 10); SGOPV 3052, partial left mandible with p3–m3 (Fig. 9B); SGOPV 3060, left ?M1; SGOPV 3067, skull and mandible with mildly worn dentitions, partially prepared (Fig. 9A, mandible only); SGOPV 3080, palate with left and right P1, dP2–4, M1 (Fig. 11B); SGOPV 3260, partial right mandible with m1–3; SGOPV 3261, partial left mandible with p4–m2.

Type Locality—Locality C-89-21b, purple-brown volcaniclastic sediment of the Abanico Formation (Charrier et al., 1996; Flynn et al., 2003); 34°59′S, 70°26′W, approximately 1 km north of pass identified by its elevation, 2738 m (Anonymous, 1985), known locally as Portezuelo El Fierro (Charrier et al., 1996), south of the Río Tinguiririca, northeast of Cerro Alto del Padre, and about 3 km south of Termas del Flaco, Chile.

Age and Distribution—Earliest Oligocene Tinguirirican SALMA (Flynn et al., 2003) of east-central Chile (see above).

Diagnosis—As for *Archaeotypotherium.* Differs from *A. propheticus* in its smaller size (approx. 20% smaller), less persistent fossettes on upper molars, and absence of trigonid and talonid fossettids on lower molars. Differs from *A. pattersoni* (new species, below) in smaller size (approx. 20% smaller), shallower mandible, and

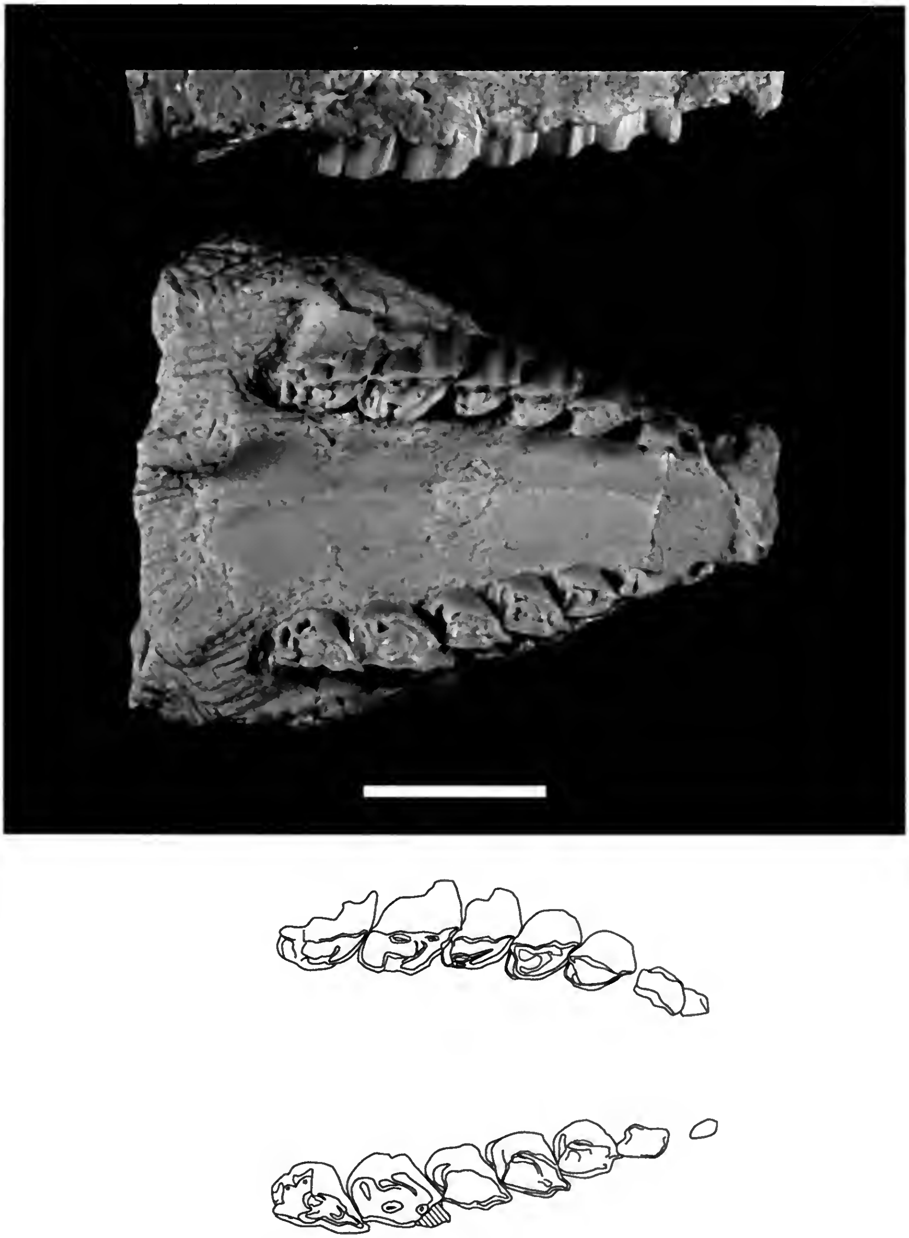

Fig. 7. Epoxy cast of SGOPV 2823, holotype of *Archaeotypotherium tinguiriricaense,* palate with left and right C1–M2 (canines barely erupted), in right lateral view (above) and occlusal view (middle and below). Specimen illustrates relatively unworn dental morphology of *Archaeotypotherium tinguiriricaense.* Scale bar = 2 cm.

proportionately smaller and more triangular premolars.

Etymology—In reference to the Río Tinguiririca and the Tinguiririca Fauna of Chile, the type locality and fauna for the species.

Description—*A. tinguiriricaense* is the most common archaeohyracid in the Tinguiririca Fauna; numerous specimens are referable to it, including two skulls (only the second and third published for an archaeohyracid), a palate bearing a deciduous dentition, and several other upper and lower dentitions. It is slightly larger than the com-

FIG. 8. Epoxy cast of SGOPV 2851, palate with left I1–3, left and right P2–M3, in occlusal view. Specimen illustrates heavily worn upper dental morphology of *Archaeotypotherium tinguiriricaense*. Scale bar = 2 cm.

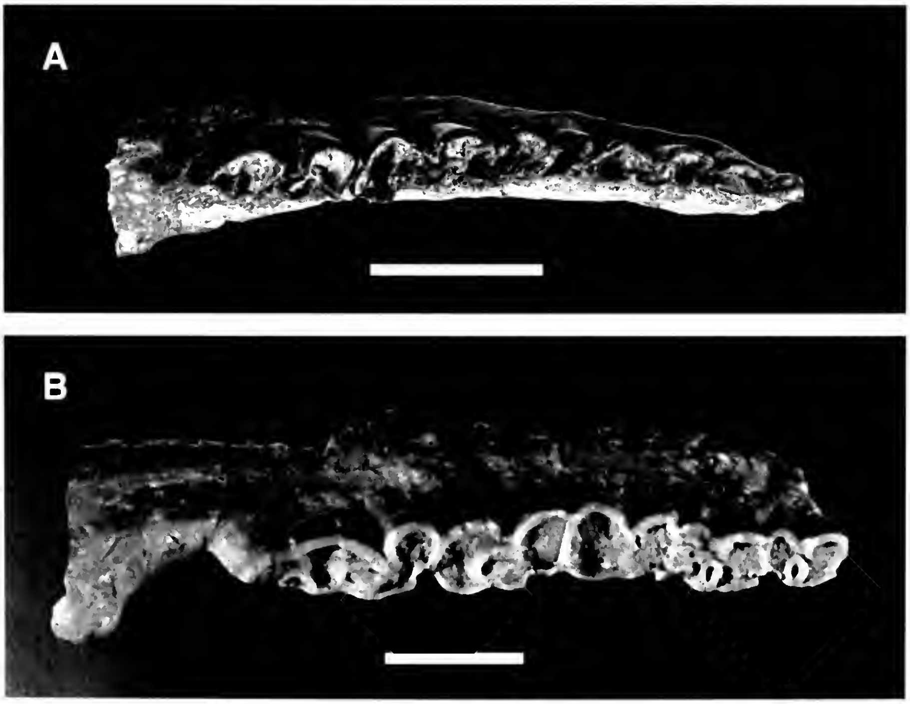

FIG. 9. Lower dentition of *Archaeotypotherium tinguiriricaense*. **A.** Portion of SGOPV 3067, little worn left mandible showing p2–m2, occlusal view. **B.** Epoxy cast of SGOPV 3052, partial left mandible with p3–m3, occlusal view. Scale bars = 1 cm.

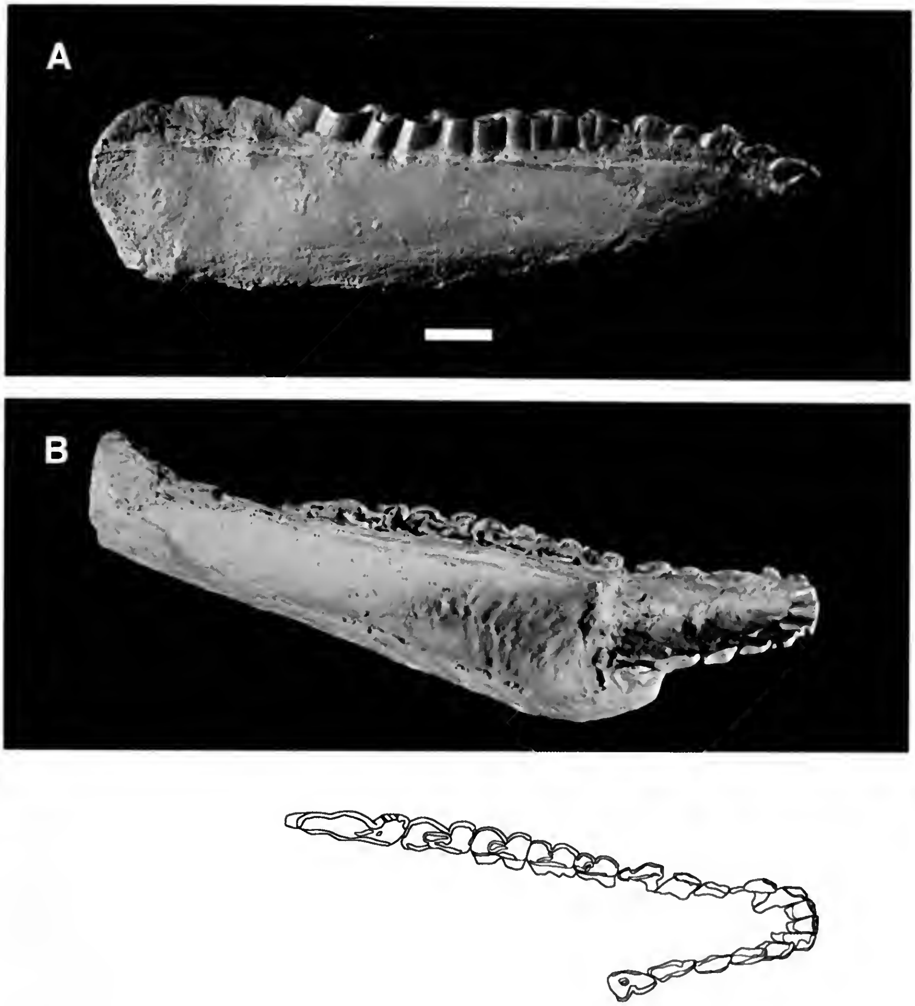

FIG. 10. Epoxy cast of SGOPV 3043, partial left and right mandibles (fused) of *Archaeotypotherium tinguiriricaense* with left i1–3, p1–m3, and right i1–p3. **A.** Left lateral view (shown as right lateral). **B.** Occlusal view. Scale bar = 1 cm.

mon *Archaeohyrax* sp. nov. from the younger fauna at Salla, Bolivia (Deseadan SALMA) but much less hypsodont. Dental measurements are presented in Table 4. A rostrum with upper dentition (SGOPV 2823) is designated the holotype for this new taxon because it preserves many diagnostic features, and archaeohyracid taxa typically are most easily distinguished on the basis of the upper dentition. A skull was not designated the holotype because in one (SGOPV 2900), the teeth are crushed, and in the other (SGOPV 3067), some adult teeth are unerupted and deciduous teeth are present.

Upper Dentition—In the current state of preparation, the relatively unworn upper dentition is best represented by the holotype specimen SGOPV 2823 (Fig. 7), a rostrum with both left and right C1–M2. No incisors are preserved. The upper canines are visible within their alveoli and are in the process of erupting. M3, if present, is completely unerupted. The lateral surface of the maxilla is present on the left side of the rostrum, but is not preserved on the right.

