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## THE HEGETOTHERIIDAE (MAMMALIA, NOTOUNGULATA) ASSEMBLAGE FROM THE LATE OLIGOCENE OF MENDOZA, CENTRAL-WESTERN ARGENTINA

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**ABSTRACT**—This study describes new remains of Hegetotheriidae (Notoungulata), including a new species, from the Deseadan (late Oligocene) of Quebrada Fiera, Mendoza Province, Argentina. The assemblage is composed of four hegetotheriines, *Prohegetotherium* cf. *P. sculptum*, *Prohegetotherium* sp., *Prohegetotherium schiaffinoi*, and *Prohegetotherium malalhuense*, sp. nov., and the pachyrukhine *Propachyruco* cf. *P. simpsoni*. The presence of *Prosotherium* cannot be totally discounted because lower molariforms are rather similar between the two pachyrukhine genera. The new species *Prohegetotherium malalhuense*, sp. nov., differs from all previously described hegetotheriines by having a lingually projecting, sharp parastyle and marked parastyle groove on the ectoloph of M2–3; talonid of m1–2 posterolabially projected; talonid of m3 with marked posterolabial groove; and the smaller size. Its phylogenetic affinities are not well resolved. *Prohegetotherium* is paraphyletic, with *P. sculptum* sister taxon to the remaining hegetotheres, and the new taxon more closely related to *Hegetotherium mirabile* than to *P. schiaffinoi*. The recognition of *P. schiaffinoi* and *Prohegetotherium* cf. *P. sculptum* emphasizes that the fauna from Quebrada Fiera shares elements with roughly contemporaneous Deseadan faunas from northern and southern latitudes, but important faunal particularities distinguish the region as well. The record of pachyrukhines at Quebrada Fiera more closely resembles Deseadan faunas in Patagonia than temporally correlative faunas from Bolivia and Uruguay, and indicates the presence of suitable habitats in mid-latitudes of Argentina for this hypselodont clade. Faunal affinities together with particular taxa from Quebrada Fiera appear to support a significant faunal provinciality in South America during the late Oligocene.

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**SUPPLEMENTAL DATA**—Supplemental materials are available for this article for free at [www.tandfonline.com/UJVP](http://www.tandfonline.com/UJVP)

### INTRODUCTION

Studies on Paleogene South American fossil mammals have traditionally focused on faunas from high latitudes, especially those coming from Patagonia, Argentina (Patterson and Pascual, 1972; Simpson, 1980). Lately, different extra-Patagonian areas have yielded interesting faunal assemblages that increase their knowledge, such as the case of Quebrada Fiera, Mendoza, Argentina.

Herein a new hegetotheriine species (Hegetotheriidae, Notoungulata) and four other hegetotheriids from the late Oligocene of Quebrada Fiera are described. This assemblage provides new insights into hegetother diversity during the Paleogene and allows comparisons between high latitude Deseadan faunas and similarly aged mid- and low-latitude faunas.

The Deseadan (late Oligocene) mammal-bearing horizons of Quebrada Fiera are located about 15 km south of El Zampal in the Malargüe Department, south of Mendoza Province, in central-western Argentina (Fig. 1). The white-grayish tuffs and tobaceous paleosols that constitute the fossiliferous level are presently considered to be the base of the Agua de la Piedra Formation (Combina and Nullo, 2008, 2011). Field work since 2006 have greatly increased the faunal list from Quebrada Fiera (Gorroño et al., 1979; Bond and Pascual, 1983; Pascual and de la

Fuente, 1993) and provided new data on this Deseadan extra-Patagonian assemblage (Prámparo et al., 2006; Pujos et al., 2008; Cerdeño and Vera, 2010, 2014a, 2014b; Cerdeño et al., 2010a; Cerdeño, 2011; Forasiepi et al., 2014), which includes typical Deseadan taxa together with unique faunal elements.

Hegetotheriids are small tyothere notoungulates; some of the latest representatives were very similar in overall morphology to modern rabbits (leporids) or certain caviomorph rodents (e.g., *Dolichotis*) (Elissamburu, 2004; Elissamburu and Vizcaíno, 2004; Reguero et al., 2007). Two hegetotheriid subfamilies are recognized (Simpson, 1945a): Hegetotheriinae and Pachyrukhinae.

Phylogenetic analyses indicate the Hegetotheriinae as a paraphyletic group; the monophyletic subset of Miocene taxa obtained by some authors (Cifelli, 1993; Croft and Anaya, 2006) is not supported in a recent analysis (Kramarz and Paz, 2013). All Argentinean Paleogene ‘hegetotheriines’ have been referred to *Prohegetotherium*, a genus that occurs at La Cantera (Chubut), early Oligocene, and various Deseadan, late Oligocene, localities in Patagonia (Reguero and Prevosti, 2010); and also recognized in ?early Miocene beds at Divisadero Largo, Mendoza (López, 2002, 2010; Reguero and Cerdeño, 2005; Cerdeño et al., 2008). It is also present in the early Oligocene (Tinguirican SALMA [South American Land Mammal Age]) of Cachapoal, Chile, (Croft et al., 2008a, 2008b). A second genus, *Sallatherium*, was defined in the Deseadan locality of Salla, Bolivia (Reguero and Cerdeño, 2005). Hegetotheriids are absent from the early Oligocene Tinguiririca Fauna (Chile) and the APS (‘Astraponotéen plus supérieur’) level at Gran Barranca (Chubut, Argentina). A previous record in Tinguirirican levels from Cañadón Blanco,

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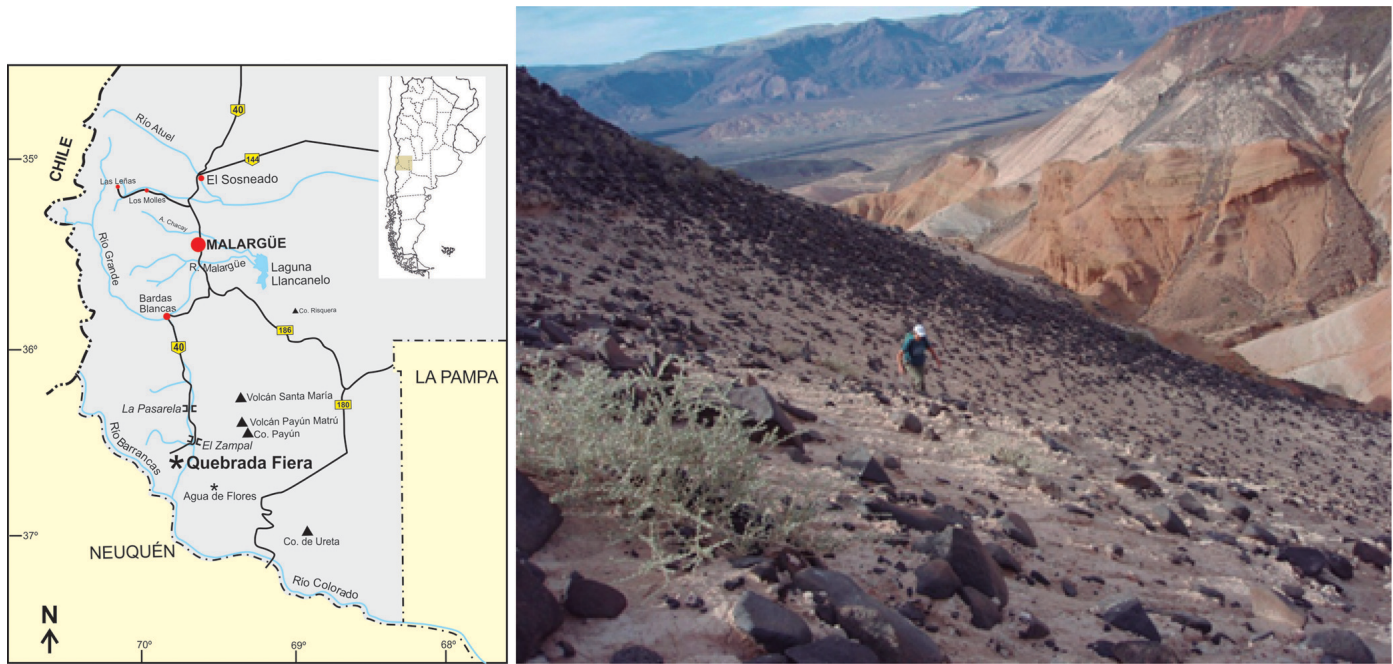


FIGURE 1. Geographic location and general landscape of Quebrada Fiera, Mendoza, Argentina.

Chubut (Bond, 1991; Reguero, 1999), was taxonomically reinterpreted as an Archaeohyracidae (Cerdeño et al., 2010b).

In turn, Pachyrukhinae are broadly considered to constitute a monophyletic group (Cerdeño and Bond, 1998); the clade is recognizable in the Deseadan SALMA, late Oligocene (Loomis, 1914; Simpson, 1945b; Reguero et al., 2007), and reaches the early Pleistocene in Argentina (Cerdeño and Bond, 1998). Three genera are recognized during the Paleogene: *Prosotherium*, *Propachyruco*, and *Medistylus*.

MATERIALS AND METHODS

The studied material from Quebrada Fiera belongs to the paleontological collection of the Museo de Ciencias Naturales y Antropológicas ‘J. C. Moyano,’ Mendoza City, Argentina. It mainly consists of maxillary and mandibular fragments, as well as some postcranial remains, which are detailed in the Systematic Paleontology section. Morphological and metric descriptions are based on comparative material from Argentina and Bolivia as well as bibliographic data. Measurements were taken with vernier and digital calipers and mainly refer to maximal diameters of each tooth as well as the series lengths.

Based on previous studies, a phylogenetic analysis of Hegetotheriidae was performed by means of cladistic methodology with the computer program T.N.T. (Goloboff, 1995; Kitching et al., 1998; Goloboff et al., 2008), as detailed in the corresponding section.