The canine is small and bladelike (approximately 2.8 mm in length) and appears to be separated from P1 by a small diastema. The posterior edge of P1 abuts the anterior edge of P2. It is a simple tooth, consisting primarily of a single,

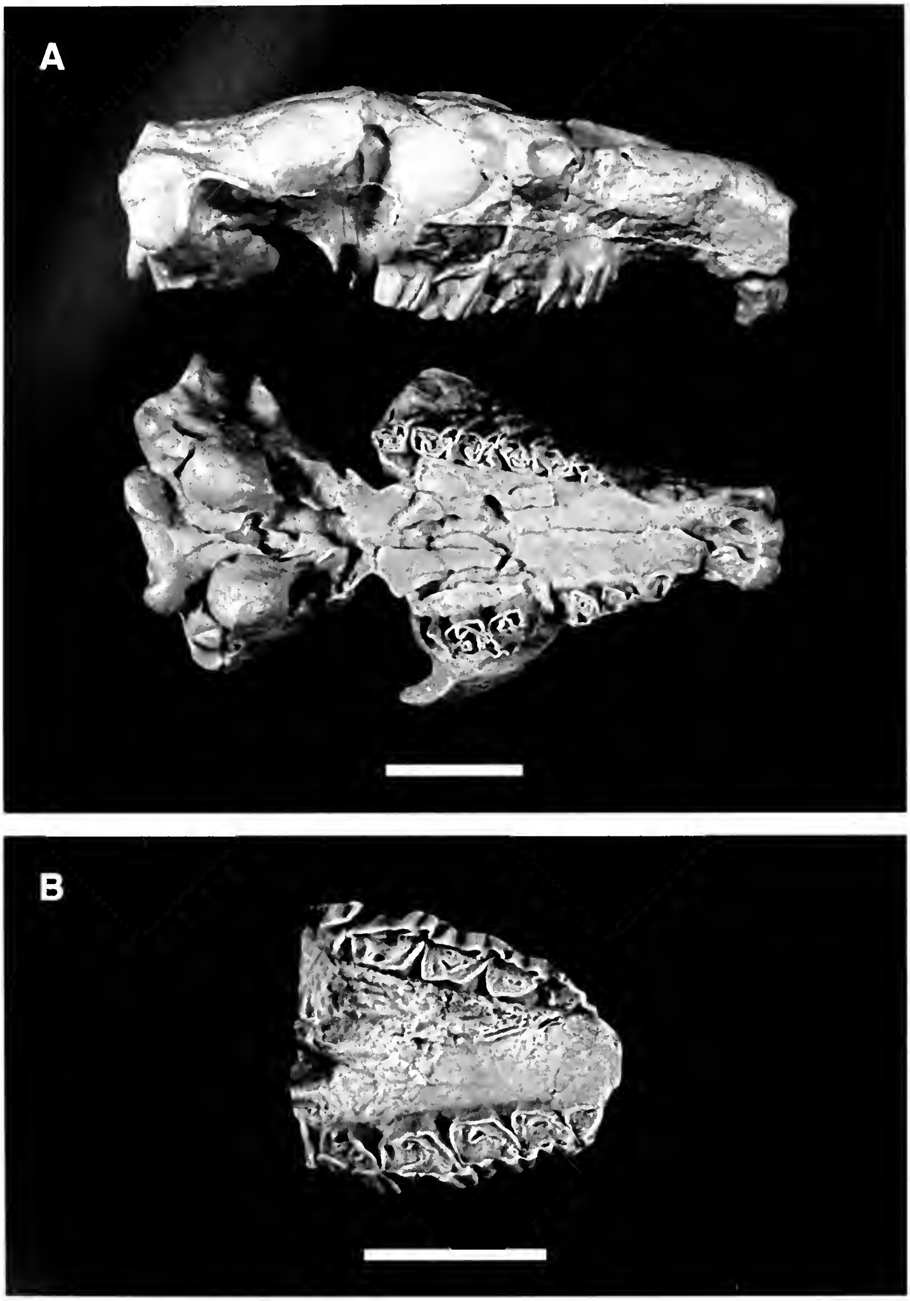

FIG. 11. Epoxy casts of skull and deciduous dentition of *Archaeotypotherium tinguiriricaense*. **A.** SGOPV 2900, slightly distorted skull with crushed teeth (left and right I1, right P2–M3, left P2–3, M1–2) in right lateral view (above) and occlusal view (below). **B.** SGOPV 3080, palate with left and right P1, dP2–4, and M1 in occlusal view. Scale bar = 2 cm.

rounded cusp occupying nearly the entire anterior half of the tooth. A small, sloping shelf is located distolingual to this main cusp.

The other premolars (P2–P4) more closely resemble the molars in shape and complexity. An anterolabially projecting parastyle is present on all premolars, but the parastyle does not extend as far apically as does the adjacent paracone. Strong la-

TABLE 4. Measurements to the nearest 0.1 mm for specimens of *Archaeotypotherium tinguiriricaense*. Specimens are arranged in order of increasing wear, as determined by various morphologic indicators (e.g., presence or absence of fossettes, height of cheek teeth). Measurements in parentheses are estimated.

Upper dentition

		P1		P2		P3		P4		M1		M2		M3	
Specimen	**Wear**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**
SGOPV 2823	Light			4.9	3.9	7.5	5.2	7.2	6.0	10.0	6.6	(10.6)	(6.6)	—	—
SGOPV 2853	Light			6.4	—	(6.4)	—	7.1	—	9.0	—	10.3	—	(11.2)	—
SGPOV 3060†	Moderate									9.1	7.6				
SGPOV 2909	Moderate									8.2	8.4	9.6	8.2		
SGOPV 2851	Heavy			5.5	4.6	4.2	6.5	5.0	7.5	6.3	9.6	8.5	8.3	13.1	7.5

Lower dentition

		p1		p2		p3		p4		m1		m2		m3	
Specimen	**Wear**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**
SGOPV 3261	Light							7.0	4.1	9.3	4.7	10.4	3.8		
SGOPV 3067	Light							6.8	3.2	8.8	4.5	10.2	3.8	—	—
SGOPV 3043	Heavy	5.0	2.3	6.6	2.5	5.9	3.5	6.6	3.8	8.2	4.7	8.9	4.7	15.0	4.9
SGOPV 3052	heavy					6.0	3.6	6.5	4.1	8.1	5.1	9.6	5.3	(14.4)	4.7

bial ridges demarcate both the parastyle and paracone; the two are separated by an asymmetric concavity that is steeper at the anterior face of the paracone ridge than it is on the posterior face of the parastylar ridge. Differentiation of the paracone and metacone increases distally in the tooth row. A posterior cingulum is present on all premolars at a height about halfway between the alveolar margin and the occlusal surface of the metaloph. No differentiation of the protocone or the hypocone is evident along the lingual face of the premolars. Each premolar roughly resembles a right triangle, with the ectoloph forming the long leg and a convex, anterolingual protoloph forming the hypotenuse.

The second upper premolar exhibits a simple occlusal morphology. Lingual to the paracone there is a very weakly developed first crista. Posterior to this is a second crista, which is united with a well-developed crochet. Two spaces are thus isolated: an internal fossa and a postero-external fossette. The internal fossa is oriented slightly obliquely to the long axis of the tooth. Its anterior end is expanded between the protoloph and the second crista, and the incipient first crista can be seen projecting into the fossa from the ectoloph. The lingual face of the tooth is smoothly convex, gently grading into the posterior cingulum.

The third and fourth upper premolars are similar in size, shape, and morphology, but P4 is more worn. Of the cheek teeth, these show the greatest development of the labial groove between the parastylar and paracone ridges. The cristae and crochet are better developed on the occlusal surfaces, and an antecrochet projects into the anterior end of the internal fossa and contacts the first crista, isolating an anterior external fossette with wear. This crochet closely parallels the protoloph along a portion of the lingual side of the crown, nearly pinching out the middle portion of the internal fossa. With wear, this creates a constricted internal fossa that is slightly expanded both anteriorly and lingually. The crochet contacts the short second crista, isolating a posterior external fossette that is larger than the anterior external fossette. In a little-worn tooth, the internal fossa can be seen to extend laterally to the ectoloph, situated between the two cristae opposite the paracone and metacone. This portion of the internal fossa disappears with wear, and the two cristae become confluent; there is no median external fossette. A posterior cingulum is present on both teeth, positioned well below the occlusal surface of the metaloph.

The first upper molar is the most heavily worn cheek tooth, but still is relatively unworn. Its anterior portion resembles the posterior premolars, but due to wear the posterior cingulum is joined with, and forms the distal portion of, the occlusal surface. Additionally, the protocone and hypocone (the latter not being evident in the premolars) are differentiated and separated at their bases by a short internal cingulum. At this slightly worn stage, the internal cingulum is slightly below the occlusal surface of the lingual portion of the tooth. The presence of a hypocone and the distal lengthening of the tooth create a more trapezoidal tooth shape in which the labial and lingual sides form roughly parallel edges and the segment along the distal edge of the tooth is perpendicular to both.

Five fossae/fossettes are present on the occlusal surface of M1. Most anterior is a small fossette resulting from the joining of the antecrochet with the first crista (i.e., the anterior portion of the conjoined first and second cristae). Posterior to this, situated approximately halfway along the labial edge of the tooth, is the posterior external fossette. Between these two fossettes, but located more lingually, is a small anterolingual fossette formed by the "pinching off" of the internal fossa by the well-developed crochet; it is not a true external fossette, as the first and second cristae become confluent with wear, preventing the fossette from reaching the ectoloph. The posterior portion of the internal fossa is situated lingually, just lateral to the small internal cingulum. The internal fossa is connected to the anterolingual fossette by the elongate remnant of the internal fossa. Finally, a mediolaterally elongate posterior fossette is present between the posterior cingulum and the metaloph.

The second upper molar is partially erupted; only the anterior half of the tooth has undergone any wear and the posteriormost portion of the tooth is nearly flush with the surface of the palate. Two cingula are clearly demonstrated in this tooth: a small, somewhat papillate posterior cingulum and a slightly shorter, gently rounded, and more robust internal cingulum. The hypocone arises from between these two structures and is the lowest of the cusps. Its apex is flat and is already confluent with the rest of the metaloph. The metastyle lies opposite the hypocone, along the labial margin of the tooth. It is significantly larger than the hypocone and has a distinct, pointed apex. It is confluent with the rest of the ectoloph, but only near its base. The second crista is well developed and is nearly as high as the worn anterior portion of the tooth. The crochet, however, is not nearly as tall, but extends anteriorly from the metaloph to contact the second crista. As on M1, an anterior external fossette is present along the lingual margin of the ectoloph, just anterior to the combined first and second cristae. Two bands of enamel extend lingually from the fossette, suggesting a possible connection of the fossette with the internal fossa before wear had taken place.

Although the incisors are not present in SGOPV 2823, they are at least partially preserved in SGOPV 3067 (the remaining teeth are unprepared), and SGOPV 2851 (Fig. 8), a specimen with highly worn teeth. In SGOPV 3067, the left first incisor is recently erupted and displays little or no wear. It appears to be much less robust than in *Archaeohyrax,* but, owing to the unprepared lingual surface of the tooth, this is uncertain. The occlusal edge of the tooth is approximately 6.5 mm in length. I1 is about twice as large as I2, and I2 is slightly larger than I3. I3 is in the process of erupting, and I2 may be broken away from its root, precluding a more detailed description of their morphology. In SGOPV 2851, all teeth have undergone significant wear and all three incisors have been worn nearly to their roots. They are separated by small diastemata (each approximately 1 mm long) and all have less than 2 mm of enamel present labially.

Measurements of upper cheek teeth for specimens of *Archaeotypotherium tinguiriricaense* are listed in Table 4. It should be noted that the measurements of teeth of different specimens vary in the orderly fashion predicted from the aforementioned studies of changes with wear in other archaeohyracid taxa.

Lower Dentition—The relatively unworn lower dentition of *Archaeotypotherium tinguiriricaense* is best exemplified by SGOPV 3067 (Fig. 9A). Both mandibles are preserved, but the posterior portion of the right mandible remains unprepared. The two mandibles are joined at a completely fused symphysis that is approximately 21 mm in length; in lateral view, the symphysis is oriented at an angle of about 30° below the level of the mandibular tooth row.

The lower incisors are small and procumbent, their size increasing from mesial to distal. The first two incisors are very small and are the only teeth of the mandible exhibiting significant wear. The third incisor exhibits no wear and is much larger than the first two. Because SGOPV 3067 represents a young individual of A. *tinguiriricaense* (most teeth are unworn and m3 is unerupted), comparisons with specimens of older individuals of this taxon (e.g., SGOPV 3043, described below) suggest that the first two incisors in SGOPV 3067 are deciduous. The identification of the third incisor is ambiguous; it may be either a late-erupting deciduous tooth or an early-erupting permanent tooth. Based on its similar size and structure to i3 in other specimens, we favor the latter alternative, pending additional specimens that might suggest otherwise. Tooth replacement in notoungulates has yet to be thoroughly investigated, and the presence of i3 in this specimen would suggest that the third incisor may not have a deciduous precursor in archaeohyracids.[5]

In SGOPV 3067, the greatest occlusal dimension is perpendicular to the sagittal plane in di1, 45° to this plane in di2, and nearly parallel to this plane in i3. A slight differentiation of two cusps is present on the lingual surface of i3, dividing the tip of the lingual face into a large, rounded posterior cusp and a smaller anterior cuspule. This division is even more pronounced on the canines; the two cusps show greater separation and are more similar in size than they are in i3. The right canine has recently erupted, but on the left side the tip of the already fully erupted tooth is partially broken off.

The teeth of the premolar series grade from caniniform to molariform. The first premolar is caniniform, consisting of a simple pointed crest. The second premolar is significantly longer than p1 and shows a differentiated trigonid and talonid. The trigonid of p2 consists of a single sigmoid crest with its highest point located at the metaconid. The short segment of the trigonid crest posterior to the metaconid hooks around the lingual side of the talonid, which is low, narrow, and c-shaped. The highest point of the talonid is at its posterior end, where a cuspule lies just medial to the most anteriorly projecting part of p3. The third premolar is similar in morphology to p2, but both the trigonid and talonid are expanded buccolingually. The metaconid and its posterior crest are still the highest points on the occlusal surface, but the trigonid has expanded to form a small basin instead of merely a crest. Lingual expansion of the paraconid, which is much better developed than on p2 (best seen in lingual view), creates this basin. A similar expansion of the entoconid occurs in the talonid, creating a talonid basin. The structure of p4 is very similar to that of p3, except the talonid is proportionately longer. In both p3 and p4 a very slight vertical groove is present on the posterolingual portion of the talonid, separating the entoconid from the hypoconulid. This structure is much more evident in the molars, especially with increasing wear.

The molars of SGOPV 3067 have undergone little wear and there is still much relief between the metaconid, with its posterior crest, and the remainder of the occlusal surface. The m1 trigonid is a long, thin structure with two grooves on its internal face. The first of these grooves is located anteromedially on the trigonid, dividing the paraconid from the metaconid. The second groove is located on the lingual side of the posterior metaconid crest; it divides the crest into two unequal portions, the more posterior one being about twice as long as the anterior. On m2, the paraconid is enlarged lingually, creating a trigonid basin much larger than on m1 (though the larger basin may be due, in part, to increased wear). The more anterior of the lingual trigonid grooves is essentially absent in m2, but a small protuberance is still evident on the anteromedial side of the trigonid, just anterior to the more posterior groove. As on the premolars, a lingual groove is present on the m1 talonid, creating a bifid posterolingual talonid face. The internal talonid groove is short in m1, extending perhaps a quarter of the distance from the occlusal surface to the alveolus. On m2, however, the groove is much deeper and extends below the level of the alveolus. The m3 is unerupted.

The morphology of a heavily worn lower dentition is shown by SGOPV 3043 (Fig. 10) and 3052 (Fig. 9B). SGOPV 3052 is slightly more worn, but other than small wear-related differences, the two specimens are almost identical in size and morphology (Table 4).

SGOPV 3043 includes the anterior portion of the right mandible (with i1–p3) and a complete left mandible and associated dentition. The first incisor on each side is small, peglike, and oriented at approximately 45° to the long axis of the mandible (in lateral view). In occlusal view, the surface of i1 is nearly perpendicular to the sagittal plane, whereas i2 is nearly parallel to it. Both i1 and i2 are larger and more robust than their deciduous counterparts in SGOPV 3067. The third incisor and the canine possess a high anterior portion and low posterior portion, similar to the configuration of the trigonid and talonid in many generalized mammal lower molars. The size of each tooth increases progressively from i1–c. In both SGOPV 3043 and 3067, the unusual spoutlike nature of the symphysis is evident, appearing "pinched in" on both sides. A mental foramen is

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[5] Sinclair (1909) noted that P1/p1 do not have deciduous precursors in Santacrucian SALMA interatheriids, so the lack of deciduous precursors for some teeth is not unprecedented in notoungulates.

present within the lateral depressions on the symphysis, almost directly beneath the canine.

The premolars are all heavily worn, and the p1 occlusal surface level is approximately equal in height to that of the posterior portion of the canine. No occlusal morphology is retained on p1 or p2, while on p3–p4 and m1 only a single fossa is present separating the trigonid from the talonid. Enamel height on the labial surface of p3 is approximately 4.2 mm. Both the m2–3 talonid and trigonid are slightly damaged, but most of the morphology remains discernible. In both SGOPV 3043 and 3052 the hypoconulid is directed posteriorly. Although not evident in SGOPV 3043, SGOPV 3052 appears to demonstrate that on m3, in addition to the fossa between the trigonid and talonid, a fossettid forms between the hypoconid and hypoconulid.

DISCUSSION—Owing to the large number of well-preserved specimens of this taxon from the Tinguiririca Fauna, *A. tinguiriricaense* will likely prove to be one of the best-known archaeohyracids. Since many of these specimens have yet to be fully prepared from the exceptionally hard volcaniclastic matrix, however, a complete description of the skull and preserved/available parts of the appendicular skeleton is not yet possible. These specimens will be thoroughly described when preparation has been completed. Of note, however, is the well-preserved basicranium of SGOPV 2900, which illustrates two characters Patterson (1936, unpublished manuscript) recognized as linking *Archaeohyrax* and hegetotheriids: the absence of a hamular process on the pterygoid and an anteriorly located carotid foramen (see phylogenetic analysis below).

A. tinguiriricaense includes both of the specimens (SGOPV 2823 and SGOPV 2900) previously referred to "archaeohyracid new taxon A" and one of the specimens (SGOPV 2851) referred to "archaeohyracid new taxon D" in Wyss et al., 1994 (see discussion below).

Archaeotypotherium pattersoni
(Figure 12)

HOLOTYPE—SGOPV 2918 (Fig. 12A), right maxilla with P2–M3, labial portions of teeth incompletely preserved.

HYPODIGM—Holotype of *A. pattersoni*; SGOPV 2917 (Fig. 12B), right mandible with p2–m3 (likely from the same individual as SGOPV 2918).

TYPE LOCALITY—Locality C-89-37, otherwise as for *A. tinguiriricaense.*

AGE AND DISTRIBUTION—Earliest Oligocene Tinguirirican SALMA (Flynn et al., 2003) of east-central Chile (see above).

DIAGNOSIS—As for *Archaeotypotherium.* Differs from *Archaeotypotherium propheticus* in less persistent fossettes on upper molars, smaller and more quadrangular upper premolars, and absence of trigonid and talonid. Differs from *A. tinguiriricaense* in larger size (approx. 20% larger), proportionately larger premolars, deeper mandible, and thicker labial enamel on upper molars.

ETYMOLOGY—After Bryan "Pat" Patterson, in honor of his extensive contributions to South American paleontology in general and archaeohyracids in particular.[6]

DESCRIPTION—A maxilla with upper dentition is designated the holotype for *A. pattersoni* because it preserves many diagnostic features, and archaeohyracid taxa typically are most readily distinguished using characters of the upper dentition. A well-preserved mandible with moderately worn p3–m3 (SGOPV 2917; Fig. 12B) probably represents the lower dentition of *A. pattersoni.* This specimen matches the holotype maxilla very well in size, degree of hypsodonty, and state of wear. The two specimens were found near each other in the field and exhibit similar preservation, and it is quite possible that they represent the same individual.

Upper Dentition—Specimen SGOPV 2918 (Fig. 12A) consists of a right maxilla with moderately worn P2–M3; most of the teeth have incompletely preserved labial surfaces. A very small portion of P1 is also present within its alveolus. The specimen is quite high-crowned, with a level of hypsodonty comparable to, or perhaps slightly exceeding, that of *A. tinguiriricaense.* Because the teeth have undergone moderate wear, little occlusal morphology is evident, except the central fossa. Because the first and second upper molars are broken labially, we are unable to discern the pattern of external fossettes (if present). However, as M3 exhibits no external fossettes and

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[6] Most of Patterson's research on archaeohyracids exists only in the form of an unpublished manuscript. Simpson (1967) alluded to this work-in-progress and chose to honor Patterson's research by erecting a new taxon, *Bryanpattersonia.* Because the present publication formally invalidates the name *Bryanpattersonia* (based on the principle of priority), it is especially appropriate that one of the new species in this group be named for Pat in its place.

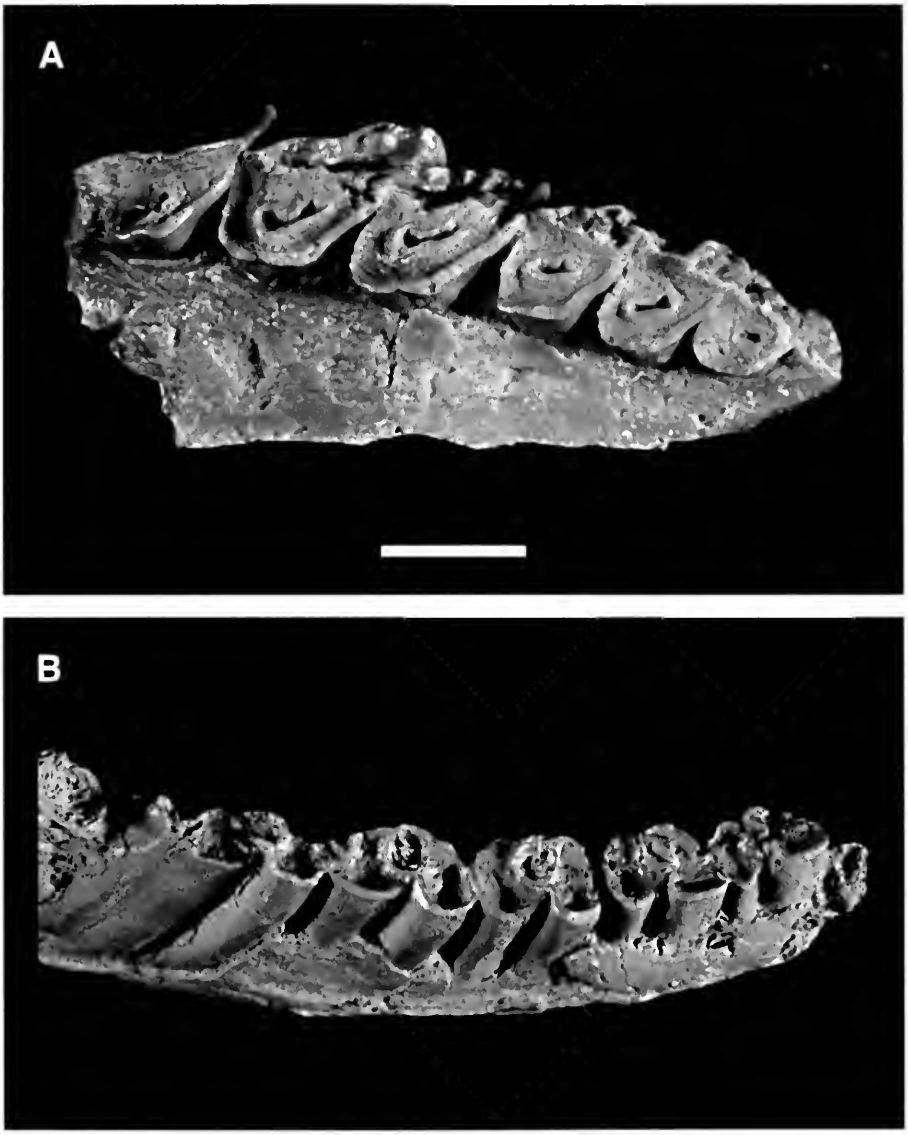

FIG. 12. Epoxy casts of specimens of *Archaeotypotherium pattersoni.* **A.** SGOPV 2918 (holotype), right maxilla with P2–M3, slightly damaged labially, occlusal view. **B.** SGOPV 2917, right mandible with p2–m3 (likely same individual as SGOPV 2918), occlusal view. Scale bar = 1 cm.

is the least worn of the molars, it is likely that these fossettes (if indeed present in more anterior molars) disappeared early in wear. The premolars all are trapezoidal in outline, as are M2 and M3. Well-defined parastyle and paracone grooves are present on all cheek teeth and are the only pronounced features of the labial surface. Dental measurements are presented in Table 5.

Lower Dentition—A single fossettid is located between the trigonid and the talonid on p4–m2, resulting from an isolated fragment of the internal groove; this has not yet been isolated through wear in m3. The lingual sides of the teeth are nearly flat, although a short groove is present on the posterointernal corner of the talonid, separating the entoconid from the hypoconulid; it has been obliterated by wear in m1 but is still present as a wide sulcus in m3.

The mandibular ramus is substantially deeper than in *A. tinguiriricaense* (SGOPV 3043, 3067). In *A. pattersoni* the mandible is 18.6 mm deep just anterior to m1 and perpendicular to the lower

TABLE 5. Measurements to the nearest 0.1 mm for specimens of *Archaeotypotherium pattersoni.* Measurements in parentheses are estimated.