**Institutional Abbreviations**—**AMNH**, American Museum of Natural History, New York, U.S.A.; **FMNH**, Field Museum of Natural History, Chicago, U.S.A.; **MACN**, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia,’ Buenos Aires, Argentina; **MCNAM-PV**, Museo de Ciencias Naturales y Antropológicas ‘J. C. Moyano,’ Vertebrate Paleontology Collection, Mendoza, Argentina; **MLP**, Museo de La Plata, La Plata, Argentina; **MNHN-Bol-V**, Museo Nacional de Historia Natural, Vertebrate Paleontology Collection, La Paz, Bolivia; **MNHN-DP**, Museo Nacional de Historia Natural de Montevideo, Montevideo Uruguay; **MNHN-T**, Muséum national d’Histoire naturelle, Tournouër collection, Paris, France; **PZ-Ctes**, Paleozoology

Collection, Universidad Nacional del Noreste, Corrientes, Argentina; **UF**, University of Florida, Gainesville, U.S.A.

**Anatomical Abbreviations**—**C**, canine; **I**, incisor; **L**, length; **l**, left; **M/m**, upper/lower molar; **P/p**, upper/lower premolar; **r**, right; **W**, width.

SYSTEMATIC PALEONTOLOGY

NOTOUNGULATA Roth, 1903

TYPOTHERIA Zittel, 1893

(sensu Reguero and Castro, 2004)

TYPOTHERIOIDEA Reguero and Prevosti, 2010

HEGETOTHERIIDAE Ameghino, 1894

**Remark**—Reguero and Prevosti (2010) diagnosed the taxon Hegetotheriidae as all notoungulates more closely related to *Prohegetotherium* (the most basal member of the clade) and *Paeodotherium* (or any other hegetotheriid) and all of its descendants.

HEGETOTHERIINAE Ameghino, 1894

The taxa classically considered to compose the Hegetotheriinae are paraphyletic according to the analysis in Reguero and Prevosti (2010).

PROHEGETOTHERIUM Ameghino, 1897

**Diagnosis**—Based on Reguero and Cerdeño (2005): I1 less hypertrophied than *Sallatherium*, *Hegetotherium*, and *Hemihegetotherium*. Maxillary root of the zygomatic arch less developed than in *Hegetotherium* and *Hemihegetotherium*. I2 and I3 less reduced than in *Hegetotherium*, *Sallatherium*, and *Hemihegetotherium*. Upper canine present. M3 with more convex lingual face and more reduced metastyle than *Hegetotherium*. Lower canine reduced (*Prohegetotherium sculptum*). Lower third molar with elongated second lobe.

**Type Species**—*Prohegetotherium sculptum* Ameghino, 1897.

PROHEGETOTHERIUM cf. P. SCULPTUM (Fig. 2A–D)

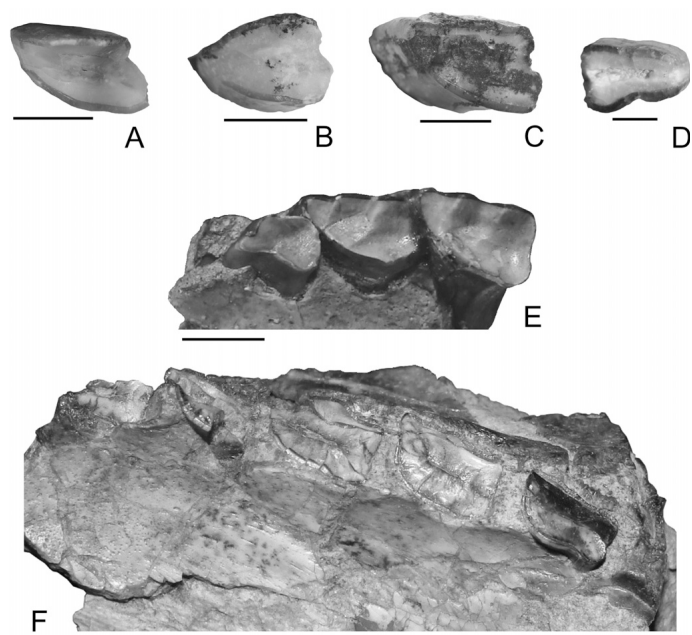


FIGURE 2. (A–D) *Prohegetotherium* cf. *sculptum*. A, MCNAM-PV 4655, right (reversed) P3; B, MCNAM-PV 4662, right (reversed) P3; C, MCNAM-PV 4660, left P4 or M1; D, MCNAM-PV 4659, right p2. (E, F) *Prohegetotherium sculptum*, E, MACN A 52-443, lectotype, left P2–4; F, MACN A 52-444, syntype, left P3–M3. Occlusal views. Scale bars equal 5 mm.

**Referred Material**—MCNAM-PV 4655 and PV 4662, right P3s; MCNAM-PV 4660, left P4 or M1; MCNAM-PV 4408, fragment of left upper premolar; and tentatively MCNAM-PV 4659, right p2.

**Description and Comparison**—The large specimens of hegetotheriids (Table 1) include some isolated teeth that display similarities with those of *Prohegetotherium sculptum*. Among them, three upper premolars are triangular teeth, with a wide, smooth labial anterior sulcus (Fig. 2A–C). MCNAM-PV 4660 also shows a shallow depression on the posterolabial half, which is more characteristic of the molars, based on comparison with the type specimens of the species (Fig. 2E–F), but the anterolingual profile is more similar to the premolars. A lower p2, MCNAM-PV 4659 (Fig. 2D), is tentatively assigned to the same taxon; it appears to be less elongated than the p2 of AMNH 29605 (Reguero and Cerdeño, 2005), but it is also more worn; its dimensions are L = 5.8 mm, W = 4.0 mm.

*PROHEGETOTHERIUM* sp.  
(Fig. 3)

**Referred Material**—MCNAM-PV 3984, left M1 or M2; MCNAM-PV 4406, right P2 or P3; MCNAM-PV 4652, right M1 or M2; MCNAM-PV 4656 left P3; MCNAM-PV 4666, right P3; and MCNAM-PV 4620, right m3.

**Description and Comparison**

All the included upper teeth are large (Table 1) and differ from those assigned to *P. cf. sculptum* by the presence of a deeper anterolabial groove, a well-marked parastyle directed

TABLE 1. Upper tooth dimensions (mm) of Hegetotheriidae from Quebrada Fiera and compared specimens.

Specimen	P1		P2		P3		P4		M1		M2		M3	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W
<i>P. malalhuense</i> , sp. nov.														
PV 3848			(3.2)	(2.3)	4.6	2.9	4.5	3.1	5.4	3.2	5.5	3.3	4.9	3.1
<i>P. schiaffinoi</i>														
PV 3959														
r.	3.9	1.9	5.2	2.5	5.2	3.7	5.9	3.7	6.4	3.8	6.5	4.0	4.9	3.1
l.	4.2	1.9	4.8	2.7	5.0	3.1	5.6	3.5	6.7	3.9	6.0	4.0	4.8	3.0
PV 3963														
r.	4.0	2.1	4.6	3.3	4.9	3.4	5.4	3.7	6.6	4.1	6.9	4.1	6.3	3.3
l.	—	—	4.6	3.2	4.0	3.7	5.6	3.9	6.8	4.2	6.7	4.1	(5.4)	3.4
PV 4188			(3.8)	(2.0)	4.8	2.9	4.9	3.3	5.2	3.6	5.8	3.7	4.7	3.2
PV 3961 <sup>a</sup>			3.9	2.2	4.9	2.6								
PV 4062							5.3	4.0						
PV 4220					3.6	3.3	(4.5)	3.7						
PV 4649							5.0	3.9	5.8	3.7	5.8	4.4	5.5	3.3
PV 4663					5.4	3.3								
<i>P. cf. sculptum</i>														
PV 4655					6.1	4.9								
PV 4662					6.9	5.5								
PV 4660							8.7	6.1						
<i>P. sculptum</i>														
MACN A 52-444			4.4	3.3	6.1	4.2	7.2	4.7	8.5	4.6	8.0	5.3	7.4	4.3
MLP 84-XII-5-1					5.5	3.9	7.1	4.2	6.9	3.9				
<i>Prohegetotherium</i> sp.														
PV 3984									9.5 <sup>b</sup>	6.4 <sup>b</sup>				
PV 4406			6.0	—										
PV 4652									9.4	6.3				
PV 4656					6.2	5.6								
PV 4666					6.1	5.2								
cf. <i>Pr. smithwoodwardi</i>														
PV 4189							4.7	4.0	6.3	4.4	5.7	4.1	5.4	3.6
PV 4654									5.0	4.0	5.2	4.3		
<i>Prosotherium garzoni</i>														
MACN A 52-455 <sup>c</sup>	3.5	3.4	5.6	3.3	6.2	3.4	—	—	6.9	4.7	6.9	4.4	6.0	3.8

PV corresponds to MCNAM material. **Abbreviations:** *P.*, *Prohegetotherium*; *Pr.*, *Propachyrucos*.

<sup>a</sup>Without wear.

<sup>b</sup>(6.9) × (5.1) at the base of the tooth.

<sup>c</sup>Reguero (1999).

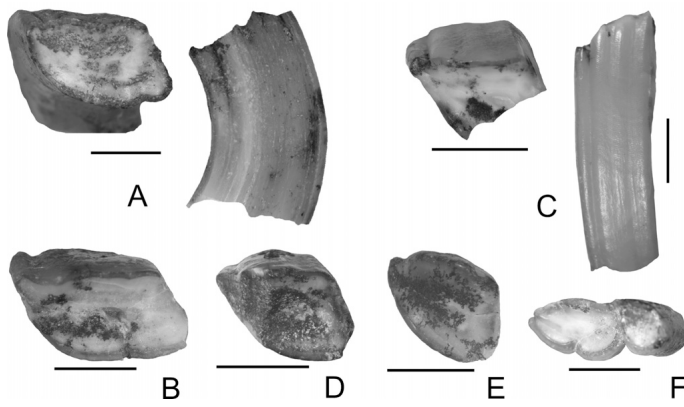


FIGURE 3. *Prohegetotherium* sp. **A**, MCNAM-PV 3984, left M1 or M2, occlusal and posterolabial views; **B**, MCNAM-PV 4652, right (reversed) M1 or M2, occlusal view; **C**, MCNAM-PV 4406, right P2 or P3, occlusal (reversed) and labial views; **D**, MCNAM-PV 4656, left P3, occlusal view; **E**, MCNAM-PV 4666, right (reversed) P3, occlusal view; **F**, MCNAM-PV 4620, right m3, occlusal view. Scale bars equal 5 mm.

labially instead of anteriorly, but lacking a projection from the wall, and a less triangular outline of premolars (Fig. 3A–E). In addition, MCNAM-PV 3984 shows a neat posterolingual sulcus (Fig. 3A) that is not comparable to the groove observed in some

specimens assigned to *P. schiaffinoi* because there is no posterolingual projection of the tooth (see below). Instead, it recalls that observed on the molars of *Sallatherium altiplanense* from Salla, but the parastyle and paracone folds of this taxon are more developed (Reguero and Cerdeño, 2005).

The lower m3 MCNAM-PV 4620 (Fig. 3F) is a large tooth without posterolingual inflection and with a well-marked posterolabial groove; this gives a trilobed aspect to the m3, better defined in labial than in occlusal view; the talonid is wide and shows a general oval outline. We tentatively ascribe this specimen to the same taxon as the large upper teeth described as *Prohegetotherium* sp., but it also is similar to the m3 of MACN Pv CH2014 assigned to the Colhuehuapian species *Hegetotheriopsis sulcatus*, which is slightly smaller (Kramarz and Paz, 2013).

These premolars and molars are close in size to the teeth described above and to *P. sculptum* (Tables 1–3). More material is needed to provide more precise taxonomic determination, and we provisionally refer them to *Prohegetotherium* sp.

*PROHEGETOTHERIUM SCHIAFFINOI* (Kraglievich, 1932) (Figs. 4–5)

**Holotype**—MNHN-DP-186, partial maxilla with P2–M2. Fray Bentos Formation, Cañada de las Mulas, Santa Lucía River, Canelones Department, Uruguay. Deseadan SALMA.

**Referred Material from Quebrada Fiera**—MCNAM-PV 3959, maxillary fragments and isolated teeth including most of the whole series: both I1, a fragmented I2 or I3, and both C–M3;

TABLE 2. Lower tooth dimensions (mm) of Hegetotheriidae from Quebrada Fiera and *Propachyrukhos* and *Prosotherium* specimens.

Specimen	p2		p3		p4		m1		m2		m3	
	L	W	L	W	L	W	L	W	L	W	L	W
<i>?P. malalhuense</i>												
PV 3847							(6.5)	3.2	—	—	(7.7)	(2.9)
PV 4679							6.0	3.4				
<i>P. schiaffinoi</i>												
PV 4061	(3.4)	(1.7)	3.7	2.6	4.7	2.9	5.2	2.9	5.6	2.9	6.4	2.3
PV 4071			(3.8)	2.0	4.4	2.7	4.6	2.9				
PV 4054					4.9	3.1	5.5	3.3				
PV 4242a, c, d			4.4	2.2	4.6	2.7			6.7	3.4	7.8	2.8
			4.1	1.8	5.0	3.1						
PV 4242b			4.3	2.1								
PV 4224							(5.9)	(2.9)	(6.0)	(2.7)		
PV 4604	—	—	5.2	3.0	5.4	3.4	6.0	3.6	6.3	3.6		
PV 4637					4.7	3.0	5.2	3.1	5.6	3.0	6.6	2.6
PV 4706											6.7	2.5
PV 4764							5.8	3.0				
PV 4796					5.9	3.4	6.4	3.6				
PV 4797											6.8	2.4
PV 4800							5.3	3.2				
MLP 96-XI-20-9							5.0	2.8	5.0	2.8		
<i>Prohegetotherium</i> sp.												
PV 4620											10.7	4.2
cf. <i>Pr. smithwoodwardi</i>												
PV 3960			5.3	3.0	5.4	3.1	6.5	3.0	6.6	3.2		
PV 3962							4.5	2.7	5.0	2.5	(7.0)	2.5
PV 3964	3.8	2.2	3.7	2.6	(4.2)	2.6	—	—	4.6	2.6	6.2	2.4
PV 4190			4.6	2.4	4.5	2.6	5.2	2.7	(5.8)	(2.5)		
PV 4223	(3.3)	(1.5)										
PV 4642											6.5	3.7
PV 4711	4.2	2.1	4.8	2.5	5.2	2.8						
PV 4793	3.7	2.0	3.7	2.6	3.8	2.8						
PV 4805			3.7	2.4								
<i>Pr. smithwoodwardi</i>												
MACN A 52-451	3.1	1.8	3.8	2.3	3.9	2.4	4.6	2.5	4.8	2.1	5.2	2.1
<i>Prosotherium garzoni</i>												
AMNH 14154			4.7	2.6	4.8	2.7	5.9	2.8				
AMNH 29604												
r.	4.3	2.6	4.3	2.9	4.3	2.9	5.3	2.9	5.4	2.8	6.8	2.5
l.	4.2	2.5	4.7	2.9	4.5	2.8	5.6	3.0	5.8	2.9	7.0	2.6

PV corresponds to MCNAM material. **Abbreviations:** *P.*, *Prohegetotherium*; *Pr.*, *Propachyrukhos*.

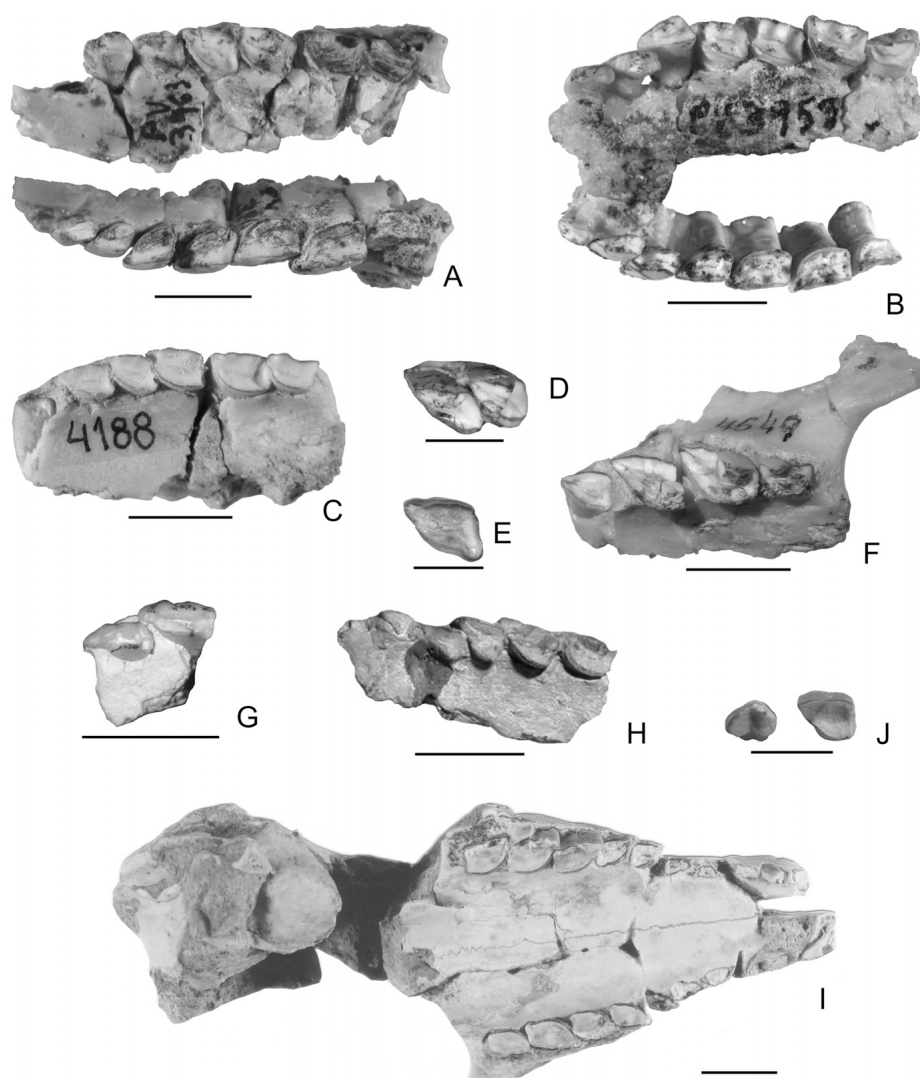


FIGURE 4. Upper dentition of *Prohegetotherium schiaffinoi*. **A–G**, Quebrada Fiera: **A**, MCNAM-PV 3963, palatal fragment with right P1–M3 and left P2–M3, anterior to the left; **B**, MCNAM-PV 3959, palatal fragment with right and left P1–M3, anterior to the left; **C**, MCNAM-PV 4188, left P2–M3; **D**, MCNAM-PV 4220, right (reversed) P2–3; **E**, MCNAM-PV 4062, right (reversed) P4; **F**, MCNAM-PV 4649, left maxillary fragment with P4–M3; **G**, MCNAM-PV 3961, unworn left P2–3; **H**, holotype, MNHN-DP-186, partial maxilla with P2–M2, Fray Bentos Formation, Uruguay; **I**, UF 91661, partial skull, Salla, Bolivia; **J**, ‘*Ethegotherium carettei*,’ right (reversed) P2 and P3 of the holotype MACN 16609, Divisadero Largo, Mendoza, Argentina. Occlusal views. Scale bars equal 10 mm (**A–C**, **F–J**) and 5 mm (**D**, **E**).