Upper dentition

		P2		P3		P4		M1		M2		M3	
Specimen	**Wear**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**
SGOPV 2918	Moderate	(5.7)	(6.3)	(6.5)	7.2	8.5	8.1	10.1	—	10.3	(9.1)	12.5	6.9

Lower dentition

		p2		p3		p4		m1		m2		m3	
Specimen	**Wear**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**
SGOPV 2917	Moderate	—	—	8.4	5.2	8.3	6.0	8.8	6.4	11.0	5.9	12.2	5.0

edge of the mandible, whereas in *A. tinguiriricaense* (SGOPV 3043) it measures only 15.7 mm. Posterior to m3, the mandibular depth is just over 28 mm in *A. pattersoni,* whereas it is about 24 mm in *A. tinguiriricaense.*

DISCUSSION—Wyss et al. (1994) tentatively attributed SGOPV 2918 and the highly worn SGOPV 2851 (Fig. 8) to "archaeohyracid new taxon D" based on a number of shared characteristics. These included: (1) the two specimens are within 30% of each other in size; (2) the morphology of SGOPV 2851 could plausibly be derived from SGOPV 2918 through significant wear; (3) the concave form and the texture of the molar bases are similar in both specimens; (4) the general cheek tooth outlines are similar in both specimens.

Two of the characteristics listed above as supporting the assignment of SGOPV 2918 and 2851 to the same taxon do not distinguish these specimens from *A. tinguiriricaense*: SGOPV 2851 can also plausibly be derived from specimens of *A. tinguiriricaense* through wear (No. 2 above) and the general cheek-tooth outlines are comparable (No. 4 above). The primary characteristic that distinguishes *A. tinguiriricaense* and *A. pattersoni* is size, the latter being significantly larger and the former comparing much more favorably with SGOPV 2851. This is especially apparent when the state of wear of each specimen is taken into account. Additionally, the labial surfaces of the teeth of SGOPV 2918 have been exposed to their bases, permitting basal lengths (presumably similar to lengths after much wear) to be compared directly. In SGOPV 2851, the bases of P2–M3 measure 41.2 mm, whereas the corresponding length in SGOPV 2918 is approximately 51 mm, a difference of 20%. Although this would not normally be considered a significant difference when comparing individual tooth values between archaeohyracid specimens, it is considerable for a tooth-row length. Unfortunately, no upper teeth of *A. tinguiriricaense* have been exposed to their bases, precluding a comparable measurement in that taxon. As Table 4 illustrates, the tooth measurements of SGOPV 2851 are what would be expected for a specimen of *A. tinguiriricaense* with heavily worn teeth.

The lack of comparable specimens of *A. tinguiriricaense* again does not allow for a proper comparison of features of the tooth bases (i.e., concave nature and similar texture, No. 3 listed above). The variation in these characters within the species (and within individuals) is not known, but it is interesting to note that the right M3 of SGOPV 2851 is much more concave than the left M3 of the same specimen. Additionally, there are differences in the morphology of SGOPV 2851 and SGOPV 2918, including a much more gently tapering shape to the edge of the enamel in SGOPV 2851, although this also could be a variable character. In light of the metric similarities between SGOPV 2851 and *A. tinguiriricaense* and the lack of discrete morphologic differences, it seems more likely that SGOPV 2851 represents a specimen of *A. tinguiriricaense* with heavily worn teeth, rather than *A. pattersoni.* Thus, we here refer to *A. pattersoni* two of the three specimens, SGOPV 2918 and SGOPV 2917, previously attributed to "Archaeohyracid new taxon D" (Wyss et al., 1994).

Pseudhyrax Ameghino, 1901
(Figures 13–17)

TYPE SPECIES—*Pseudhyrax eutrachytheroides* Ameghino, 1901.

INCLUDED SPECIES—The type species, *Pseudhyrax strangulatus* (Ameghino, 1901), and the indeterminate material described here.

DIAGNOSIS—Simpson (1967, p. 109) diagnosed *Pseudhyrax* as "Closely similar to *Eohyrax* and probably intergrading with that genus, but more progressive, more hypsodont, lower molars tending to develop a second closed talonid fossette and a closed trigonid fossette." As emended here, *Pseudhyrax* is a member of the Hegetotheria that differs from Hegetotheriidae in absence of hypselodont (ever-growing) cheek teeth, absence of hypselodont I1, absence of straight lingual face on lower molars, presence of fossettes/fossettids at some stages of wear in upper and lower molars, and presence of significant change in cheek tooth shape with wear. Differs from *Archaeotypotherium, Protarchaeohyrax, Archaeohyrax* and the new archaeohyracid taxon from Antofagasta de La Sierra (López, 1997; Reguero & López, 1999) by lower degree of hypsodonty, greater persistence of accessory fossettes with wear, presence of internal sulcus on endoloph, more pronounced ectoloph ridges, and more quadrangular cheek teeth. Larger than *Protarchaeohyrax* and the new archaeohyracid taxon from Antofagasta de La Sierra (López, 1997; Reguero & López, 1999). Protoloph less transverse than the new archaeohyracid taxon from Antofagasta de La Sierra (López, 1997; Reguero & López, 1999).

AGE AND DISTRIBUTION—Latest Eocene Mustersan of Patagonia and earliest Oligocene Tinguiririican SALMA (Flynn et al., in press) of Patagonia and east-central Chile (see above).

COMMENTS—Simpson (1967) recognized two species of *Pseudhyrax*: *P. eutrachytheroides* and *P. strangulatus*. These two are differentiated by size only, and Simpson (1967), while still recognizing the specific status of *P. strangulatus*, expressed doubt as to whether its smaller size was due to taxonomic distinction or merely intraspecific variation.

In order to examine size variation within the Argentine sample of *Pseudhyrax*, molar lengths and widths from a large number of specimens (N = 23) were recorded and examined on a bivariate plot (Fig. 13). This plot reveals the following points. First, a gap in the size distribution appears to be present, and is most pronounced for m3. This distribution suggests that *Pseudhyrax* specimens with m3 longer than 11.5 mm and wider than 5.0 mm should be referred to *P. eutrachytheroides*, while those with m3 shorter than 9.2 mm and narrower than 5.0 mm should be referred to *P. strangulatus*. Second, based on this plot, one large specimen identified as *P. strangulatus* (MLP 67-II-27-272) is probably referable to *P. eutrachytheroides*. Finally, the uneven ratio of *P. eutrachytheroides* to *P. strangulatus* specimens (approx. 10:1) suggests that this size difference is not due to sexual dimorphism, and more likely represents taxonomic distinction.

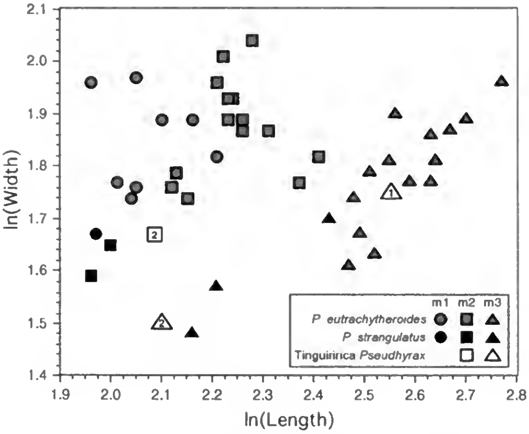

FIG. 13. Bivariate plot of lower molars of *Pseudhyrax* from the Mustersan of Chubut, Argentina. Tinguiririca specimen 1 represents SGOPV 2985 (*P. eutrachytheroides*) and Tinguiririca specimen 2 represents SGOPV 2887 (*P. strangulatus*).

Pseudhyrax eutrachytheroides Ameghino, 1901
(Figures 14–16)

HOLOTYPE—MACN A-11662, maxillary fragment with dP2–4, M1 (Simpson, 1967).

REFERRED SPECIMENS—SGOPV 2985, right mandibular fragment with partial m2, m3 (Fig. 14B); SGOPV 2877 (tentatively), left and right I1 and left P3–M3 (Fig. 15).

TYPE LOCALITY—Unknown.

AGE AND DISTRIBUTION—As for *Pseudhyrax*.

DIAGNOSIS—Differs from *P. strangulatus* in its larger size.

COMMENTS—SGOPV 2985, a right mandibular fragment with partial m2, m3, compares well with moderately worn specimens of *Pseudhyrax* from Argentina. Based on its size and indistinguishable morphology, SGOPV 2985 is referred to *P. eutrachytheroides* (see Fig. 13 and Table 6).

No upper teeth attributable to *Pseudhyrax* have been previously recorded from the Tinguiririca assemblage. Wyss et al. (1994) noted the possibility that, given the conservative nature of

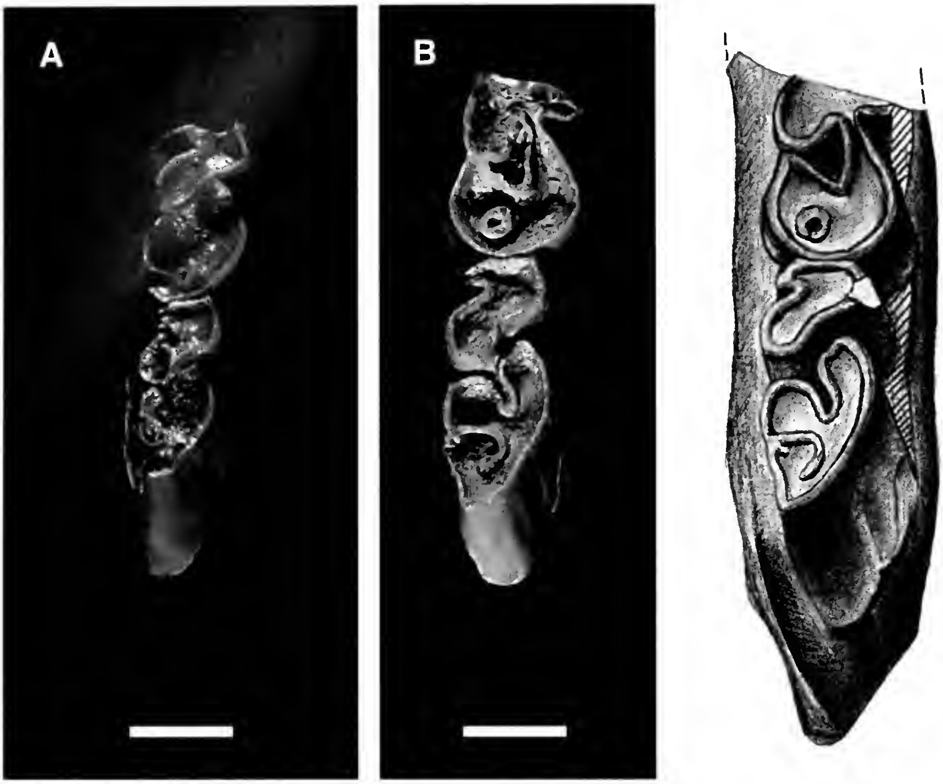

FIG. 14. Mandibles from the Tinguiririca Fauna referred to *Pseudhyrax*. **A.** Epoxy cast of SGOPV 2887, *Pseudhyrax strangulatus,* right partial mandible with m2–3. **B.** SGOPV 2985, *Pseudhyrax eutrachytheroides,* right mandibular fragment with partial m2, m3, photo of epoxy cast (left) and illustration (right). Scale bar = 5 mm.

archaeohyracid lower dentitions, one or both of the Tinguiririca Fauna lower dentition specimens identified as *Pseudhyrax* might instead pertain to another archaeohyracid species from Tinguiririca, better known from upper teeth. The other possibility, endorsed here, is that some (or at least one) of the well-known upper dentitions from Tinguiririca is/are actually referable to *Pseudhyrax* (viz., SGOPV 2877, "archaeohyracid new taxon B" of Wyss et al., 1994; Table 7).

SGOPV 2877 is a well-preserved upper dental series, including left and right I1 and left P3–M3 (Fig. 15; Table 6). Although a small fragment of P2 is preserved, the morphologies of the posterior incisors, canine, and anteriormost premolar (if they were present) are unknown. No bone of the palate or maxilla is present, so the presence of teeth cannot be discerned from alveoli. The cheek teeth are relatively low-crowned (at least as compared with other contemporaneous archaeohyracids), similar to that exhibited by *Pseudhyrax*. The teeth are moderately worn, except for M3, which is only slightly worn.

The two incisors are enlarged and spatulate. They curve posteriorly and are obliquely implanted, meeting at the tips. A strong enamel face is present on the anterior face of each tooth, but enamel appears to be absent from the back, thus creating a long, self-sharpening edge.