MCNAM-PV 3961, left P2–3 unworn; MCNAM-PV 3963, maxillary fragment with right P1–M3 and left P1–M2; MCNAM-PV 4062, left P4; MCNAM-PV 4188, left maxillary fragment with P2 (broken), P3–4, and M1–3; MCNAM-PV 4220, right maxillary fragment with P2 (broken) and P3; MCNAM-PV 4649, left maxillary fragment with P4–M3 and a part of the zygomatic arch; MCNAM-PV 4663, right P3; MCNAM-PV 4054, right mandibular fragment with p4–m2; MCNAM-PV 4061, right mandibular fragment with p2–m3; MCNAM-PV 4071, left mandibular fragment with p3 incomplete and p4–m1; MCNAM-PV 4224, right mandibular fragment with m1–2; MCNAM-PV 4242a–d, set including mandibular fragments of at least two individuals: right and left fragments with p3–4, right p3, left m2, and right m3; MCNAM-PV 4604, right mandibular fragment with p3–m2; MCNAM-PV 4637, right mandibular fragment with p4–m3; MCNAM-PV 4685, right dp3; MCNAM-PV 4706, right mandibular fragment with m3; MCNAM-PV 4723, right dp3; MCNAM-PV 4764, left m1; MCNAM-PV 4797, left m3; MLP 79-XII-18-42, left ?p4; MLP 96-XI-20-9, right mandibular fragment with m1–2.

**Geographic and Stratigraphic Distribution**—Uruguay: Fray Bentos Formation; Bolivia: Salla, ‘Upper Salla Beds’; and Argentina: Corrientes and Entre Ríos, Fray Bentos Formation; Mendoza, base of the Agua de la Piedra Formation and ?middle

Member of the Mariño Formation. Late Oligocene, Deseadan SALMA, and ?early Miocene.

**Remark**—The mandible PZ-Ctes No. 3748-49 from the Fray Bentos Formation, figured by Bond et al. (1998) and recognized as *P. schiaffinoi* by Reguero and Cerdeño (2005), differs from the specimens herein described by the general convexity of the labial walls and the absence of posterolabial inflection on m3 and posterolabial projection on m1 (m2 broken). Consequently, it is removed from *P. schiaffinoi*.

#### Description and Comparison

Most hegetothere remains from Quebrada Fiera are identified as *P. schiaffinoi*. The most complete, MCNAM-PV 3963 and MCNAM-PV 3959 (Fig. 4A, B), are very similar to each other, with some difference in tooth width (Tables 1, 3) due to less wear on MCNAM-PV 3959. In this specimen, I2(3?) and C are reduced; the left C, more complete, is hardly larger than the tooth fragment identifiable as I2(3?). The left I1 measures 5.6 mm × 2.1 mm. These dimensions and the canine somewhat larger than I2 or I3 are similar to that observed in the Bolivian *P. schiaffinoi* (Reguero and Cerdeño, 2005).

P1 is a simple tooth, with a marked paracone fold, more convex in MCNAM-PV 3963; this fold is hardly marked on P2–4,

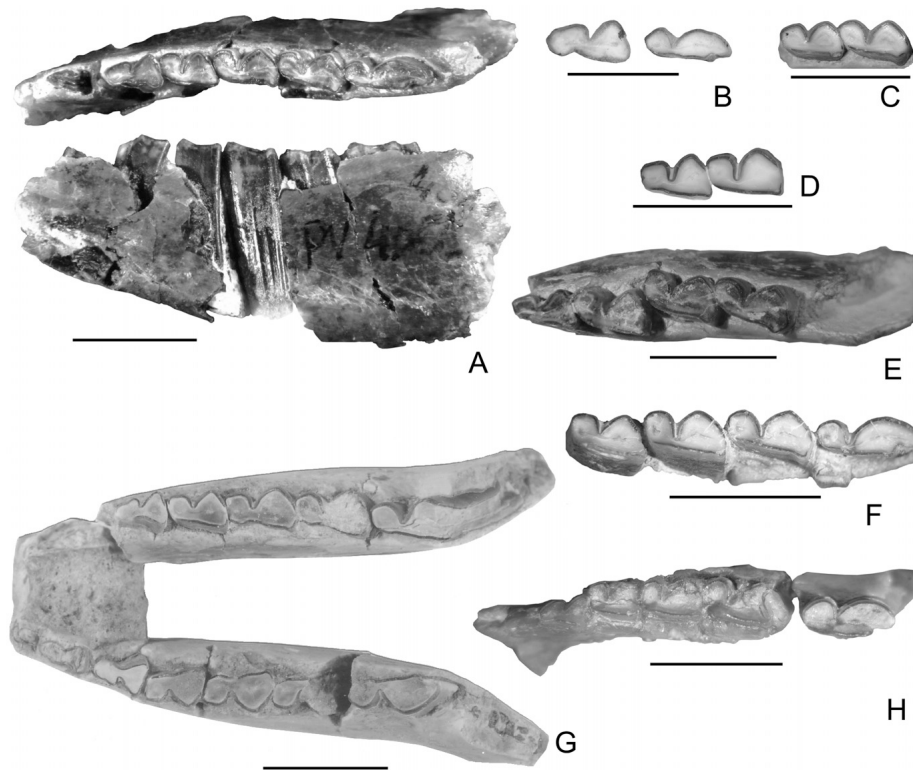


FIGURE 5. Lower dentition of *Prohegetotherium schiaffinoi*. **A**, MCNAM-PV 4061, right mandibular fragment with p2–m3, occlusal and lingual views; **B**, MCNAM-PV 4242b and d, right p3 and m3; **C**, MCNAM-PV 4054, right p4–m1; **D**, MCNAM-PV 4071, left (reversed) p4–m1; **E**, MCNAM-PV 4604, right mandibular fragment with p3–m2; **F**, MCNAM-PV 4637, right mandibular fragment with p4–m3; **G**, UF 91661, incomplete mandible, Salla, Bolivia; **H**, '*E. carettei*,' mandibular fragment of the holotype MACN 16609, Divisadero Largo, Mendoza. Anterior to the left. **B–G**, occlusal views. Scale bars equal 10 mm.

although it is more pronounced in P2 and P3 of MCNAM-PV 3963 than in MCNAM-PV 3959. The development of the paracone fold in P2–4 is close to that of the holotype of *P. schiaffinoi* (Fig. 4H); instead, the specimen UF 91661 from Salla assigned to this species (Fig. 4I; and Reguero and Cerdeño, 2005) shows a marked paracone fold in P2 and P3, but not in P1 (broken, apparently labially convex) or P4. The Bolivian specimen MNHN-Bol-V-010873 (E.C., pers. data) shows this fold on all premolars, although less marked on P4. These differences represent intraspecific variation.

In MCNAM-PV 3963, M1–2 present a labially centered groove (persistent along the crown height) that separates the smooth paracone and metacone convexities. This groove is clearly observable on the M1 of the holotype MNHN-DP-186, where it is slightly more anteriorly placed. The groove is more centered in upper molars of UF 91661 and MNHN-Bol-V-009279 from Salla. Another difference with respect to these Bolivian specimens is that they present an incipient posterolingual groove in P4–M3, better observable in P4 and M2 of UF 91661 (Fig. 4I). M3 is smaller than M1 and M2; this difference is greater in MCNAM-PV 3959 (Table 1), probably due to the younger age of this individual. Upper premolars and molars are slightly imbricated.

MCNAM-PV 4188 (Fig. 4C) is smaller than MCNAM-PV 3963 and PV 3959, and closer in size to the holotype of the new taxon (see below; Table 1). In morphology, it is more similar to MCNAM-PV 3959 than to MCNAM-PV 3963 because of the more pointed parastyle of M2. The parastylar groove is more evident on M2, but the parastyle does not project labially. The centered groove on the ectoloph is also present in the M1–2 of MCNAM-PV 4188, as in MCNAM-PV 3963. The premolars are triangular, P3–4 with a weakly developed posterolingual groove (Fig. 4C), which is more difficult to observe in the other specimens (Fig. 4A, B). Instead, this groove is more evident in MCNAM-PV 4062, a larger P4 (Fig. 4E), more similar to the P4

of UF 91661 (Fig. 4I) and closer in size to MCNAM-PV 3963 (Table 1). Both MCNAM-PV 4188 and MCNAM-PV 4062 also present an occlusal, centered enamel line. This line does not seem to be present on the holotype of *P. schiaffinoi* (Fig. 4H), but it occurs in different specimens from Salla (i.e., UF 91661 or MNHN-Bol-V-003816 and Bol-V-006351; E.C., pers. data). MCNAM-PV 4220 (Fig. 4D) presents small P2–3 (Table 1), close to MCNAM-PV 4188. Also similar to the latter and slightly larger, is MCNAM-PV 4649 (Fig. 4F; Table 1), which preserves the beginning of the zygomatic arch, behind M3.

The specimen MCNAM-PV 3961 (Fig. 4G) bears two teeth identified as unworn P2–3, irrespective of their deciduous condition based on the relatively high crowns, the lack of differentiated roots, and small size (Table 1). They are relatively long and narrow, the width increasing slightly to the base of the tooth. The labial cusps are well defined. The parastyle is well projecting anteriorly, especially in P2, and delimited by a shallow labial groove. Another labial groove is centered on the ectoloph, similar to that described before (more anteriorly placed on P3). The P2 exhibits a short metaloph that delimits a posterior fossette together with the posterior and lingual walls; this fossette is shallow and would become rapidly incorporated in the occlusal surface with little wear. Anterior to the metaloph, there is a longitudinally narrow fossette (still as a lingually open valley in P3; Fig. 4G) that would originate at the enamel line observed in the adult specimens. The P3 shows a more developed protoloph, strongly inclined posteriorly and in contact with the metaloph. The separation of these lophs is less than 1 mm in height, and consequently they become fused with wear. In this tooth, the posterior fossette appears shallower and a narrow longitudinal valley is also present. The posterolingual corner of both teeth shows a minimum lingual projection, as occurring in some of the above-mentioned teeth.

A form recognized as *P. schiaffinoi* is '*Ethegotherium carettei*' (Minoprio, 1947) from the Divisadero Largo area, Mendoza

Province (Simpson and Minoprio, 1949; López, 2002; Reguero and Cerdeño, 2005). The only known material is the holotype, MACN 16609, a skull and mandible whose teeth are poorly preserved, some of them separated from the skull. The most complete is identified as the right P3 (Fig. 4J; see also López, 2002: fig. 2), a triangular tooth, relatively shorter than those studied herein, closer to the P4 (e.g., MCNAM-PV 3959), with a smooth undulating ectoloph and without median occlusal enamel line. The P2 of MACN 16609 (Fig. 4J) differs by its marked anterolingual groove, which provides a more interatheriid aspect (i.e., *Miocochilius* in Croft, 2007). This material corresponds to the Mariño Formation (Cerdeño et al., 2008; López and Manasero, 2008), early Miocene in age, and its taxonomic status and biostratigraphic position need to be reevaluated.

Among mandibular fragments, MCNAM-PV 4061 (Fig. 5A) shows a horizontal ramus that increases in height posteriorly, from 9.6 mm at the level of p2–3 (lingual face) to 15.3 mm behind m3; its ventral border is slightly convex and the posterior end of the symphysis reaches the level of the trigonid of p3. In lateral view, it is closer to UF 91661 of *Prohegetotherium schiaffinoi* from Salla than to UF 91621 of *Sallatherium* (Reguero and Cerdeño, 2005). The p2, broken at the alveolar level, is long and narrow, triangular, pointed anteriorly, and with smoothly undulating labial and lingual walls. The p3 is a larger tooth, long but not anteriorly pointed, with two smooth, wide labial grooves. The trigonid is quadrangular, whereas the talonid is clearly triangular and larger. This difference between trigonid and talonid is also observed in p4 and the molars, but their trigonids are shorter. The m1–2 present a marked posterolabial projection (observed along the crown height on m2; Fig. 5A), and the m3 shows a posterolabial inflection point on the talonid, as a wide groove, similar to, but more marked than, that of *Prohegetotherium sculptum* AMNH 29605. In addition, this species differs by having p3–4 with a more elongated, pointed trigonid; molars not projected posterolingually; m3 with more developed trigonid and smooth labial and lingual sulci in the talonid; and more imbricated teeth (Chaffee, 1952; Reguero and Cerdeño, 2005).

The mandible associated with the partial skull UF 91661 of *P. schiaffinoi* from Salla (Fig. 5G; Reguero and Cerdeño, 2005) also displays a posterolingual projection on the m1 (not clearly observable on m2 because it is incomplete on both sides), and the inflection in m3 appears present; UF 91661 differs from MCNAM-PV 4061 by the more lingually convex trigonid of the molars. This same feature is observed in the specimen MNHN-Bol-V-006132 from Salla, which is larger (E.C., pers. data) than MCNAM-PV 4061 and closer to MCNAM-PV 4064 (Table 2). These small differences are interpreted as intraspecific variation.

The mandible of *P. schiaffinoi* from Divisadero Largo (MACN 16609, ‘*E. carettei*’; Fig. 5H) differs from MCNAM-PV 4061 in having the trigonid of p4 more rectangular and short, and m1 hardly projected posterolingually; its m3 has a similar inflection (the enamel is missing on this part).

Other specimens from Quebrada Fiera present similarities with MCNAM-PV 4061. Among them, MCNAM-PV 4242 includes several mandibular fragments, some assumed to belong to the same individual, which have been differentiated as follows: MCNAM-PV 4242a, right and left fragments with p3–4 (both p2 broken); MCNAM-PV 4242b, right p3, which shows the presence of a second individual (Fig. 5B); MCNAM-PV 4242c, left m2; and MCNAM-PV 4242d, right m3 (Fig. 5B). They are larger than MCNAM-PV 4061 (Table 2), but present the same morphology, such as the posterolingual groove of m3, the posterolingual projection of m2 (more subtle), and the elongated p3, with its anterolingually directed trigonid. Similar characteristics and size (Table 2) to MCNAM-PV 4061 are also present in MCNAM-PV 4054 (Fig. 5C), PV 4071 (Fig. 5D), PV 4224, PV 4604 (Fig. 5E), PV 4637 (Fig. 5F), PV 4706, and MLP 96-XI-20-9, while some specimens are slightly larger, such as

MCNAM-PV 4604 or PV 4796 (Table 2), but without significant differences.

*PROHEGETOTHERIUM MALALHUENSE*, sp. nov.  
(Fig. 6)

**Holotype**—MCNAM-PV 3848, partial right maxilla with P2–M3.

**Referred Material**—Besides the holotype, we tentatively refer MCNAM-PV 3847, right mandibular fragment with incomplete m1–3, and MCNAM-PV 4679, right m1, to this species.

**Diagnosis**—Differs from other species of *Prohegetotherium* in having P3–4 more triangular; M1–2 wider and labially rounded; M2 with a lingually projecting, sharp parastyle and marked parastylar sulcus on the ectoloph, giving a more sinuous profile; M3 with a distinctive parastyle and a posterior face with an irregular surface; m1–2 posterolingually projected; talonid of m3 with marked posterolingual groove; and significantly smaller size than *P. sculptum* in tooth dimensions (20–25% in M1 length).

**Etymology**—From the Mapuche words ‘Malal’ (corral) and ‘Huel’ (place) from which ‘Malalhue’ and the present name Malargüe are derived, the department of Mendoza Province where Quebrada Fiera is located.

**Geographic and Stratigraphic Origin**—Quebrada Fiera (36°33′13.3″S, 69°42′3.5″W), Malargüe Department, Mendoza Province, central-western Argentina. Base of the Agua de la Piedra Formation, late Oligocene, Deseadan SALMA.

**Description and Comparison**

The upper premolars of MCNAM-PV 3848 (Fig. 6A) are similar to each other, triangular in shape, and increase in size from P2 to P4. They are broader distally and taper mesiolabially. The enamel is continuous. A high pointed paracone and metacone cusps are present on the ectoloph of the P3–4, because the teeth are not very worn. The occlusal surfaces are almost featureless, but there is a longitudinal, thin enamel band in the center of

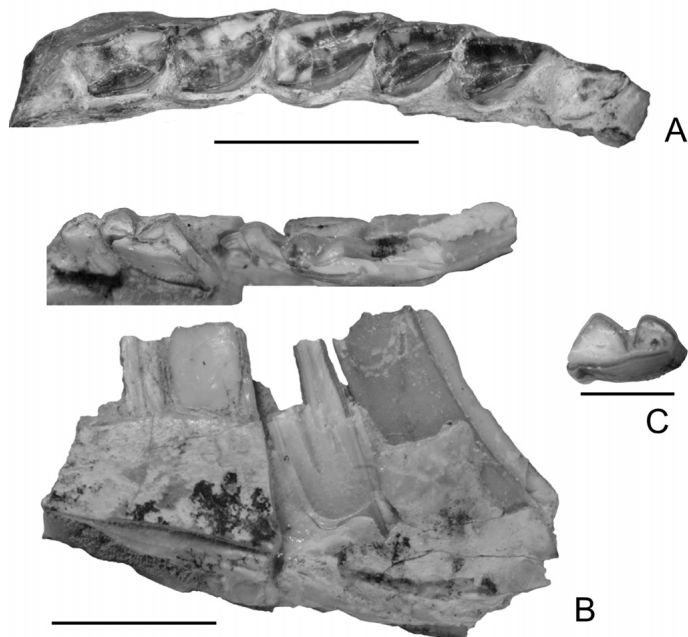


FIGURE 6. *Prohegetotherium malalhuense*, sp. nov. (B and C tentatively assigned), Quebrada Fiera, Mendoza. A, MCNAM-PV 3848, partial right maxilla with P2–M3, occlusal view; B, MCNAM-PV 3847, right mandibular fragment with incomplete m1–3, occlusal and lingual views; C, MCNAM-PV 4679, right m1, occlusal view. Scale bars equal 10 mm (A, B) and 5 mm (C).



each tooth (including molars), a remnant of an original, shallow central fossette, such as was observed in *P. schiaffinoi* (see above). The P2 (broken at the level of the alveolus) presents a shallow groove on the anterior part of the ectoloph, which is not observed on P3–4.

The molars are subequal in size, the M1 being slightly longer and the M2 slightly wider (Table 1). The main characteristic of these molars is the presence on M2 and M3 of a small, rounded parastyle, directed labially, more constricted labially and anteriorly in M3. In contrast, M1 presents a more anteriorly directed parastyle and a smoother labial groove. As in the posterior premolars, the molars also have high, pointed paracone and metacone cusps. The respective folds are evident on M1, but the paracone fold is better marked on M2 and M3. The M3 has a smoothly concave lingual wall, differing from the more regularly convex wall of M1–2.

This specimen differs from other described material from Quebrada Fiera. *Prohegetotherium sculptum* and *P. sp.* are larger (Table 1; Fig. 7), have more marked anterolabial sulci in the premolars, and do not present the projected parastyle of the molars. *Prohegetotherium schiaffinoi* is more similar in size. MCNAM-

PV 4188 shows similar dimensions, although other specimens, such as MCNAM-PV 3959 and PV 3963, are slightly larger (Tables 1, 3; Fig. 7). Compared with the holotype of *P. schiaffinoi*, MNHN-DP-186 possesses slightly longer premolars, an M2 without a projecting parastyle, and a more undulating ectoloph of the molars. The referred specimen UF 91661 (Reguero and Cerdeño, 2005) and other material from Quebrada Fiera have molars that lack projecting parastyles. Some also differ in the relative length of the premolars, the more concave ectoloph of M3, and the more angular outline of the anterolingual wall of the molars.