The premolars in SGOPV 2877 show a relatively high degree of molarization. In lateral view, the metacone, paracone, and parastyle ridges are easily distinguishable, the latter two being confluent at the base of the tooth. In occlusal view, the ridges of the paracone and parastyle are more pronounced than that on the metacone, but no parastylar "spur" is present. Each premolar is subquadrangular and longer than wide; the lingual and labial sides are essentially parallel, and the anterior and posterior faces are nearly so. The only feature on the tooth distinguishing the two internal cusps is a slight sulcus on the lingual face. Both premolars are worn and have nearly

FIG. 15. SGOPV 2877, *Pseudhyrax* cf. *P. eutrachytheroides,* left and right I1, left P3–M3. **A.** Occlusal view. **B.** Reconstruction of SGOPV 2877 with M3 in life position. Scale bar = 1 cm.

featureless occlusal surfaces, save for an elongate central fossa oriented anterolabially.

The first two molars also display moderate wear. As in the premolars, the amount of wear on each tooth increases posterolingually, resulting in the anterolabial corner of each tooth being the highest part of the crown. The ectoloph is at least half again as high as the endoloph in these teeth, and the front edge of each tooth is higher than the posterior edge of the tooth directly in front of it. The molars possess a better-developed parastylar spur than do the premolars, but this structure overlaps little, if any, with the proximate anterior tooth. Enamel is absent along the labial portion of the anterior and posterior faces of M1–2, permitting a confluence of the dentine of the occlusal surfaces just medial to the ectoloph.

Both M1 and M2 retain a central fossa that is confluent with the median external fossette. In M1 this fossa is concave anteromedially. The central fossa is larger in M2, owing to the lesser amount of wear. Additionally, whereas the external fossette is a small circular structure abutting the central fossa in M1, in M2 it is located further labially and is joined to the central fossa by a long, thin isthmus. Only M2 retains a posterior external fossette. Due to the high angle of wear along the internal face of the ectoloph, the posterior external fossette appears as an elongate structure, roughly parallel to the median external fossette and its isthmus.

The third molar is separated from M2 by a sizable gap (5 mm), presumably the result of postmortem dislocation. As expected with the eruption pattern, M3 shows the least amount of wear and preserves the greatest occlusal detail among the molars; the lesser degree of wear is especially evident in the shape of the tooth (subtriangular), the high protocone (it is flush with the occlusal surface in worn teeth), and the shape of the ectoloph in lateral aspect (the ectoloph is tapered at both the base and the occlusal surface in M3, whereas it only tapers at the base in worn teeth like M1–2). It possesses a pronounced metastylar ridge that becomes more prominent toward the base of the tooth.

As in M2, a more posteriorly located external fossette is evident on M3, in addition to the central fossa and associated median external fossette. This posterior external fossette has less occlusal exposure than does the corresponding fossette in M2 (owing to a less oblique angle of wear) and it appears as an oval structure that is approximately the same size as the posterior end of the central fossa. Other very small, isolated enamel lakes (microfossettes) are located on the surface

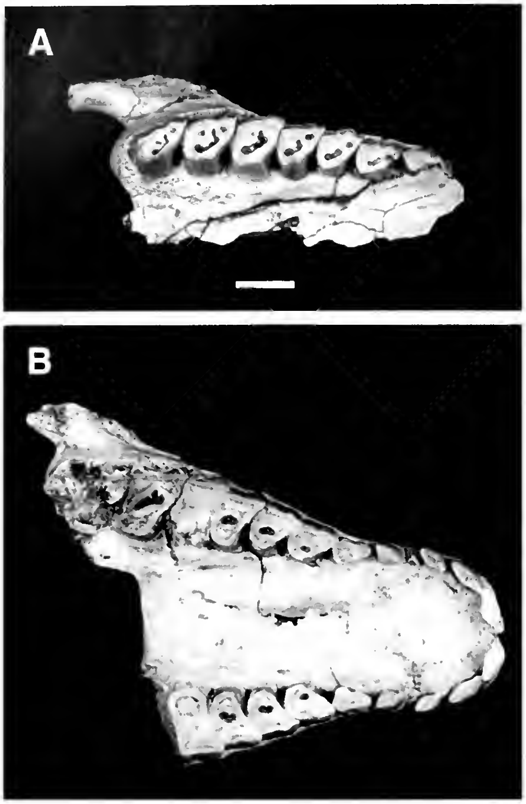

FIG. 16. Occlusal views of *P. eutrachytheroides* specimens from the Mustersan of Chubut, Argentina. **A.** MLP 61-IV-9-1, slightly worn left maxilla with P1–M3 from Laguna del Mate, shown as right. **B.** MLP 67-II-27-359, heavily worn palate with left and right I1–M1, right M2 and partial M3 from La Gran Hondonada. Scale bar = 1 cm.

of M3. Two microfossettes form a transversely oriented pair in the anteroexternal region of the tooth; two others form an obliquely oriented pair in the posteroexternal region of the tooth; and a single microfossette is located posteriorly and internal to the posterior external fossette.

SGOPV 2877 has been described as one of the more unusual typotheres known from the Tinguiririca Fauna, and was designated "archaeohyracid new taxon B" by Wyss et al. (1994) and as Typotheria incertae sedis by Croft (2000). However, further comparisons among a wider series of specimens and a better understanding of wear-related change in archaeohyracid teeth suggest that the atypical morphology of SGOPV 2877 may result from unusual preservation (e.g., the lack of bone and the absence of some teeth), a relative scarcity of appropriate comparative material, and unusual wear-related shape changes in the teeth relative to other taxa.

SGOPV 2877 can be excluded from all other typotheres except the Archaeohyracidae based on the following characteristics: differs from Campanorcidae in presence of more hypsodont teeth, presence of more deeply rooted I1, absence of undulating ectoloph on upper molars; differs from Archaeopithecidae in presence of spatulate first incisors, premolars with enlarged hypocone, absence of lingual sulcus on upper molars, more pronounced parastyle ridge on molars, and large size; differs from Oldfieldthomasiidae in more hypsodont cheek teeth and enlarged incisors; differs from Notopithecinae in large size and lack of bilobed incisors; lacks hypsodont, bilobed upper cheek teeth of Interatheriinae; lacks hypsodont, trilobed upper cheek teeth of Mesotheriidae; and

TABLE 6. Measurements to the nearest 0.1 mm for specimens of *Pseudhyrax* (*P. eutrachytheroides*: SGOPV 2985 and tentatively SGOPV 2877; *P. strangulatus*: SGOPV 2887; *Pseudhyrax* sp. indet.: SGOPV 2901). Measurements in parentheses are estimated.

Upper dentition

		P2		P3		P4		M1		M2		M3	
Specimen	**Wear**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**
SGOPV 2877	Moderate	—	—	5.8	7.2	7.0	7.6	7.6	8.6	9.8	7.9	10.3	6.8

Lower dentition

		p2		p3		p4		m1		m2		m3	
Specimen	**Wear**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**
SGOPV 2985	Moderate	—	—	—	—	—	—	—	—	—	6.8	12.7	5.8
SGOPV 2887	Moderate	—	—	—	—	—	—	—	—	8.1	5.3	(8.2)	4.5
SGOPV 2901	Moderate	—	—	—	—	—	—	(7.2)	(65)	(8.1)	(7.3)	(10.0)	(5.3)

TABLE 7. Identifications of archaeohyracid specimens included in Wyss et al., 1994.

Specimen	Wyss et al., 1994	Flynn et al., 2003	Reguero et al., 2003; present study
SGOPV 2823	archaeohyracid new taxon A	*Archaeotypotherium* new sp. 1	*Archaeotypotherium tinguiricaense*
SGOPV 2851	archaeohyracid new taxon D	*Archaeotypotherium* new sp. 1	*Archaeotypotherium tinguiricaense*
SGOPV 2877	archaeohyracid new taxon B	*Pseudhyrax* cf. *P. eutrachytheroides*	*Pseudhyrax* cf. *P. eutrachytheroides*
SGOPV 2887	*Pseudhyrax* sp. (smaller morph)	*Pseudhyrax strangulatus*	*Pseudhyrax strangulatus*
SGOPV 2900	archaeohyracid new taxon A	*Archaeotypotherium* new sp. 1	*Archaeotypotherium tinguiricaense*
SGOPV 2901	archaeohyracid new taxon C	*Pseudhyrax* sp. indet.	*Pseudhyrax* sp. indet.
SGOPV 2917	archaeohyracid new taxon D	*Archaeotypotherium* new sp. 2	*Archaeotypotherium pattersoni*
SGOPV 2918	archaeohyracid new taxon D	*Archaeotypotherium* new sp. 2	*Archaeotypotherium pattersoni*
SGOPV 2954	cf. "*Bryanpattersonia suicidens*"	New Taxon A1	*Protarchaeohyrax gracilis*
SGOPV 2985	*Pseudhyrax* sp. (larger morph)	*Pseudhyrax eutrachytheroides*	*Pseudhyrax eutrachytheroides*
SGOPV 3065	interatheriine new gen. et sp. B	New Taxon A2	*Protarchaeohyrax intermedium*

lacks hypselodont, simplified upper cheek teeth of Hegetotheriidae.

Among the Archaeohyracidae, the following characters suggest affinities with *Pseudhyrax*: hypsodonty greater than that exhibited by *Eohyrax*, but less than that in *Archaeotypotherium, Protarchaeohyrax,* and *Archaeohyrax*; upper cheek teeth with prominent paracone and parastyle ridges on molar ectolophs; accessory fossettes present on molars even after moderate wear; presence of elongate central fossa, oriented anterolabially; and presence of a slight sulcus on endoloph dividing protocone and hypocone.

The total absence of the maxillary bones (and associated alveoli) does not permit the presence or absence of I2–P1 to be ascertained. Although it has been speculated that a significant diastema could have been present (Wyss et al., 1994; Croft, 2000), the presence of a closed dentition is equally plausible. Nothing in the morphology of the preserved dentition precludes referral to *Pseudhyrax.*

In overall form, SGOPV 2877 is most similar to MLP 61-IV-9-1 (Fig. 16A), a *Pseudhyrax* left maxilla from Laguna del Mate (reference) with all premolars and molars preserved. If such a specimen were to undergo further wear, one would expect the prominence of the external fossettes to decrease and the teeth to become shorter (anteroposteriorly), wider, and more quadrangular. Such a hypothetical specimen would likely be very similar to SGOPV 2877. Unfortunately, few *Pseudhyrax* specimens containing the upper cheek tooth series are known, and so a direct comparison between SGOPV 2877 and a *Pseudhyrax* specimen of comparable wear state is not possible. MLP 67-II-27-359 (Fig. 16B) represents a *Pseudhyrax* palate with most of the teeth preserved, but it has undergone even more wear than SGOPV 2877. A comparison of tooth outlines in MLP 61-IV-9-1, SGOPV 2877, and MLP 67-II-27-359 suggests that these specimens may represent a reasonable wear series for *Pseudhyrax.*

If the upper dentition of SGOPV 2877 does represent *Pseudhyrax,* it solves the "problem" of the lack of good candidates for the lower dentition of SGOPV 2877 (see further discussion below); there do exist good candidates, they just were never recognized as such. Similarly, the recognition of SGOPV 2877 as *Pseudhyrax* also provides an explanation of why no upper remains referable to *Pseudhyrax* had been found previously within the extensive archaeohyracid collections from the Tinguiririca Fauna. Again, at least one example

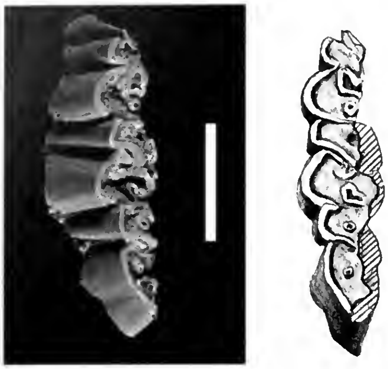

FIG. 17. SGOPV 2901, *Pseudhyrax* sp. indet., left mandibular fragment with partial m1–m3 in oblique labial view (left) and occlusal view (right). Scale bar = 1 cm.

would have been present, but was unrecognized. As *P. eutrachytheroides* is the better known of the two species of *Pseudhyrax,* and because SGOPV 2877 is similar in size and morphology to Argentine specimens referred to *P. eutrachytheroides,* SGOPV 2877 is tentatively referred to that taxon.

Pseudhyrax strangulatus **(Ameghino, 1901)**
(Figure 14A)

HOLOTYPE—MACN 10774, partial right mandible with p4–m2.

REFERRED SPECIMEN—SGOPV 2887, right mandibular fragment with m2–3 (Fig. 14A).

TYPE LOCALITY—Unknown.

AGE AND DISTRIBUTION—As for *Pseudhyrax.*

DIAGNOSIS—Differs from *P. eutrachytheroides* in its smaller size.

COMMENTS—SGOPV 2887, a right mandibular fragment with m2–3, is morphologically similar to relatively unworn specimens of *Pseudhyrax* from Argentina. Based on its size, SGOPV 2887 is referred to *P. strangulatus* (see Fig. 13 and Table 6).

Pseudhyrax **sp. indet.**
(Figure 17)

REFERRED SPECIMEN—SGOPV 2901, left mandibular fragment with partial m1–m3 (Fig. 17), from the Tinguiririca-aged Tinguiririca Fauna of Chile (see above for age discussion).