Most of the studied mandibular fragments present common characteristics and size (Table 2; Fig. 7) and were assigned to *P. schiaffinoi*. Only one fragment, MCNAM-PV 3847, shows a different feature on m3. This specimen has very fragmented molars (Fig. 6B), but the m3 shows a posterolingual groove that forms a short but marked folding along the crown height, different from the posterolingual inflection observed on the m3 of specimens assigned to *P. schiaffinoi*. Instead, MCNAM-PV 3847 is similar in the posterolingual projection of m1–2. The described fold on m3 has been also observed in some

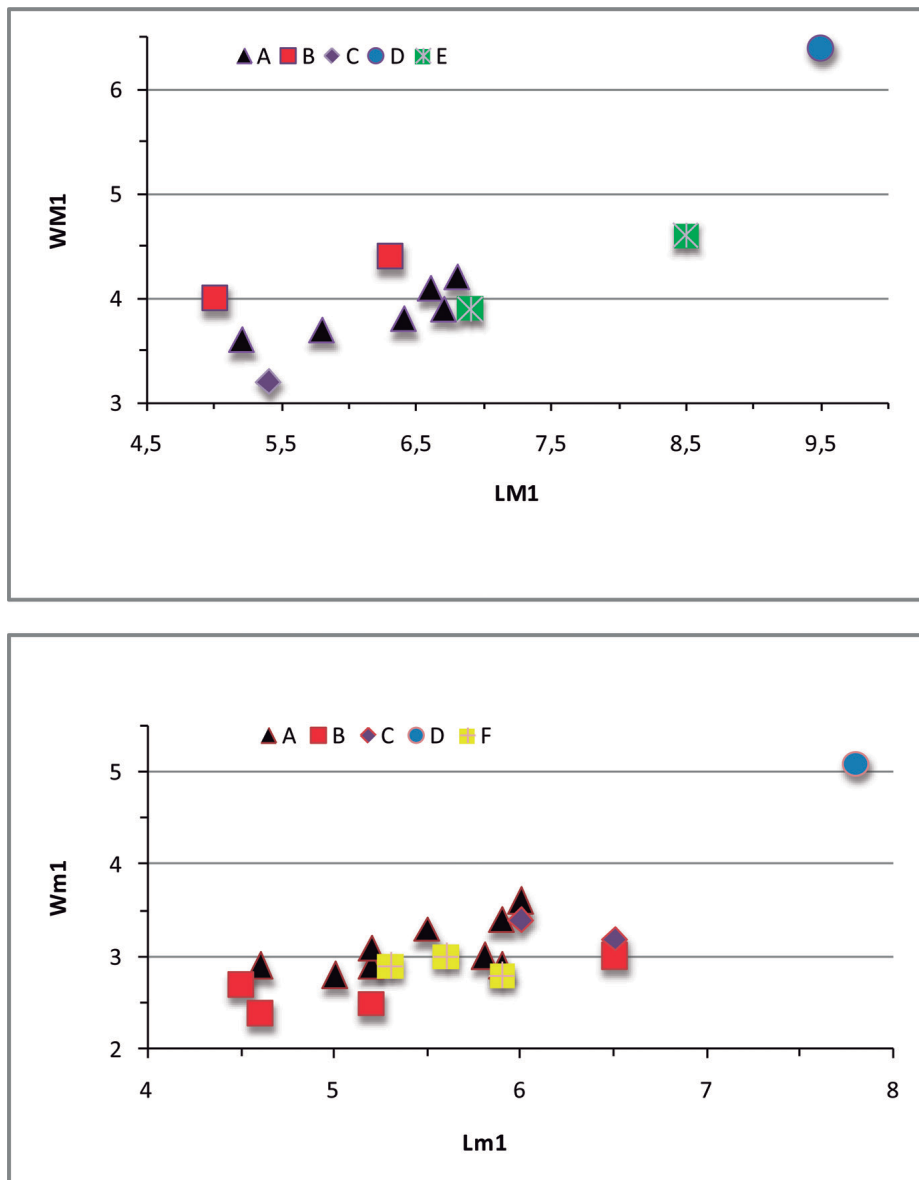


FIGURE 7. Length and width distributions of M1 and m1 of hegetotheriids from Quebrada Fiera. **A** = *Prohegetotherium schiaffinoi*; **B** = *Propachyrucos*; **C** = *Prohegetotherium malalhuense*, sp. nov.; **D** = *Prohegetotherium* sp. (M1/2); **E** = *Prohegetotherium sculptum*; **F** = *Prosotherium garzoni*. Axes in units of mm.

specimens from Salla, such as the m3 of MNHN-Bol-V 005595 and the m1 and m2 of MNHN-Bol-V 004409, which lacks m3 (E.C., pers. data). The taxonomic relevance of this character needs to be confirmed with more material to consider MCNAM-PV 3847 as a case of intraspecific variation; consequently, we provisionally refer it to the new taxon. Another specimen questionably assigned to *P. malalhuense*, sp. nov., is MCNAM-PV 4679 (Fig. 6C), a lower m1 distinguished from other described molars in having a posterolingual end that is separated as a fold, with an anterior groove.

PACHYRUKHINAE Kraglievich, 1934  
(Diagnosis in Cerdeño and Bond, 1998)  
*PROPACHYRUCOS* Ameghino, 1897

**Type Species**—*Propachyrucos smithwoodwardi* Ameghino, 1897.

*PROPACHYRUCOS* cf. *P. SMITHWOODWARDI*

**Referred Material**—MCNAM-PV 4189, left maxillary fragment with P4–M3; MCNAM-PV 4654, left maxillary fragment

with M1–2; MCNAM-PV 3960, right mandibular fragment with p3–m2; MCNAM-PV 3962, left mandibular fragment with m1–3; MCNAM-PV 3964, right mandibular fragment with p2–m3 (m1 broken); MCNAM-PV 4191, left m1?; MCNAM-PV 4223, left mandibular fragment with p2; MCNAM-PV 4642, right m3; MCNAM-PV 4644, left p3; MCNAM-PV 4793, right mandibular fragment with p2–4; MCNAM-PV 4805, left p4 or m1. We also questionably refer: MCNAM-PV 4190, right mandibular fragment with p3–m2; and MCNAM-PV 4711, right mandibular fragment with p2–4.

**Geographic and Stratigraphic Distribution**—Argentina: Chubut (Cabeza Blanca and Scarritt Pocket), Sarmiento Formation, Upper Puesto Almendra Member; and Mendoza, Agua de la Piedra Formation. Late Oligocene, Deseadan SALMA.

#### Description and Comparison

The P4 of MCNAM-PV 4189 (Fig. 8A; Table 1) is subtriangular, without a lingual groove, and labial and lingual faces smoothly convex. The molars are linguallly bilobed by a wide groove, slightly anteriorly directed. The M1 and M2 present a smooth paracone fold, giving some convexity to the ectoloph, in

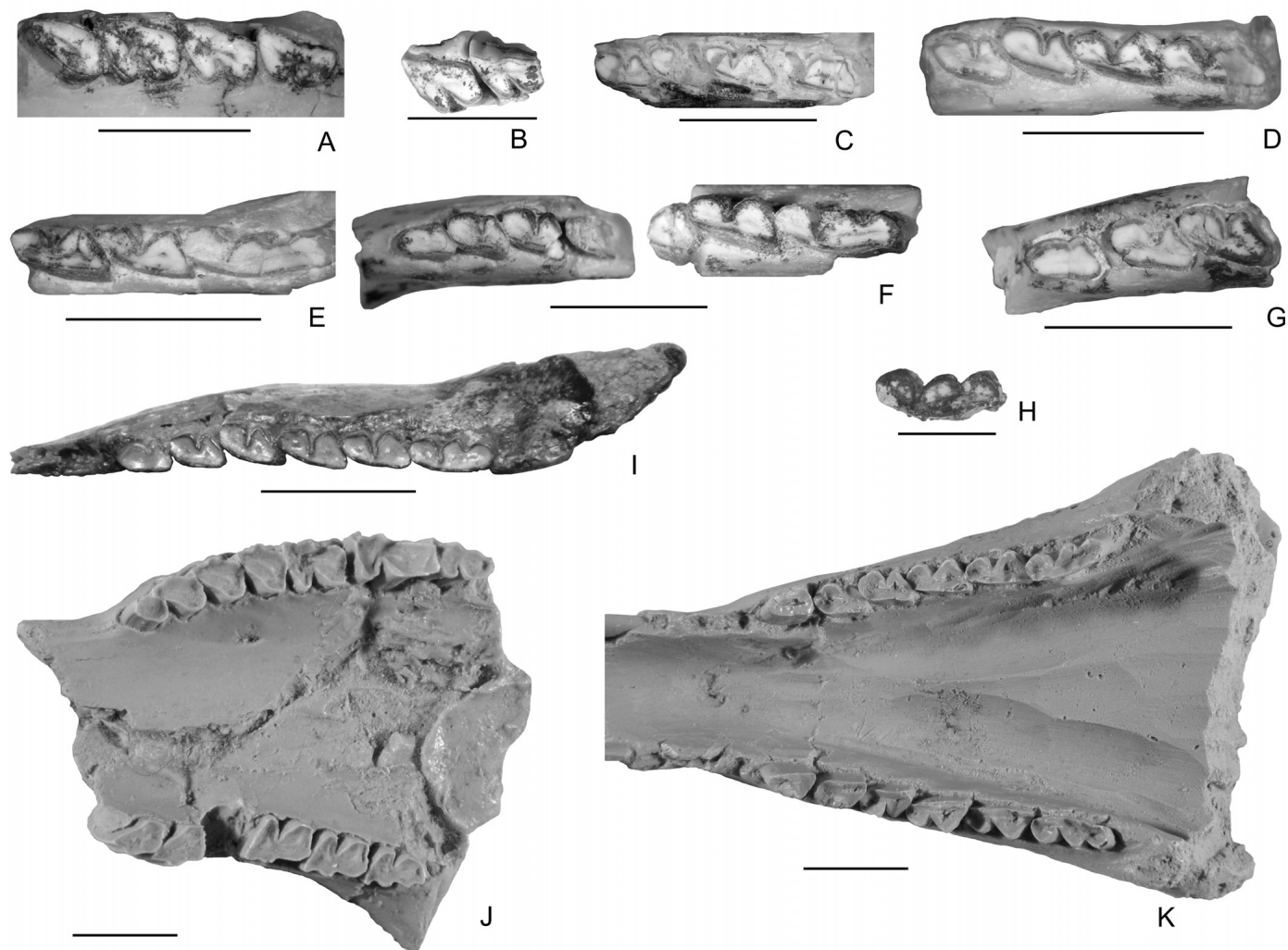


FIGURE 8. (A–H) *Propachyrucos* cf. *smithwoodwardi* from Quebrada Fiera: A, MCNAM-PV 4189, left P4–M3; B, MCNAM-PV 4654, left M1–2; C, MCNAM-PV 3960, right p3–m2; D, MCNAM-PV 4190, left (reversed) p3–m2; E, MCNAM-PV 3962, left (reversed) m1–3; F, MCNAM-PV 3964, right p2–m3 (m1 broken); G, MCNAM-PV 4711, right p2–4; H, MCNAM-PV 4642, right m3. (I) *Propachyrucos smithwoodwardi*: holotype MACN A 52-451, right mandibular fragment with p2–m3. (J, K) *Prosotherium garzoni*: J, AMNH 14154 (cast), palate with both P1–M3 series (except left P4); K, AMNH 29604 (cast), mandible with right and left i1–2 and p2–m3. Scale bars equal 10 mm.