COMMENTS—SGOPV 2901 is a peculiar specimen. As noted by Wyss et al. (1994: 18), it resembles specimens of *Pseudhyrax,* but the "bizarre anteroposteriorly shortened talonid on m2" and "its posteroexternal termination which forms a tight, nearly 90° corner" make this taxon "unmistakably distinct from any archaeohyracid known." A similar shortening of the talonid is described in the new archaeohyracid taxon from Antofagasta de La Sierra (López, 1997; Reguero & López, 1999), an archaeohyracid allied to *Pseudhyrax* (Reguero & López, 1999, in prep.) from probable Mustersan-aged strata from northwest Argentina (López, 1997). However, the degree to which the m2 talonid is compressed and the abrupt angle of the posteroexternal corner of SGOPV 2901 make the specimen distinct from any other notoungulate currently known.

Wyss et al. (1994) referred SGOPV 2901 to "archaeohyracid new taxon C" and suggested, based on size and morphology, that it might represent a portion of the lower dentition of what they called "archaeohyracid new taxon B" (SGOPV 2877, discussed above). The plausibility of SGOPV 2877 and SGOPV 2901 representing the same taxon was also supported by Croft (2000). If the conclusions reached above regarding the taxonomic affinities of SGOPV 2877 are correct (viz., that SGOPV 2877 is referable to *Pseudhyrax eutrachytheroides*), the potential for the referral of SGOPV 2901 to that taxon warrants consideration.

Indeed, certain attributes of SGOPV 2901 support the interpretation that the very unusual features of this specimen may be the result of incomplete preservation and post-mortem deformation, rather than peculiar attributes of a new taxon. First, although the lingual portions of the talonids of both m1 and m2 are preserved, only the talonid of m2 exhibits the unusual, 90° posteroexternal termination. In other notoungulates, the morphologies of the talonids on m1 and m2 are generally very similar to each other. This suggests that one of the two talonids in SGOPV 2901 may have been deformed, probably the talonid of m2. Second, a slight ridge is present on the lateral surface of the mandible in SGOPV 2901, oriented nearly perpendicular to the long axis of the mandible. The ridge terminates at the base of the talonid of m2 and looks as if it might have resulted from a small anteroposterior compression fold in that portion of the mandible. If this deformation took place plastically, it might have altered the typical rounded talonid morphology (exhibited by m1) into the peculiar, sharply angled morphology exhibited by m2. Third, the talonid of m1 presents a small fossettid directly posterior to the central fossa, a condition characteristic of *Pseudhyrax*; no other characters of m1, the trigonid of m2, or m3 preclude assignment to that taxon. Finally, the dimensions of at least m3 suggest that SGOPV 2901 falls within the range exhibited by Argentine and Tinguiririean *Pseudhyrax* material (Fig. 13; Table 6).

Taking into consideration these observations, there is a reasonable possibility that SGOPV 2901 represents *Pseudhyrax eutrachytheroides*. However, if the unusual structure of the talonid is not due to deformation, the specimen surely represents a new archaeohyracid, perhaps allied to the new archaeohyracid taxon from Antofagasta de La Sierra (López, 1997; Reguero & López, 1999). Given the abundance of poorly founded and/or synonymous names that already exist for so many notoungulates, we refrain from proposing a new taxon based on SGOPV 2901, at least until additional specimens come to light that further clarify the specimen's affinities. SGOPV 2901 is therefore provisionally referred to *Pseudhyrax* sp. indet.

Phylogenetic Relationships

To determine the phylogenetic relationships of the new Tinguiririean archaeohyracids, a preliminary analysis of the five currently recognized archaeohyracid "genera" was undertaken. Two well-known basal typotheres were chosen as outgroups, *Oldfieldthomasia* (Oldfieldthomasiidae) and *Acropithecus* (Archaeopithecidae). A representative hegetotheriid (*Hegetotherium*) was also included in the analysis, since many recent phylogenetic analyses have suggested that hegetotheriids are nested within the series of taxa traditionally included with the Archaeohyracidae (Cifelli, 1993; Hitz, 1995; Croft, 1998; Reguero, 1999; Croft, 2000). The eight taxa were scored for 22 craniodental characters, most modified from the more detailed analyses in Croft (2000). The complete list of characters follows. Characters with multiple derived character states are ordered unless designated by an asterisk. The character-taxon matrix is presented in Table 8.

1. Height of cheek tooth crowns: brachydont, HI < 1.0 (0); moderately hypsodont, 1.0 < HI < 1.75 (1); very hypsodont, HI > 1.75 (2); rootless, HI undefined (3).
2. Cementum: absent (0); present (1).
3. Relative size of I1: mesiodistal length < 50% premaxilla length (0); mesiodistal length ≥ 50% premaxilla length (1).
4. Enamel on I1: present on anterior and posterior faces (0); present only on anterior face (1).
5. I2: present (0); significantly reduced (peg-like and < 50% size of M1) or absent (1).
6. Upper dentition: closed (0); with diastemata separating anterior teeth (1).
7. Upper molars: with lingual sulcus (0); without lingual sulcus (1).
8. Accessory fossettes on upper molars after isolation of central fossa: present (0); absent (1).

9.* Shape of lingual notch separating upper molar protocone and hypocone; broad-based, "u-shaped" (0); sharp-based, "v-shaped" (1); no notch present (2).

10. M3: without posterior lobe (0); with posterior lobe formed by metastyle (1).
11. Lower incisors: implanted subvertically (0); markedly procumbent (1).
12. Relative size of p3 and p4: smaller than anterior molars (0); similar in size to anterior molars (1).
13. Lower molar central trigonid fossettid: absent (0); present (1).
14. Lower molar lingual fossettid between trigonid and talonid: absent (0); present (1).
15. Lingual side of lower molars: with sulcus (0); flat after advanced wear (1); present as salient, straight wall (2).
16. Lower molar shape: varies little with wear (0); develops lingual talonid extension with heavy wear (1).

17.* Shape of lingual notch separating m3 entoconid and hypoconulid: narrow and deep (0); wide and shallow (1); notch absent (2).

18. Small fossettid between m3 entoconid and hypoconulid: absent (0); present (1).
19. Labial surface of m3 talonid: relatively smooth (0); with sulcus between hypoconid and hypoconulid (1); with pronounced notch (2).
20. Carotid foramen: located posterior to auditory bulla (0); shifted anteriorly, medial to auditory bulla (0).
21. Vertical septum in auditory bulla: absent (0); present (1).
22. Hamular process of pterygoid: present (0); absent (1).

TABLE 8. Matrix of characters used in phylogenetic analysis of archaeohyacid relationships.

	01	**02**	**03**	**04**	**05**	**06**	**07**	**08**	**09**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**
Oldfieldthomasia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acropithecus	1	0	0	0	0	0	0	0	?	0	0	1	0	1	0	0	0	0	2	0	0	0
Eohyrax	1	0	0	1	0	0	0	0	0	0	?	0	0	1	0	0	0	0	0	?	?	?
Pseudhyrax	1	0	?	1	?	0	0	0	0	0	?	0	1	1	0	0	0	1	1	?	?	?
Archaeotypotherium	2	0	1	1	0	1	1	0	0	0	1	0	1	1	1	0	1	1	1	1	?	1
Protarchaeohyrax	2	0	?	?	?	?	0	1	1	1	1	0	1	1	1	1	1	0	0	?	?	?
Archaeohyrax	2	1	1	1	0	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1	1
Hegetotherium	3	1	1	1	1	1	1	1	2	1	1	1	0	0	2	0	2	0	1	1	1	1

The data matrix, analyzed using the exhaustive search option in PAUP 3.1.1, resulted in four equally most parsimonious trees of 36 steps each. The strict consensus of these four trees is presented in Figure 18. Consistent with previous analyses, *Hegetotherium* nests within a clade that would traditionally be termed the Archaeohyracidae, suggesting that Archaeohyracidae (in its classical sense) is paraphyletic. Specifically, *Hegetotherium* and two archaeohyracids (*Protarchaeohyrax* and *Archaeohyrax*) are united in an unresolved polytomy based on shared, derived features of the upper dentition: No. 8(1): accessory fossettes on upper molars absent after isolation of central fossa; No. 10(1): M3 with posterior lobe formed by metastyle; No. 9(1): lingual notch between protocone and hypocone "v-shaped" ("u-shaped" is ancestral condition; no notch is present in *Hegetotherium*). The identity of the closest relative of *Hegetotherium* is uncertain, an ambiguity arising from the relatively large amount of missing data for *Protarchaeohyrax*; pending the recovery of material permitting the scoring of these missing characters, either *Archaeohyrax* or *Protarchaeohyrax* is the likeliest proximal outgroup to Hegetotheriidae. Of particular utility would be recovering of specimens preserving the anterior dentition of *Protarchaeohyrax*. The temporally later occurrence of *Archaeohyrax* (Table 9) and the presence of at least one synapomorphy shared by *Archaeohyrax* and *Hegetotherium* to the exclusion of *Protarchaeohyrax* (No. 2(1): cementum present), predict that future analyses will find support for an exclusive closest relationship between *Archaeohyrax* and Hegetotheriidae. (In the present analysis, no synapomor-

TABLE 9. Currently recognized archaeohyracid species.

Taxon	**SALMA**	**Region**	**Reference**
FORMALLY NAMED TAXA			
Eohyrax rusticus	Casamayoran	Patagonia	Simpson, 1967
Eohyrax isotemnoides	Casamayoran	Patagonia	Simpson, 1967
Eohyrax praerusticus	Casamayoran	Patagonia	Simpson, 1967
Pseudhyrax strangulatus	Mustersan	Patagonia	Simpson, 1967
	Tinguirirican	Central Chile	Present study
Pseudhyrax eutrachytheroides	Mustersan	Patagonia	Simpson, 1967
	Tinguirirican	Central Chile	Present study
Protarchaeohyrax gracilis	Tinguirirican	Patagonia; central Chile	Reguero et al., 2003
Protarchaeohyrax intermedium	Tinguirirican	Central Chile	Reguero et al., 2003
Protarchaeohyrax minor	Tinguirirican	Patagonia	Reguero et al., 2003
Archaeotypotherium propheticus	Tinguirirican	Patagonia	Present study
Archaeotypotherium tinguiriricaense	Tinguirirican	Central Chile	Present study
Archaeotypotherium pattersoni	Tinguirirican	Central Chile	Present study
Archaeohyrax patagonicus	Deseadan	Patagonia	[Ameghino, 1897]
INFORMAL TAXA			
Gen. et sp. nov.	Mustersan	Catamarca, Argentina	Reguero & López, 1999
Protarchaeohyrax sp. nov.	Deseadan	Uruguay	Reguero et al., 1995
		Bolivia	Reguero & Cifelli, 1997
Archaeohyrax sp. nov.	Deseadan	Bolivia	Reguero & Cifelli, 1997

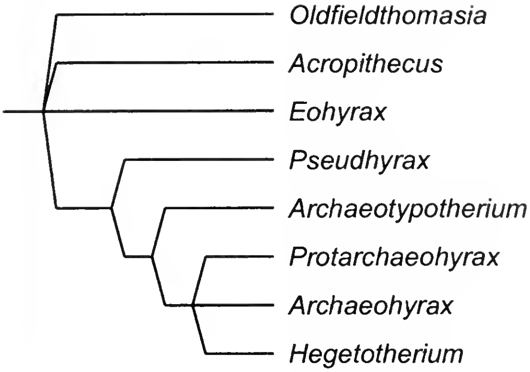

FIG. 18. Strict consensus tree representing the phylogenetic relationships among archaeohyracids. The outgroups for the analysis are *Oldfieldthomasia* (Oldfieldthomasiidae) and *Acropithecus* (Archaeopithecidae). Consistency Index (CI) = 0.78; Rescaled Consistency Index (RCI) = 0.59; Retention Index (RI) = 0.76; Length = 36 steps.

phies uniting *Protarchaeohyrax* and *Hegetotherium* to the exclusion of *Archaeohyrax* were identified.)

The taxa forming the focus of the present study, *Archaeotypotherium* and *Pseudhyrax,* represent successive outgroups to the *Protarchaeohyrax–Archaeohyrax–Hegetotherium* triad. Five synapomorphies link *Archaeotypotherium* with these three taxa, making it the most robustly supported clade in the analysis: No. 1(2~3): HI of cheek teeth > 1.75; No. 6(1): upper dentition with diastemata separating anterior teeth; No. 7(1): upper molars without lingual sulcus (reversed in *Protarchaeohyrax*); No. 15(1~2): lingual side of lower molars flat; No. 17(1): wide and shallow lingual notch separating m3 entoconid and hypoconulid (the notch is absent in *Hegetotherium*). The three basicranial characters (Nos. 20–22) and two incisor characters (3 and 11) represent derived states shared by at least these taxa (and possibly more basal archaeohyracids as well, although the lack of skulls and anterior dentitions for those earlier diverging taxa precludes more definitive identification of the node[s] to which these synapomorphies pertain).

Three synapomorphies diagnose *Pseudhyrax* and later diverging archaeohyracids (plus *Hegetotherium*) to the exclusion of *Eohyrax* (the earliest diverging archaeohyracid): No. 13(1) presence of lower molar central trigonid fossettid (lost in *Hegetotherium*); No. 18(1): presence of small fossettid between m3 entoconid and hypoconulid (either lost in *Protarchaeohyrax* and *Hegetotherium* [ACCTRAN optimization] or independently derived in *Pseudhyrax, Archaeotypotherium,* and *Archaeohyrax* [DELTRAN optimization]); No. 19(1): labial surface of m3 talonid with sulcus between hypoconid and hypoconulid (lost in *Protarchaeohyrax*).

Eohyrax is located at the base of the tree in a polytomy with the two outgroup taxa and the clade of remaining ingroup taxa. Although this topology does not indicate that *Eohyrax* and other archaeohyracids share a most recent common ancestor (MRCA) exclusive of the outgroups, the presence of a single derived character in *Eohyrax* and all archaeohyracids for which the character could be coded [No. 4(1): lack of enamel on the posterior face of I1] suggests more detailed analyses will find greater support grouping *Eohyrax* and other archaeohyracids. Based on their distribution, the derived character states present in *Acropithecus* appear to have been acquired independently in some archaeohyracids and/or *Hegetotherium.*

A notable feature of this analysis is the strong congruence between the branching order of the cladogram and the relative stratigraphic positions of the taxa (cf. Fig. 18 and Table 9); in no instance does the proximal outgroup to a clade have a first appearance later than any of the ingroup taxa. Since many of the derived character states in this analysis are likely correlated with the consumption of more abrasive vegetation (e.g., higher HI values, simplified occlusal surfaces in the cheek teeth, increased emphasis on the anterior dentition and cheek teeth), the tight correlation between cladogenesis and morphologic evolution suggests that dietary selection strongly influenced archaeohyracid evolution. The most robustly supported clade in the analysis (*Archaeotypotherium, Protarchaeohyrax, Archaeohyrax, Hegetotherium*) records its first appearance in the earliest Oligocene Tinguiririan SALMA (Flynn et al., 2003); this implies an initial divergence approximately coincident with, and possibly causally related to, the Eocene-Oligocene climatic deterioration (see below). From a phylogenetic perspective, most (if not all) of the characters conventionally used to diagnose hegetotheriids (enlarged and hypselodont I1, hypselodont cheek teeth, complete lack of dental fossettes and fossettids; Cifelli, 1993; Reguero, 1998; Croft, 2000) can be interpreted as elaborations of derived character states already present in the later diverging archaeohyracids. It is therefore not surprising that Archaeohyracidae (in the classical sense of that name) is now shown to be paraphyletic.

From the perspective of phylogenetic taxonomy (de Quieroz & Gauthier, 1990), however, whereby names are defined by linking them to specified clades, names refer to monophyletic groups (by definition). Thus, if one were to fashion a phylogenetic definition for the least inclusive clade including *Eohyrax* and *Archaeohyrax* (e.g., Archaeohyracidae = MRCA of those two taxa plus all its descendants), Archaeohyracidae would refer to a clade happening to have as one of its members a group (viz., Hegetotheriidae) of "equivalent" taxonomic rank (at least as far as traditional taxonomic suffixes are concerned). Whether or not this "clash of suffixes" is viewed as significant, the present phylogenetic analysis points to the need for a comprehensive review of the names associated with major clades of typothere notoungulates.

Based on the topology obtained in this analysis, the species classically referred to as archaeohyracids and hegetotheriids (with the possible exception of *Eohyrax*) share an exclusive common ancestry, and thus form an evolutionary entity worthy of naming. A phylogenetic definition of a name for this clade can be fashioned any number of ways, each with pros and cons. For example, in naming this clade, the clade itself might be described (in the definition statement) with reference to the MRCA of its earliest diverging member (*Eohyrax*) and some other constituent (e.g., *Archaeohyrax, Hegetotherium*), plus all of its descendants. Which taxon is specified in the second position of this definition statement is relatively unimportant, as any number of options would encompass all species presently termed archaeohyracids or hegetotheriids and would exclude other notoungulates.

One potential disadvantage of phrasing a definition in such a node-based fashion is that it would not accommodate the discovery of earlier diverging members of the clade. A stem-based definition (sensu de Queiroz & Gauthier, 1990), however, would overcome this problem. Mesotheriidae has been advocated as the proximal outgroup to archaeohyracids plus hegetotheriids (e.g., Cifelli, 1993; Croft, 2000), but the interrelationships of typotheres have yet to be thoroughly examined. Pending a comprehensive examination of the phylogenetic relationships among typotheres, a stem-based definition for archaeohyracids plus hegetotheriids could be formulated as all typotheres more closely related to *Archaeohyrax* (or *Hegetotherium*) than to *Mesotherium, Interatherium, Acropithecus,* or *Oldfieldthomasia.*

Perhaps the more difficult question is which names to attach to the major subclades of typotheres about whose existence we are confident. The names most commonly associated with the groups discussed herein are the "family" names Archaeohyracidae and Hegetotheriidae. If conserving both of these long-used names is considered desirable, Archaeohyracidae could be defined such that it refers to all taxa previously referred to both of these "families" collectively. As noted above, however, having Hegetotheriidae nested within another clade bearing a name with the same suffix (Archaeohyracidae) could potentially cause confusion. This problem might be circumvented by amending Hegetotheriidae to Hegetotheriinae (and changing the included groups Hegetotheriinae and Pachyrukhinae to Hegetotherini and Pachyrukhini, respectively), but this tactic would not preserve the two "family" names (the original intention of such a scheme) and would likely cause more confusion than clarification. Alternatively, the name Hegetotheriidae could be defined such that it applies to hegetotheriids plus the taxa traditionally termed archaeohyracids, but again, this arrangement would fail to preserve the two "family" names. In either case, these names would dramatically differ from their traditional conceptions.

Rather than employ a traditional "family" name to refer to the clade including both archaeohyracids and hegetotheres, an alternative would be to redefine a name traditionally used to encompass a similar group. One obvious choice would be Simpson's Hegetotheria (Simpson, 1945). This suborder of Notoungulata originally included only the Hegetotheriidae, but was later modified to also include the Archaeohyracidae (Simpson, 1967). It would thus seem reasonable to tie either a node-based or a stem-based definition to this name to encompass both hegetotheriids and archaeohyracids, concordant with Simpson's conception of the group. Another option would be Hegetotheroidea, proposed by Romer (1966) as including both archaeohyracids and hegetotheriids. Since Romer's recognition of the association between archaeohyracids and hegetotheriids was proposed a year prior to Simpson's revision of Hegetotheria, use of the name Hegetotheroidea would be an appropriate tribute. Similar (but novel) names based on the earliest diverging members of the group (e.g., Archaeohyracia, Archaeohyracoidea) or a combination of the members (e.g., Archaeohegetotheria, Hegetoarchaeohyracoidea) could also be used.

Some combination of these higher-level and/or traditional "family" names could be used if there were sufficient justification to attach names to multiple components of the preferred phylogeny. The precise phrasing of such definitions may be tailored to insure nomenclatural stability in the face of potential future changes in topology.

None of the potential combinations of definitions and names discussed above is ideal; each represents a compromise. As the present phylogenetic study is not a comprehensive examination of relationships among archaeohyracids and hegetotheriids, we do not propose new definitions of names at this time. We raise these issues to illustrate potential options for doing so, since we ourselves have grappled with the question of how best to refer to the clades in question. We defer the naming of clades to a more comprehensive cladistic analysis.

Conclusions

One of the most striking aspects of the Tinguiririca Fauna of Chile is its high diversity of archaeohyracids. In the preliminary description of the fauna, Wyss et al. (1994) argued that no fewer than five and perhaps as many as nine archaeohyracid taxa might be represented. The present study (combined with the findings of Reguero et al., 2003) recognizes at least six archaeohyracid taxa from the Tinguiririca Fauna, and notes the possibility of a seventh. The revised identifications of archaeohyracid specimens considered in Wyss et al. (1994) are listed in Table 7.

This remarkably high diversity represents the peak for the Archaeohyracidae. Besides Tinguiririca, no single fauna is known to have had more than three contemporaneous archaeohyracid species, and among South American Land Mammal Ages, the Tinguirirican records the occurrence of eight of the 15 currently recognized species, almost triple that of any other SALMA (no others have more than three species, Table 9; see also Flynn et al., 2003, Table 2). With increasingly precise age constraints for middle Cenozoic South American fossil localities (Flynn & Swisher, 1995; Madden et al., 1997; Kay et al., 1999; Flynn et al., 2003), it has become apparent that the archaeohyracid radiation that resulted in this peak diversity during the Tinguirirican SALMA took place over a relatively short period of time—the entire stratigraphic range of the group may be as little as 15 million years, depending on the age of the beginning of the Casamayoran SALMA (wherein the first archaeohyracids are recorded). With the exception of the Archaeopithecidae (a small group of basal notoungulates known exclusively from the Casamayoran) and Campanorcidae (a monotypic family, also from the Casamayoran), this is likely the shortest range of any of the 14 traditional notoungulate "families."

Although the reason for such a rapid diversification of archaeohyracids is unknown, its temporal proximity to the Eocene/Oligocene boundary suggests the group might have been "preadapted" to exploit, or at least were able to respond extremely rapidly to, the changing habitats associated with the Eocene-Oligocene transition and early Oligocene "climatic deterioration" (Wolfe, 1971; Prothero & Berggren, 1992; Prothero, 1994). Alternatively, these changes may have led to greater habitat fragmentation and increased isolation of archaeohyracid populations, with allochthony yielding higher levels of speciation and cladogenesis. Current evidence suggests that the global events that marked the Eocene-Oligocene transition also resulted in cooler, drier climates and more open habitats in South America (e.g., MacFadden, 1985; Pascual & Ortiz Jaureguizar, 1990; Wyss et al., 1993, 1994, 1996; Pascual et al., 1996; Flynn & Wyss, 1998, 1999; Kay et al., 1999; Croft, 2001; Flynn et al., 2003). As modern mammalian herbivores that graze in open habitats tend to exhibit high levels of hypsodonty (Janis 1984, 1988, 1990, 1995), the environmental changes associated with the Eocene-Oligocene transition would likely have favored more hypsodont herbivores. Indeed, most clades of early Oligocene Tinguirirican notoungulates exhibit sharply increased hypsodonty as compared with their late Eocene Mustersan relatives (e.g., interatheriids, archaeohyracids, notohippids), suggesting across-clade responses to these changing habitats (Flynn et al., 2003). Since archaeohyracids were among the first hypsodont members of the Notoungulata (as illustrated by the late Eocene Casamayoran *Eohyrax*; Simpson, 1967), the group might have diversified so rapidly during the Tinguirirican as a result of already having initiated hypsodonty and thus being "better positioned" to quickly respond evolutionarily to the dramatically changing climate and habitats. This advantage seems to have been short-lived, however, as archaeohyracids are last known from the mostly late Oligocene Deseadan SALMA. Filling a niche that presumably was similar to that of the hypsodont archaeohyracids, other small notoungulates with hypselodont (ever-growing) cheek teeth (e.g., hegetotheriids, interatheriids, mesotheriids) diversified during the late Oligocene (Deseadan SALMA) and into the early Miocene. Nevertheless, Tinguiririican SALMA assemblages document a short, previously unrecognized burst of exceptional evolutionary success for Archaeohyracidae, the first notoungulate "family" dominated by hypsodont species.

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Literature Cited

Ameghino, F. 1897. Les Mammifères crétacés de l'Argentine. Deuxième contribution à la connaissance de la faune mammalogique des couches à *Pyrotherium*. Boletín del Instituto Geográfico Argentino, **18:** 406–521.

———. 1901. Notices préliminaires sur des ongulés nouveaux des terrains crétacés de Patagonie. Boletín de la Academia Nacional de Ciencias de Córdoba, **16:** 350–426.

———. 1902. Notices préliminaires sur des mamifères nouveaux des terrains crétacés de Patagonie. Boletín de la Academia Nacional de Ciencias de Córdoba, **17:** 5–73.

Bond, M., G. López, and M. Reguero. 1996. "Astraponoteén plus supérieure" of Ameghino: Another interval in the Paleogene record of South America. Journal of Vertebrate Paleontology, **16**(Suppl. to No. 3): 23A.

———. 1997a. Rocas Bayas, una localidad fosilífera Paleógena de la Provincia de Río Negro, República Argentina. Ameghiniana, **34**(4): 533.

Bond, M., M. Reguero, G. López, A. A. Carlini, F. Goin, R. H. Madden, M. G. Vucetich, and R. F. Kay. 1997b. The "Astraponotéen plus supérieur" (Paleogene) in Patagonia. Ameghiniana, **34**(4): 533.