TABLE 3. Upper and lower tooth series dimensions (mm) of Hegetotheriidae from Quebrada Fiera and compared specimens.

Specimen	L P2–4	L M1–3	L P1–M3	L P2–M3
<i>P. malalhuense</i> , sp. nov.				
PV 3848	(11.0)	16.0	—	26.7
<i>P. schiaffinoi</i>				
PV 3959	13.7	17.5	35.0	31.8
PV 3963	13.4	18.5	35.4	32.6
cf. <i>Pr. smithwoodwardi</i>				
PV 4189		16.5		
	L p2–4	L m1–3	L p2–m3	
? <i>P. malalhuense</i>				
PV 3847		(18.8)		
<i>P. schiaffinoi</i>				
PV 4061	13.5	16.3	29.4	
PV 4637		18.0		
PV 4071	14.6			
PV 3964	10.7	(16.2)	(26.3)	
cf. <i>Pr. smithwoodwardi</i>				
PV 3962		15.8		
PV 3964 <sup>a</sup>	10.4	(16.0)	(25.9)	
<i>P. sculptum</i>				
AMNH 29605	13.0	21.2	39.1	
<i>Pr. smithwoodwardi</i>				
MACN-A 52-451		13.4	23.2	
<i>Pro. garzoni</i>				
AMNH 29604	18.4	18.0	31.0	

PV corresponds to MCNAM material. **Abbreviations:** *P.*, *Prohegetotherium*; *Pr.*, *Propachyrucos*; *Pro.*, *Prosotherium*.

<sup>a</sup>Broken at m1 level.

contrast to the longer M3, which has a general labial concavity, although the ectoloph is undulating. The greater length of the M3 is due to the relatively longer metaloph. All teeth present a longitudinally compressed enamel ridge, as occurs in the other hegetotheriid teeth from Quebrada Fiera. The bilobed molars and the absence of a developed fold on the ectoloph allow referral of the specimen to *Propachyrucos smithwoodwardi*. In contrast, the lectotype of *Prosotherium garzoni*, MACN A 52-445 (Reguero, 1999:pl. 12), and the referred specimen AMNH 14154 (Fig. 8J) present premolars molars with developed paracone folds; this fold is less marked on the molars of the lectotype, but more developed than in MCNAM-PV 4189.

The specimen MCNAM-PV 4654, with M1–2, is comparable to MCNAM-PV 4189 in size and morphology (Table 1; Fig. 8B). Both are similar to MLP 93-XI-21-50 from Las Cascadas, Chubut (pers. data). The latter preserves the P3 (broken), showing a labial fold that is more marked than that of P4 but less than in *Prosotherium garzoni*.

The third Deseadan pachyrukhine, *Medistylus dorsatus*, differs in having a narrow, very detached mesostyle (Reguero et al., 2007).

The lower dentition is similar in *Propachyrucos* and *Prosotherium*. Major differences are the dissimilar development of incisors and canines, which cannot be examined in the studied material. Therefore, the identification of different mandibular fragments or isolated lower teeth is difficult. According to Ameghino (1897) and Reguero (1999), *Propachyrucos* has narrower lower teeth and a shallower posterior labial groove in m3, but the observed differences in our sample are not significant (Table 2).

The studied lower teeth (Fig. 8C–H) include premolars with long and more or less labially rounded trigonids, together with short and triangular talonids. Both lobes are more similar to each other in m1–2. The m3 has three labially well defined lobes, while its lingual wall has a convex outline, but with a slight concavity between the second and the third lobes.

Examination of the holotype of *Propachyrucos smithwoodwardi*, MACN A 52-451 (Fig. 8I), reveals a similarity with most specimens from Quebrada Fiera, and only MCNAM-PV 4190

and MCNAM-PV 4711 (Fig. 8D, H) exhibit more rounded trigonids. However, the mandibular fragment associated with the maxilla AMNH 14154 of *Prosotherium garzoni* also presents angular trigonids. In addition, some variation is observed among the Quebrada Fiera specimens; for instance, MCNAM-PV 4793 has more angular trigonid in p3 than in p4 (Fig. 8G), and MCNAM-PV 3964 has greater angularity in the premolars than in m2.

On the other hand, the mandible AMNH 29604 (Fig. 8L), described as *Propachyrucos simpsoni* (Chaffee, 1952) and assigned later to *Prosotherium garzoni* (Reguero, 1999), presents molars with the talonid better defined as a triangle, with straight anterior sides, whereas in MACN A 52-451 the outline is more trapezoidal (but pointing labially). Based on this feature, MCNAM-PV 3962 and MCNAM-PV 4190 are closer to *P. garzoni*, because their talonid is more triangular, but with a less straight anterior side. However, MCNAM-PV 3962 has pointed trigonids, whereas they are more rounded in MCNAM-PV 4190. Consequently, these characters do not seem to be sufficient to separate our sample into two pachyrukhine taxa with certainty. Concerning size (Table 2), MCNAM-PV 3960 is larger than the other pachyrukhine specimens from Quebrada Fiera, and all of them have relatively larger molars than the holotype of *P. smithwoodwardi*. Therefore, we include all in the same taxon, without eliminating the possibility that they may represent two different taxa. The taxonomic significance of the mentioned features needs to be confirmed with more complete material.

#### PHYLOGENETIC ANALYSIS

In order to establish the phylogenetic relationships of the new hegetotheriid species, we performed a cladistic analysis (Goloboff, 1995; Kitching et al., 1998) based on previous studies. The analysis of Billet (2009) included hegetotheres, but at a generic or group level, because it was mainly focused on archaeohyracids. More recently, Kramarz and Paz (2013) used the same data matrix to establish the relationships of the hegetotheriid *Hegetotheriopsis sulcatus*, also adding two other hegetotheriine species as terminal units (*Prohegetotherium sculptum* and *Hegetotherium*

*novus*). A first attempt using the same data matrix provided 48 trees whose consensus tree revealed a large polytomy for hegetotheriids, with *Prohegetotherium* as paraphyletic, and two small monophyletic groups: pachyrukhines, on the one hand, and *P. schiaffinoi* and *Sallatherium*, on the other hand. Even without adding the new species, the replication of the analysis using TNT, instead of PAUP (see Billet et al., 2009), did not provide the same result as that presented by Kramarz and Paz (2013). Therefore, for the purpose of our study, we chose to use the data matrix made by Croft and Anaya (2006) focused on hegetotheriids. Based on this, we added terminal units at the species level, including *P. malalhuense*, sp. nov., *Hegetotheriopsis sulcatus* after data from Kramarz and Paz (2013) and original photographs, and *Medistylus dorsatus* after Reguero et al. (2007). Concerning characters (numbered from 0 to 24), we added three new ones and modified some others. The new characters (22–24) were listed at the end of the original list (Croft and Anaya, 2006) to facilitate the comparison of matrices. Modifications include (1) changes of coding with respect to the analysis in Croft and Anaya (2006): character 0 has been modified for *Paedotherium* and *Tremacyllus* (0<sup>1</sup>), because both have a thick layer of cement on the teeth, especially lingually; character 4 has been coded as not applicable in *Medistylus*, *Pachyrukhos*, *Paedotherium*, and *Tremacyllus*, because they lack the canine; character 6 is coded 6<sup>0</sup> for *P. schiaffinoi* and 6<sup>1</sup> for the type material of *P. sculptum*, although it was previously coded as 6<sup>0</sup> for the genus *Prohegetotherium*; character 11 is variable in *Archaeohyrax*, because this

genus can also have a notch (see below for the added state); characters 22 and 23 are variable in *Pachyrukhos* based on specimens FMNH P12051 (22<sup>0</sup>, 23<sup>0</sup>), FMNH P12994 (22<sup>1</sup>, 23<sup>0</sup>), MNHN-T-1900-18 (22<sup>1</sup>), and MNHN-T-1899-7 (22<sup>1</sup>, 23<sup>1</sup>); finally, the variation in *P. schiaffinoi* for characters 9<sup>0,1</sup> and 24<sup>1,2</sup> reflects the only different coding concerning '*E. carettei*' (= *P. schiaffinoi* in Reguero and Cerdeño, 2005); (2) changes in previously considered character states: the former character 2 was divided into two (characters 1 and 2) due to the presence of I2 and the lack of C in *Medistylus*; in character 7, we introduced three character states instead of two to differentiate the condition in *H. sulcatus* from that in *Prosotherium*, *Propachyrukos*, and *Medistylus*; character 10, the triangular shape of M3 (previous character state 0) is split into two different states according to the orientation of the triangle (implying distinct development or placement of cusps), as seen in archaeohyracids and pachyrukhines; in character 11, a new character state is added, because we consider that the presence of a posterior notch in M3 shows two different conditions.