Charrier, R., A. R. Wyss, J. J. Flynn, C. C. Swisher, M. A. Norell, F. Zapatta, M. C. McKenna, and M. J. Novacek. 1996. New evidence for late Mesozoic–early Cenozoic evolution of the Chilean Andes in the upper Tinguiririca Valley (35°S), central Chile. Journal of South American Earth Sciences, **9**(5/6): 393–422.

Charrier, R., A. R. Wyss, M. A. Norell, J. J. Flynn, M. J. Novacek, M. C. McKenna, C. C. Swisher III, D. Frassinetti, and P. Salinas. 1990. Hallazgo de mamíferos fósiles del Terciario Inferior en el sector de Termas del Flaco, Cordillera Principal, Chile Central: implicaciones paleontológicas, estratigráficas y tectónicas. Actas Segundo Simposio sobre le Terciario de Chile, Concepción, pp. 73–84.

Cifelli, R. L. 1993. The phylogeny of the native South American ungulates, pp. 195–216. *In* Szalay, F. S., M. J. Novacek, and M. C. McKenna, eds., Mammal Phylogeny: Placentals. Springer-Verlag, New York.

Croft, D. A. 1998. Experiments in herbivory: Evolution in the Archaeohyracidae (Mammalia: Notoungulata). Journal of Vertebrate Paleontology, **18**(Suppl. to No. 3): 36A.

———. 2000. Archaeohyracidae (Mammalia, Notoungulata) from the Tinguiririca Fauna, central Chile, and the evolution and paleoecology of South American mammalian herbivores. Ph.D. diss., University of Chicago, 311 pp.

———. 2001. Cenozoic environmental change in South American as indicated by mammalian body size distributions (cenograms). Diversity and Distributions, **7:** 271–287.

de Queiroz, K., and J. Gauthier. 1990. Phylogeny as a central principle in taxonomy: Phylogenetic definitions of taxon names. Systematic Biology, **39:** 307–322.

Flynn, J. J., M. A. Norell, C. C. Swisher, and A. R. Wyss. 1991. Pre-Deseadan, post-Mustersan mammals from central Chile: An update. Journal of Vertebrate Paleontology, **11**(Suppl. to No. 3): 29A.

Flynn, J. J., and C. C. Swisher III. 1995. Cenozoic

South American Land Mammal Ages: Correlation to global geochronologies, pp. 317–333. *In* Berggren, W. A., D. V. Kent, M.-P. Aubry, and J. Hardenbol, eds., Geochronology, Time Scales, and Global Stratigraphic Correlation. SEPM (Society of Sedimentary Geology) Special Publication No. 54.

Flynn, J. J., and A. Wyss. 1990. New early Oligocene marsupials from the Andean Cordillera, Chile. Journal of Vertebrate Paleontology, **10**(Suppl. to No. 3): 22A.

Flynn, J. J., and A. R. Wyss. 1998. Recent advances in South American mammalian paleontology. Trends in Ecology and Evolution, **13**(11): 449–454.

———. 1999. New marsupials from the Eocene-Oligocene transition of the Andean Main Range, Chile. Journal of Vertebrate Paleontology, **19**(3): 533–549.

Flynn, J. J., A. R. Wyss, D. A. Croft, and R. Charrier. (2003). The Tinguiririca Fauna, Chile: Biochronology, paleoecology, biogeography, and a new earliest Oligocene South American Land Mammal "Age." Palaeogeography, Palaeoclimatology, Palaeoecology, **195**(3–4): 229–259.

Gingerich, P. D. 1974. Size variability of the teeth in living mammals and the diagnosis of closely related sympatric fossil species. Journal of Paleontology, **48**(5): 895–903.

Hitz, R. 1995. Typothere (Notoungulata) phylogeny and proposed taxonomic revisions. Journal of Vertebrate Paleontology, **15**(Suppl. to No. 3): 34A.

Hitz, R., M. Reguero, A. R. Wyss, and J. J. Flynn. 2000. New interatheriines (Interatheriidae, Notoungulata) from the Paleogene of Central Chile and Southern Argentina. Fieldiana: Geology, New Series, **42:** 1–26.

Janis, C. M. 1984. The use of fossil ungulate communities as indicators of climate and environment, pp. 85–104. *In* Brenchley, P., ed., Fossils and Climate. John Wiley & Sons Ltd., Chichester, U.K.

———. 1988. An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preference, pp. 371–391. *In* Russell, D. E., J. P. Santoro, and D. Sigogneau-Russell, eds., Teeth Revisited: Proceedings of the VIIth International Congress of Dental Morphology. Memoires du Museum d'Histoire Naturelle de Paris, série C.

———. 1990. Correlation of cranial and dental variables with dietary preference in mammals: A comparison of macropodids and ungulates. Memoirs of the Queensland Museum, **28**(1): 349–366.

———. 1995. Correlations between craniodental morphology and feeding behavior in ungulates: Reciprocal illumination between living and fossil taxa, pp. 76–98. *In* Thomason, J. J., ed., Functional Morphology in Vertebrate Paleontology. Cambridge University Press, New York.

Kay, R. F., R. H. Madden, M. G. Vucetich, A. A. Carlini, M. M. Mazzoni, G. H. Re, M. Heizler, and H. Sandeman. 1999. Revised geochronology of the Casamayoran South American Land Mammal Age: Climatic and biotic implications. Proceedings of the National Academy of Sciences **96**(23): 13235–13240.

Loomis, F. B. 1914. The Deseado Formation of Patagonia. Runford Press, Concord, New Hampshire, 232 pp.

López, G. M. 1997. Paleogene faunal assemblage from Antofagasta de la Sierra (Catamarca Province, Argentina). Palaeovertebrata, **26:** 61–81.

MacFadden, B. J. 1985. Drifting continents, mammals, and time scales: Current developments in South America. Journal of Vertebrate Paleontology, **5**(2): 169–174.

MacFadden, B. J., K. E. Campbell, Jr., R. L. Cifelli, O. Siles, N. M. Johnson, C. W. Naeser, and P. K. Zeitler. 1985. Magnetic polarity stratigraphy and mammalian fauna of the Deseadan (Late Oligocene–Early Miocene) Salla Beds of northern Bolivia. Journal of Geology, **93**(3): 223–250.

Madden, R. H., J. Guerrero, R. F. Kay, J. J. Flynn, C. C. Swisher III, and A. H. Walton. 1997. The Laventan Stage and Age, pp. 355–381. *In* Kay, R. F., R. H. Madden, R. L. Cifelli, and J. J. Flynn, eds., Vertebrate Paleontology in the Neotropics: The Miocene Fauna of La Venta, Colombia. Smithsonian Institution Press, Washington, D.C.

Marshall, L. G., R. L. Cifelli, R. E. Drake, and G. H. Curtis. 1986. Vertebrate paleontology, geology, and geochronology of the Tapera de López and Scarritt Pocket, Chubut Province, Argentina. Journal of Paleontology, **60**(4): 920–951.

Novacek, M. J. 2002. Time Traveler: In Search of Dinosaurs and Ancient Mammals from Montana to Mongolia. Farrar, Straus and Giroux, New York, 368 pp.

Novacek, M. J., A. Wyss, D. Frassinetti, and P. Salinas. 1989. A new ?Eocene mammal fauna from the Andean Main Range. Journal of Vertebrate Paleontology, **9**(Suppl. to No. 3): 34A.

Pascual, R., and E. O. Jaureguizar. 1990. Evolving climates and mammal faunas in Cenozoic South America. Journal of Human Evolution, **19:** 23–60.

Pascual, R., E. Ortiz Jaureguizar, and J. L. Prado. 1996. Land mammals: Paradigm for Cenozoic South American geobiotic evolution. Münchner Geowissenschaftliche Abhandlungen A, **30:** 265–319.

Patterson, B. 1936. The internal structure of the ear in some notoungulates. Geological Series, Field Museum of Natural History, **6:** 199–227.

Prothero, D. R. 1994. The late Eocene-Oligocene extinctions. Annual Review of Earth and Planetary Sciences, **22:** 145–165.

Prothero, D. R., and W. A. Berggren. 1992. Eocene-Oligocene Climatic and Biotic Evolution. Princeton University Press, Princeton, New Jersey, 568 pp.

Reguero, M. A. 1993. Los Typotheria y Hegetotheria (Mammalia, Notoungulata) eocenos de la localidad Cañadón Blanco, Chubut. Ameghiniana, **30**(3): 336.

———. 1998. El problema de las relaciones sistemáticas y filogenéticas de los Typotheria y Hegetotheria (Mammalia, †Notoungulata): Análisis de los taxones de Patagonia de la Edad-mamífero Deseadense (Oligoceno). Ph.D. diss., Universidad de Buenos Aires, Buenos Aires.

Reguero, M. A., and R. L. Cifelli. 1997. Deseadan Archaeohyracidae from Salla, Bolivia. Ameghiniana, **34**(3): 539.

REGUERO, M. A., D. A. CROFT, J. J. FLYNN, AND A. R. WYSS. (2003). Small archaeohyracids (Typotheria, Notoungulata) from Chubut Province, Argentina, and central Chile: Implications for trans-Andean temporal correlation. Fieldiana: Geology, n.s. **48**: 1–17.

REGUERO, M., AND G. LÓPEZ. 1999. Un nuevo Archaeohyracidae (Notoungulata, Hegetotheria) del Paleógeno de Antofagasta de la Sierra, provincia de Catamarca, Argentina. Ameghiniana, **36**(1): 107.

ROMER, A. S. 1966. Vertebrate Paleontology. University of Chicago Press, 468 pp.

ROTH, S. 1903. Noticias preliminares sobre nuevos mamíferos fósiles del Cretáceo superior y Terciario inferior de la Patagonia. Revista, Museo de La Plata, **11:** 133–158.

SHOCKEY, B. J. 1997. Toxodontia of Salla, Bolivia (late Oligocene): Taxonomy, systematics, and functional morphology. Ph.D. diss., University of Florida, Gainesville, 275 pp.

SIMPSON, G. G. 1945. The principles of classification and a classification of mammals. Bulletin of the American Museum of Natural History, **85:** 1–350.

———. 1967. The beginning of the age of mammals in South America. Part II. Bulletin of the American Museum of Natural History, **137:** 1–260.

SINCLAIR, W. J. 1909. Typotheria of the Santa Cruz beds, pp. 1–110. *In* Scott, W. B., ed., Reports of the Princeton University Expeditions to Patagonia, 1896–1899. Princeton University, Princeton, NJ.

WOLFE, J. A. 1971. Tertiary climatic fluctuations and methods of analysis of Tertiary floras. Palaeogeography, Palaeoclimatology, Palaeoecology, **9:** 27–57.

WYSS, A. R., R. CHARRIER, AND J. J. FLYNN. 1996. Fossil mammals as a tool in Andean stratigraphy: Dwindling evidence of Late Cretaceous volcanism in the South Central Main Range. PaleoBios, **17**(2–4): 13–27.

WYSS, A. R., AND J. J. FLYNN. 1991. Phylogenetic and biostratigraphic implications of a new early Oligocene marsupial fauna from the Tinguiririca Valley, Chile. PaleoBios, **13**(Suppl. to No. 50): 10.

WYSS, A. R., J. J. FLYNN, M. A. NORELL, C. C. SWISHER III, R. CHARRIER, M. J. NOVACEK, AND M. C. MCKENNA. 1993. South America's earliest rodent and recognition of a new interval of mammalian evolution. Nature, **365:** 434–437.

WYSS, A. R., J. J. FLYNN, M. A. NORELL, C. C. SWISHER III, M. J. NOVACEK, M. C. MCKENNA, AND R. CHARRIER. 1994. Paleogene mammals from the Andes of central Chile: A preliminary taxonomic, biostratigraphic, and geochronologic assessment. American Museum Novitates, **3098:** 1–31.

WYSS, A. R., J. J. FLYNN, C. C. SWISHER III, R. CHARRIER, AND M. A. NORELL. 1992. Fossil mammals from the central Chilean Andes: A new interval in the South American land mammal succession, and implications for Eocene-Oligocene boundary events and Andean tectonics. Paleontological Society, Special Publication, **6:** 318.

WYSS, A. R., M. A. NORELL, AND J. J. FLYNN. 1993. An exceptional archaeohyracid fauna from the Tinguiririca River valley of central Chile. Journal of Vertebrate Paleontology, **13**(Suppl. to No. 3): 64A.

WYSS, A. R., M. A. NORELL, J. J. FLYNN, M. J. NOVACEK, R. CHARRIER, M. C. MCKENNA, C. C. SWISHER, D. FRASINETTI, AND M. JIN. 1990. A new early Tertiary mammal fauna from central Chile: Implications for Andean stratigraphy and tectonics. Journal of Vertebrate Paleontology, **10**(4): 518–522.

WYSS, A. R., M. A. NORELL, M. J. NOVACEK, AND J. J. FLYNN. 1992. New ?early Tertiary localities from the Chilean Andes. Journal of Vertebrate Paleontology, **12**(Suppl. to No. 3): 61A.

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