The data matrix (Supplemental Data) was analyzed under maximum parsimony (Goloboff, 1995) with the computer program TNT 1.1 (Goloboff et al., 2008), using implicit enumeration, under equal weight with all characters unordered. Bremer support was calculated with the same program and for tree editing we used the program Winclada (Nixon, 2002). The analysis provided a single tree (tree length = 50, consistency index [CI] = 66, retention index [RI] = 76; Fig. 9) whose main result is the

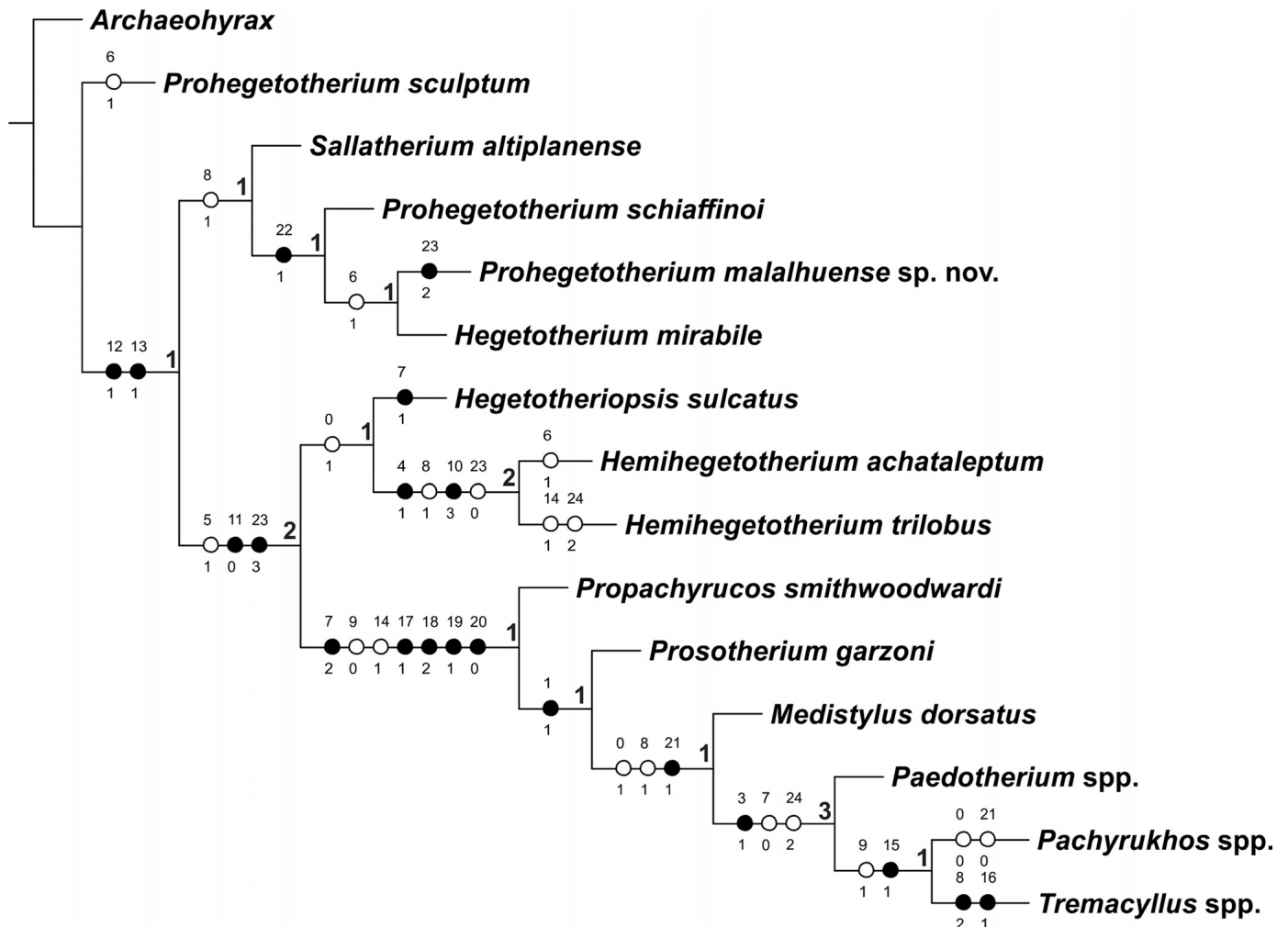


FIGURE 9. Cladogram resulting from the phylogenetic analysis of Hegetotheriidae. White circles indicate homoplasious character states. Numbers in bold at the nodes are Bremer support values.

paraphyly of Hegetotheriinae as classically considered and of the genus *Prohegetotherium*. This result also appeared in previous analyses (Reguero and Prevosti, 2010; Kramarz and Paz, 2013), although the relationships among terminal taxa are different. In the present phylogeny, *Prohegetotherium sculptum* is the sister group of the remaining hegetotheres, which are included in two large clades (Fig. 9). One is composed of (*Sallatherium altiplanense* (*Prohegetotherium schiaffinoi* (*Hegetotherium mirabile* + *Prohegetotherium malalhuense*, sp. nov.))), with low Bremer support (Fig. 9). The second large clade is better supported and encompasses, in turn, two monophyletic groups. On the one hand, *Hegetotheriopsis sulcatus* and the species of *Hemihegetotherium* and, on the other hand, the pachyrukhines, whose monophyly is well supported, as in previous analyses, by seven synapomorphies (Fig. 9). This arrangement is remarkable because the clade (*Hegetotheriopsis* + *Hemihegetotherium*) shows closer affinities with pachyrukhines than with the rest of 'hegetotheriines.' Synapomorphies are detailed in Figure 9, which show a high number of homoplasies.

These results reveal that hegetotheres, especially 'hegetotheriines,' need a revision that allows a selection of significant characters, which will result in a better understanding of the phylogenetic relationships among hegetotheriids. The incomplete knowledge of some taxa adds to the lack of high-quality character assessments. In this regard, future discoveries in Quebrada Fiera and the unpublished material from different localities could shed light on intraspecific variation and provide new data to improve the character matrix.

## DISCUSSION AND CONCLUSIONS

The specimens described herein increase the diversity of hegetotheriids during the late Oligocene in mid-latitudes (Mendoza) of South America. Four hegetotheriines, including *Prohegetotherium malalhuense*, sp. nov., and at least one pachyrukhine are recognized. Except for the new taxon and *Prohegetotherium* sp., the other species are known from the Deseadan of Argentina. On the one hand, *Prohegetotherium sculptum* and the pachyrukhine *Propachyrucos* (and *Prosotherium*) are common in Deseadan localities of Patagonia; on the other hand, *Prohegetotherium schiaffinoi* is present in Uruguay and Bolivia (Reguero and Cerdeño, 2005) and was also recognized in the Argentinean provinces of Corrientes and Entre Ríos.

The record of *Propachyrucos* from Mendoza documents the northernmost geographic distribution of pachyrukhines during Deseadan times, previously known only from various localities in Chubut, Patagonia. The geographic location of Quebrada Fiera at about 36.3°S and 69.4°W is roughly 900 km northwest from the northernmost record of Paleogene pachyrukhines in Chubut, and the group is lacking in low- and middle-latitude Deseadan faunas (Salla, Bolivia [Reguero and Cerdeño, 2005, among others]; Fray Bentos, Uruguay [Bond et al., 1998]; Moquegua, Perú [Shockey et al., 2009]). They are also absent from the late early Miocene (Santacrucian SALMA) Chucal Fauna in northern Chile (Croft et al., 2004), while still common in Patagonia at this time (Sinclair, 1909). It is in the Deseadan fauna of high latitudes (Patagonia) where pachyrukhines experienced their first radiation, with three species co-occurring, *Propachyrucos smithwoodwardi*, *Prosotherium garzoni*, and *Medistylus dorsatus* (Reguero et al., 2007). This variation in the geographic distribution of pachyrukhines suggests that geographic and/or ecological barriers may have prevented the dispersal of these hegetotheriids into lower latitudes, at least 33°S, until the late Miocene. The first report of pachyrukhines in low latitudes is *Paedotherium minor* from the late Miocene (Huayquerian SALMA) Guandacay Formation in southern Bolivia (Marshall and Sempere, 1991; Cerdeño and Bond, 1998). Their absence from lower latitude Deseadan faunas might therefore be

attributed to a lack of suitable habitats in these potentially more tropical environments. Pachyrukhinae constitutes the most hypselodont clade among Deseadan notoungulates (Reguero et al., 2010), even more than coeval Archaeohyracidae, Mesotheriidae Trachytheriinae, and Interatheriidae, which are rather hypsodont but not hypselodont (Hitz et al., 2000; Reguero and Castro, 2004). Pachyrukhines are generally reconstructed as open-habitat dwellers that might have lived in burrows and resembled rabbits (leporids) or various South American rodents (caviids, chinchillids) in lifestyle (Sinclair, 1909; Kraglievich, 1926; Cifelli, 1985; Genise, 1989; Dozo, 1997; Cerdeño and Bond, 1998; Elissamburu, 2004). Perhaps the most striking aspect of the Quebrada Fiera mammals, especially given its age, is the abundance and diversity of hegetotheriid notoungulates. In terms of abundance, Quebrada Fiera is similar to other Oligocene faunas of Bolivia (Salla), where hegetotheriids, together with archaeohyracids, constitute a significant proportion of identified specimens (Reguero and Cerdeño, 2005; Billet et al., 2009; Cerdeño et al., 2010a). Out of more than 300 specimens (without including most of the small postcranial remains) of notoungulates recognized at the family level, about 25% correspond to Hegetotheriidae. The geographic proximity of the faunas in which pachyrukhines are rare or absent (Bolivian and Chilean Altiplano) suggests that some biogeographic and/or ecological factors served to limit or exclude pachyrukhines from at least the eastern portion of these intermediate latitudes during much of the Oligocene. However, such proximity in place and time does not guarantee a great similarity of faunas, such as Shockey et al. (2009) have established for the Moquegua (Peru) and Salla (Bolivia) mammal assemblages.

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